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ANIMAL INTELLECT AND HUMAN INSTINCT:
REFLECTIONS ON THE PSYCHOBIOLOGY OF RANK

by

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Twenty years ago, when I first began the study of monkeys and apes, the nature of behavior was so well understood that it needed no discussion. Higher animals were characterized by learning, lower animals by instinct, and “physical anthropology” was the dissection of primate cadavers by former medical students.

In all fields of social science, human nature, while not actually denied, was regarded as a residual category, far off the main line of significant variables. Even Br̄anislav Malinowski, the founder of modern anthropology, whose Continental eccentricities included what he called a “biological theory of culture,” is most revealing in what he thought a human behavioral biology ought to include: “impulses for oxygen, hunger, sexual coupling, fatigue, restlessness, sleep, urination, elimination, fright, and pain.” Not even aggression is on this list, much less anything as abstract as dominance or hierarchy.

Biology itself was not much of a corrective to this point of view. Biology had only two theories of human nature, genetic determination of behavior and neurohumoral control of behavior, and neither theory gave much room to social science. Neurobiology, in fact, had come of age in the same intellectual context as the modern branches of social science, and they both shared the same nineteenth century assumptions about the relationship between nature and nurture. As I have pointed out at length in my book *On The Evolution Of Human Behavior* (University of California Press, 1981), for almost two hundred years the social and biological sciences have shared a progressive and dualistic concept of human nature that is not only contradicted by the facts but makes impossible any theoretical reconciliation among these different fields.

For example, look at the illustrations from textbooks in physical anthropology and neurobiology from the 1940's to 1960's. In Figure 1 we see the cerebral cortex, the organ of enlightenment, superimposed on the more instinctual side of human nature. In Figure 2 from Watson's *Behaviorism*, there is an explicit rendering of a two-tracks theory of behavior: innate behavior, called unconditioned responses, appears at birth and becomes subordinated to learned behaviors during development. Finally, the culmination of this tradition is shown

in Figure 3, from Paul McLean's 1949 paper on the concept of the visceral brain. Here, the instinctual functions of the brain are specifically equated with the phylogenetically older "reptilian" parts of the brain, while learning and intelligence are equated with the newer "mammalian" parts of the brain.

When I first became interested in the biological basis of primate behavior, I confess that I fell in love with McLean's diagram of the neural hierarchy. What a thrill to discover that everything I had been taught in graduate school about the relationship between nature and nurture had been scientifically validated by the exact sciences neuroanatomy and neurophysiology! The concept of human instinct as a residual category, subordinated to phylogenetically advanced mechanisms of learning and culture, was written large on the brain itself. Shortly thereafter, I was invited by Dr. Karl Pribram, the Honorary Chairman of this committee, to do my dissertation research in his laboratory at Stanford University, and it was there that I came to see these issues in a very different light. Now I use McLean's theory of the brain as a litmus paper test of a person's neurological sophistication. It fits so neatly into our cultural preconceptions about the nature of human nature that people who know nothing about the brain are immediately attracted to it. Even recently, one can see this illustration reproduced in all seriousness in Carl Sagan's book, *The Dragons of Eden*.

What is wrong with this picture? First of all, it assumes that advanced behaviors can be localized in anatomically advanced brain structures, while primitive behaviors can be localized in anatomically primitive brain structures. Second, it assumes that the relationship between primitive and advanced is one of subordination, with the latter dominating the former. Third, it assumes that anatomy is the best guide to functionally distinct systems in the brain. Virtually all of these assumptions, however, have been negated by the findings of the neurosciences over the past three decades.

- The anatomically primitive parts of the mammalian ~~fore~~ brain, such as the hippocampus, septum, and amygdala, are critically involved in such advanced behavioral functions as learning and memory

- The advanced and primitive parts of the brain are not related by subordination but by differentiation of function
- The physiological properties of the cerebral cortex are determined to a large extent by the activity in lower brain center^S
- The function of anatomical structures is determined in part by the chemical composition of the fluids that bathe them
- The brain and body are reciprocally related: the brain controls the production of hormones that affect the body, while the brain is itself a target organ for hormones produced by the body
- Many anatomical structures in the brain, such as sensory cortex, are dependent upon certain kinds of environmental information for normal growth and development
- Many functional systems, such as visual processing or aggression, involve anatomical structures developed at different evolutionary period^S
- Specifically human behavioral systems, such as language, tool use, or intellectual processes, may involve subcortical parts of the brain as well as the neocortex

Biology's own understanding of the nervous system has changed dramatically in the span of a generation, and any appeals to human nature must refer to this richer concept of the brain. Among the general public, the older neurology of animal instinct and human intellect continues to hold sway, but behavioral science cannot afford to shy away from issues because the conclusions may be misinterpreted by the misinformed or twisted by the malicious. The duty of behavioral science is to present the causation of behavior in all of its empirical complexity. By attempting to assess the role of biological variables in social phenomena, we are expanding the intellectual range of the inquiry, not narrowing it down to preconceived assumptions.

The nature of human nature is the last thing that behavioral science will discover, not its point of departure; and our research programs should be designed to discover it, not to assume it.

In primatology, my own field of expertise, the inquiry into the biological determinants of behavior has been a humbling experience, conducive to intellectual growth. Modern primatology began about 1960 as a joint venture among psychologists, zoologists, and anthropologists. At that time, each science was confident that it already knew the significant causal factors that determined why animals behaved as they did.

The zoologists began with a concept of innate behavior patterns derived from the European ethologists Niko Tinbergen and Konrad Lorenz, and they categorized primate species in terms of the species-specific behaviors they exhibited. Psychologists began with the assumption that a monkey's behavior is determined by its relationship to its mother, and they set about varying childhood experience in a systematic way. Anthropologists were convinced that membership in the social group explained the form and frequency of behavior. They made careful records of social grooming and mapped the statistics against kinship charts of who was related to whom.

After only a few years of this enthusiasm, the research paradigms of all three sciences were demonstrated to be insufficient. The same species with the same species-specific behavior patterns were found to live in different types of social groups in different places and to have localized behavioral variants not easily explained by the innate fixed-action pattern. Primate zoology suddenly shifted from Hobbes to Montesquieu, downplaying ethological models in favor of ecological studies on such environmental issues as predation rates, resource availability, and the effects of climate on behavior. Primate psychology suffered a reversal in the opposite direction. Experimental learning theorists, who had written tomes proving that behavior could be shaped more easily than putty, suddenly found themselves with infant monkeys whose developmental history could be predicted better by biological species than by rearing experience. Even closely related species of macaque

monkey differed in their response to maternal deprivation, and these differences continued in the face of cross-fostering experiments in which infants of one species were raised by mother of another. And the anthropologists? Their studies did indeed demonstrate the pervasive effects of kinship on the social organization of monkeys and apes, but they also underscored the significance of another organizing principle which they were far less happy to validate—the concept of social rank as an independent variable.

At this point, it is necessary to touch on a territory so hedged about with caveats that I have postponed approaching it at all: The characterization of social rank itself. In many respects, it is easier to characterize in a negative way by giving instances of what it is not. It is not, for example, the same as “dominance” in a brute-force sense of the term. In the early days of primatology, when Robert M. Yerkes was the science’s nearly sole practitioner, monkeys and apes were believed to have a social organization based on dominance, the monopolization of resources by more aggressive individuals. Abraham Maslow, the humanist psychologist, carried this idea a step further by devising a “pair test” to measure it. He would put two monkeys together in the same cage and toss a peanut between them. The monkey who grabbed the peanut was judged the dominant individual, and if the subordinate objected to the situation, the dominant animal would threaten him. The problem with this method is that it creates the phenomenon one is trying to measure—although it creates it reliably. If one puts monkeys in a winner-take-all situation, a winner will almost always emerge to take it all. However, situations like this are an artifact of concentrated feeding, and the social organization of primates in the wild has scarcely anything that corresponds to the monopolization of resources.

Human beings are the only species of primate that have cooperative economic production, although there are adumbrations of it in chimpanzees, and monkeys and apes forage for themselves on plant food that is scattered about, not concentrated. Even primate children fend for themselves once they are off their mother’s breast. In some species, in fact, like hamadryas baboons, where the males are almost twice the size of the females, the

sexes occupy different economic niches, with the lighter animals feeding on the tops of bushes, while the heavy adult males are restricted to more accessible food sources. Thus, the direct competition for resources that the dominance theory addresses in fact hardly ever arises in a primate's natural habitat.

Another shortcoming of the classical model of dominance was observed by Japanese primatologists. They found that an animal's dominance status when measured by the peanut tossed between two individuals was not necessarily the same as the dominance rank that could be inferred by watching the animal in its natural social group. The pair-test was not as predictive as it should have been, and additional problems of the dominance concept soon came to light in the first field studies of primate groups in their natural habitats: in most species of primates, dominance is strictly marginal to the social organization.

If one measures dominance by one individual giving way or acquiescing to the will of another, then in most species of primates such behavior is rare, and in many species almost nonexistent.

In gibbons, siamangs, and many kinds of South American monkeys for example, where the basic social unit consists of a father, mother, and their dependent offspring; ~~and~~ territoriality, not dominance, is the way in which aggression manifests itself. These species give intense displays on the borders of their territories, like male song birds in mating season, but social relations within the group are harmonious and peaceful. Dominance, as defined for laboratory monkeys and chimpanzees, does not apply at all.

After hundreds of field studies on a wide variety of species, a more realistic picture of primate social organization began to emerge. It became clear that "dominance hierarchies" are preferentially associated with a single type of primate society, the multimale troop. The multimale troop is a social group that contains *multiple, unrelated, breeding adult males*. Such a social organization is very rare in mammals but relatively common in primates. Even so, most species of primates live either in mated-pair societies, where the nuclear family is the largest social unit, or in harem societies, where a single male lives and breeds with a group of females.

In multimale troops, by definition, there are two or more adult males, and these males are unrelated in the sense of not having grown up together as children of the same mother. (Whether they have the same father is usually impossible to say.) Furthermore, these unrelated males have sexual access to females in the troop. In these social situations, it is usually easy to discern a male hierarchy, in which male alpha outranks male beta . . . down to male omega. These hierarchical relationships, once called “dominance hierarchies,” are now called “ranking systems” or “status hierarchies” by primatologists; and this alteration of terminology signals an important change in our understanding of how they work.

The classical theory of dominance predicts that rank is primarily motivated by the desire for scarce resources and that it is implemented by aggressive means primarily, but observations on free-ranging animals do not bear out these presuppositions. High-ranking animals are typically not the most aggressive as measured by the frequency of fights and threat behavior, and rank does not usually function in the allocation of resources unless these are artificially concentrated. This fact will prove extremely important in intellectual history because it undercuts conventional sociological theories on the origins of social rank. All the major sociological theories derive rank from the system of resource allocation—the monopolization of the means of production—but systems of social rank are widespread in species of nonhuman primates that have no cooperative economic production and no concentrated resources. If sociology were right, the ranking systems of monkeys would be expected to wither away.

The primatological answer is that social rank is not primarily a system for the allocation of scarce resources—even though it might subserve that function in special circumstances—but a way of integrating unrelated adults into a single social group. This explanation runs as counter to the premises of sociobiology as it does to sociology. Sociobiologists think that the highest ranking individuals should be the most successful at reproduction, but the allocation of sex in primate multimale troops is as refractory to simplistic explanations as is the allocation of material resources. If examined objectively,

the primatological evidence is exactly the opposite of what a reproductive fitness model would predict. The species where reproductive success correlates with the boundaries of aggression are the species that have lived in territorial mated-pair societies or in harems with a single breeding adult male. Ranking systems, in contrast, are correlated with sexual democracy. The species that have the most elaborated status hierarchies, —macaques, baboons, and chimpanzees—are also the species with the least exclusive system of mating. In none of these species can reproductive success be predicted from the ranking position alone. In primates with elaborate ranking systems, the lower ranks reproduce themselves—what an amazing sociological revelation!

Social rank does not determine reproductive success. It creates a two-tier system of sexuality with a matrimonial component and an adultery component. This can be seen quite clearly in Frans de Waal's monograph *Chimpanzee Politics*, about sex and power among apes in the Arnhem Zoo. In this case, the high-ranking males attempted to monopolize the females, denying other males access to them, but the females and the lower-ranking males nonetheless indulged in sexual hanky-panky outside the bounds of the ranking system. Similar behaviors have been observed in hamadryas and gelada baboons, where the males have harems, and it suggests that rank is no more involved in the regular allocation of sex than it is in the allocation of resources.

Social rank is not primarily a system of resource allocation, sexual or otherwise, but an adaptation for large-scale social aggregations containing unrelated adults of the same sex. "Unrelated" in this context means animals who have not grown up together as members of the same family, not unrelated in a genetic or genealogical sense. As numerous ethological experiments show, raising animals together as siblings inhibits the expression of aggression, enforcing cooperative relationships, even among predators and their natural prey. In troops of wild primates, all of a female's children tend to form a distinct social group, the matriline, whose members support one another. These matriline subgroups can become fault lines along which larger groups fracture; but in multimale troop species, the kinship organization is integrated into a larger social framework, the ranking system.

Not all primates have the biological dispositions to form ranking systems. Ranking systems are made possible by the transformation of aggression into display and fear into submission. In primates without the hierarchical propensity, aggression leads to defeat and defeat to flight from the scene of battle; but in rank-oriented species, defeat leads to gestures of subordination by the defeated party. Instead of fleeing, as in territorial species, the defeated animal continues to live in the social group as a subordinate member, giving gestures of dominance to those below him and ^ggestures of submission to those above. Ranking systems, in other words, make possible social aggregations of adults by both sexes without any diminution of aggressive motivation on one hand or any reduction in the importance of kin-based subgroups on the other.

Consider the ranking system of rhesus monkeys, which is composed of at least four subsystems that interact: ^(Fig 4)

- A central hierarchy composed of adult males ranked in linear order
- A peripheral hierarchy composed of young or old subordinate males who are no longer active
- A serially ranked system of matriline composed of adult females and their daughters and granddaughters
- A linear intertroop hierarchy composed of entire troops that defer to each other when sharing resources and habitat.

Ranking systems, therefore, are not the outcome of unsocialized animal instincts but a phylogenetically advanced form of social organization that presupposes kin-based social units and the evolution of signals for dominance and submission that are over and above the normal vertebrate repertory of ritualized aggression and fear. Moreover, the manipulation of rank, as careful studies of ape behavior are beginning to demonstrate, is an intentional process in higher primates based on awareness of the consequences of the behavior and the intelligent assessment of political support. Although dominance and subordination are transacted in the coinage of fear and aggression, they nonetheless are implemented through political alliances that draw on the positive feelings that sustain families and friendships.

Ranking systems are not a recent development, contingent on concentrated resources—although concentration can reinforce existing inequalities as ethological experiments show—but a universal attribute of primate species that have cooperative groups of unrelated adults with high levels of aggressiveness. Human ranking systems, far from being a radical departure from our simian forebears, are in fact one area of radical continuity. There are clear differences between humans and other primates in language, technology, and art, and these differences are incorporated into human political behavior; but no one reading De Waal's *Chimpanzee Politics* with an open mind can come away convinced of major discontinuity in the underlying motivations.

As a scientific hypothesis, it is far more parsimonious to accept these close behavioral correspondences as evidence of similarity in the underlying brain mechanisms. Far from being a reductionist fallacy, this assumption makes possible a new model of behavior that is far richer than either the cultural or biological perspectives because it can incorporate findings from both traditions into a single intellectual framework. As Figure 5 shows, brain mechanisms for the processing of information about the social environment are affected by social input during development (step 1). This is consistent with the maternal deprivation experiments in monkeys and cross-fostering experiments in mammals generally. These same mechanisms are also affected by changes in the hormonal environment (step 2), which are in turn triggered by (step 3) age, sex, physical stress, and the social context, as indicated by a host of endocrinological experiments. The brain mechanisms for processing social information, more commonly known as emotions, do not work in a vacuum but interact with the mechanisms for skill acquisition (step 4) associated with the special senses and the skeletal musculature. Although there are some innate expressive behaviors specifically associated with the emotions (step ⁶5), as revealed by cinematic and video studies of facial expression, as well as some innate instrumental actions such as biting and hitting (step ⁵6), these behaviors are always combined with nonemotional motor skills (step 7) that track the target in space and time and monitor the effect of the behavior. As a

result, the observed behavior is always a composite of learned and innate elements (step 8), as the detailed studies of emotional expression indicate. Finally, the brain mechanisms for acquiring learned behaviors are also affected by the social context in higher primates (step 9), leading to the social transmission of skills through observational learning, a phenomenon that is well-documented in home-reared apes.

Can a theory of this type, which takes seriously the interactive model of the brain with which we began this presentation, come to terms with some of the peculiar features of human aggression and rank discussed by anthropologists? It illuminates human behavior as well as that of nonhuman primates. In an intelligent species, selected for an increased ability to perceive the consequences of action, perception of the effects of innate behavior transforms these actions into learned skills. The innate connections between emotional perception and emotional response do not disappear, nor even attenuate, but they come to be represented in the nervous system as both innate programs and as intentional skills. Once a swaggering posture or broad shoulders are perceived as instrumental in the negotiation of rank, they will be simulated by intentional action and culturally elaborated, like any other efficacious technique, into a body of traditionally transmitted skills.

The Samurai warrior or the nuclear bomb are cultural phenomena by anyone's definition, but their efficacy nonetheless depends upon the underlying mechanisms of social perception that humans share with apes. The unique capacities for language and technology confer to humans a far higher level of consciousness and creativity in the implementation of social behavior than is possible in an ape, but the inherent parsimony of science forbids us from postulating two distinct principles of behavior when one will do. There are not two kinds of social ranking systems, the human and the simian, mediated by two different levels of neural control—the instinctive and the symbolic—but a single functional system such as that shown in Figure 5 that merges affect and instrumentality into composite behavioral strategies. This is not a pessimistic conclusion about the inevitability of war and the inequalities of rank. Primatology, by looking squarely at human

nature, gives us the enhanced capacity for action implicit in all good science. If the ranking systems of apes presuppose the intentional control of emotionally salient behaviors and the perception of the consequences of action, do not human beings have at least an equal ability to alter their behavior through a rational assessment of behavioral effects (step 10) and the communication (step 11 and step 12) of the implications to others?

