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The Inevitability of Evolutionary Psychology and the Limitations of Adaptationism: Lessons from the other Primates

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The arrival of Evolutionary Psychology (EP) has upset many psychologists. Partly, this reflects resistance to what is perceived as genetic reductionism, partly worry about yet another step closer to the life sciences. Are the life sciences going to devour the social sciences? This essay starts out with a list of pitfalls for the beginning Darwinists that many EP followers are, warning against simplistic adptationist scenarios, and the fragmentation of the organism, the human brain (a module for every capacity), and the genome (a gene for this and a gene for that). Despite these criticisms, the author is generally sympathetic to the evolutionary approach, however, and feels that EP is inevitable. It may show growing pains, but psychology does need to move under the evolutionary umbrella, which is the only framework that can provide coherence to a fragmented discipline. The essay concludes with several illustrations of the usefulness of evolutionary theory to explain the social behavior of primates. Primatologists face many of the same dilemmas as followers of EP in that primate behavior seems almost endlessly variable. Examples of political strategy, peacemaking, and reciprocal exchange show the complexity, the profound similarity to human behavior, and the promise of the evolutionary framework.

I am honored and pleased to address psychologists at their annual convention. You must know that, even though I am an ethologist, hence biologist, I've worked and taught in a psychology department for the past decade. As a result, I have discovered a peculiarity of psychologists: they seem worried about the definition of their discipline. For example, a student designs a research project and one of my colleagues will pose the question "but is it psychology?" I don't know what to do with such a question. Is it interesting science? Is it well designed? Is it publishable? These are good questions, but what does or does not fall under psychology is hardly interesting. This insecurity is probably related to the gradual move of psychology first out of the clutches of philosophy, then out of the clutches of black-box behaviorism, and now increasingly towards genetics, neuroscience, and evolutionary biology. This leaves many wondering what will be left of the discipline they knew. My presentation deals with one aspect of this transformation—the one relating to the rise of Darwinism in the social sciences.

Psychology has a long and distinguished history that began with speculations based on philosophy and introspection about the human mind and behavior.

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If we accept the discipline's modern origin with Wilhelm Wundt in 19th century Germany, it is obvious how much philosophy was at psychology's core. At the time, all German psychologists studied philosophy, and Wundt's goal was not to replace philosophy as an approach to the mind, but simply to improve upon it (Smith, 1997). As we shall discuss, these philosophical roots remain visible in lingering dualisms within the discipline. Breaking with the traditional distinction between the *Geisteswissenschaften*, to which it was originally assigned, and the *Naturwissenschaften*, psychology has in the meantime reached the stage of a hard, empirical science, leaning more and more toward the natural sciences. It now looks at hormones and behavior, brain and behavior, and the evolution of behavior. Psychology is becoming a branch of the life sciences, which is exactly where it belongs.

Nevertheless, or perhaps precisely because of this development, the rise of evolutionary psychology (EP) is eyed with profound anxiety by the discipline. Some people are opposed to it or at least upset by the perceived simplicity of it all. And even though I think that the growth in importance of EP cannot be stopped, I share many of the same concerns. Perhaps this is why I was invited to speak. So, I'd like to start out criticizing EP a little, making a few jokes at its expense, then explain why EP is inevitable, and finally illustrate how my own work with nonhuman primates fits the picture.

Darwinism 101

Let me start with an intriguing quote:

> The entire modern deification of survival *per se*, survival returning into itself, survival naked and abstract, with the denial of any substantive excellence in *what* survives, except the capacity for more survival still, is surely the strangest intellectual stopping place ever proposed by one man to another.

I use this 1879 remark by William James (1920, pp. 143-144) to show that this whole issue of evolutionary theory applied to human behavior is rather ancient. Of course, he wrote this right after the rise of Social Darwinism, which is still what gives EP a bad name today, yet it clearly is an issue that has been with us most of the time that psychology existed, and that will be with us for a long time to come. Books on the topic are coming out as we speak. For example, there is *The Mind Doesn't Work that Way*, which is Jerry Fodor's (2000) answer to Steven Pinker. Fodor, who proposed the modularity of mind concept, is now objecting to the proliferation of modules proposed by the adherents of EP. Next is Ullica Segerstråle's (2000) *Defenders of the Truth*, an insider's look at the history of sociobiology—not particularly critical of it. In contrast, Richard Lewontin's (2001) *It Ain't Necessarily So*, and the edited volume by Hilary and Steven Rose (2000), *Alas, Poor Darwin*, are extremely negative. But there are also books that defend EP, such as John Alcock's (2001), *The Triumph of Sociobiology*—a title that may strike some as wishful thinking—and new introductory texts, such as David Buss' (1999). All of these books are hot from the press. EP is clearly in the news, arousing strong emotions. Instead of shrugging off EP, as some try to do, I recommend books like these as a starting point for a lively graduate seminar on the merits and pitfalls of evolutionary approaches to human behavior.

Many of the problems surrounding EP have nothing to do with whether human behavior has been subject to evolution by means of natural selection—which for me a is a given—but with how broad or narrow a view of evolution one embraces. So, before getting into primate behavior, I would like to go over some of the basics of evolutionary thought—Darwinism 101, as I call it. Simple truths that come out of evolutionary theory are sometimes overlooked by the followers of EP.

The first and foremost misunderstanding concerns the concept of adaptation. My concern is summed up in the following statement by George Williams, a contemporary evolutionary biologist: "…adaptation is a special and onerous concept that should be used only when it is really necessary" (Williams, 1966, pp. 4-5). Now mind you, Williams' warning does not specifically refer to human behavior, but to the regular sort of issues that biologists address, such as plant physiology, anatomical features of animals, insect behavior, and so on. The conclusion from this work is that adaptation is a complex and difficult concept that should be applied parsimoniously. Hence, adaptive explanations would benefit from Occam's razor. If this holds for features of plants and animals, it certainly also holds for human behavior. So, why the eagerness in EP to postulate an adaptation at every turn?

The situation is—and I think I'm a bit mean here saying this, but not incorrect—that many psychologists in the U.S.A. have been trained in a school system that pays little attention to evolution. In essence, their background in evolution is weak or absent. This is due to continuing resistance against evolutionary theory in the population at large. As a result, the teaching of evolution is absent in one-third of the U.S.A. public schools and such teaching is half-hearted at best in most others. According to a 2001 Gallup poll, only 12% of Americans fully accept the tenets of evolutionary theory, whereas another 37% accepts a watered down version: the rest rejects the theory (Shermer, 2002, p. 25). Even the best universities are not immune to these attitudes. If, as Theodosius Dobzhansky (1973) famously declared "Nothing in biology makes sense, except in the light of evolution," then leaving evolution out of basic science education constitutes a fatal deficiency. After such an education, the young social scientist goes to the university where the curriculum, with a few exceptions, still neglects evolutionary theory. This forces those interested in evolution to acquire the relevant knowledge second-hand, often from other social scientists or science writers rather than biologists.

This remark does not apply to the founders of EP, who are as well-schooled in evolutionary thought as any biologist, but rather to the growing throng of followers, who have created a field riddled with curious errors. The most basic one is that the existence of a trait is taken to mean that it must be good for something. Biologists know, however, that it is not at all uncommon to find a trait in all members of a species without this trait serving any purpose whatsoever. This is why we are taught to be conservative with the postulation of adaptiveness. Just to give one example that comes straight out of the EP literature—and I could offer hundreds of examples without any problem because the error is committed over and over again—here we have a recent article with a blunder right in the opening sentence of its abstract. It starts: "Both male facial hair and male pattern baldness are genetically based, suggesting that they contributed to fitness" (Muscarella & Cunningham, 1996, p. 99). Where does this come from? Alzheimer's and cystic fibrosis have a genetic basis, as do many other diseases, but no one would argue

that they contribute to fitness. Later in the same paper we learn that male pattern baldness may signal social maturity, described as a friendly kind of dominance based on wisdom. I consider this another "just-so" story, and not a very convincing one. Is this supposed to explain why we have an entire industry that removes hair from men's heads? Obviously, every man wants to look mature and wise!

Fragmenting the Organism

The first common mistake in evolutionary explanations, then, is to think that if something is genetically influenced it must serve a purpose. What is overlooked is that many characteristics are byproducts of others, and that all that matters from an evolutionary perspective is that the entire set of traits serves survival and reproduction (By the way, survival and reproduction do not count equally. Evolutionarily speaking, survival is important only insofar as it serves reproduction). There is the problem of correlated traits, as already noted in Darwin's (1859) *The Origin of Species*, which is often due to pleiotropy. And there is the problem that the development of one trait may dictate the development, reduction, or disappearance of others.

Just to give one example of why we should look at the whole package: why did *Tyrannosaurus rex* have such little front limbs? If one looks at their front limbs in isolation, this seems a perfectly fine question, and perhaps you can come up with a proposal: perhaps these limbs served the cleaning of teeth or subtle gestural communication. But then, if you look at the whole animal, you'll understand that this predator probably didn't need any front limbs. It had a big mouth, big feet, and a huge tail. Large front limbs might have been in the way. Our contemporary kangaroo is in a similar situation: it also has reduced front limbs. Thus, with every question about a particular feature one needs to consider the whole animal (Gould & Lewontin, 1979).

It is even worse than this. Not only are certain traits dictated by others, but there exist many traits that are imperfectly designed or positively costly. A good human example is our back: our species is not fully suited for an upright posture, hence many of us suffer back problems, such as hernias, slipped disks, and neck pain. Walking upright must have had great benefits for these costs to be tolerable, even though there exists no universally accepted theory of why we walk upright. No wonder, biologists often refer to the evolutionary process as "tinkering" (Jacob, 1977), meaning that the process does the best it can given the available materials. All sorts of ballast remains visible in the end product. Ironically, then, the natural world is rampant with *flawed designs* that reflect the trouble evolution has had turning one form into another, such as a quadruped into a biped. Even the eye, often featured as this incredibly perfect organ, has major problems; for example, the optical nerve blocks incoming light creating a blind spot on the retina that organisms can only circumvent by combining the incoming information from both eyes (Zimmer, 2001).

Talking about imperfection, take the example provided by Steven Glickman and Laurence Frank for the spotted hyena. In this species, the male and female can barely be distinguished because the female's external genitals are similar to the male's. She possesses a pseudopenis and is also otherwise masculinized. Being bigger and stronger than the male, the female is the dominant sex. As it turns out,

the female's penis-like structure is awfully costly. This is mainly because nature has been unable to find a way around this structure during parturition, meaning that the female needs to press the pups through an extremely narrow tunnel. You can see how this must be a painful process: many females die during first parturition. And then I won't even go into how the males inseminate them, which may be less painful but is equally complicated.

Instead of taking the female hyena's genitalia and seek an adaptive story for them, which would be hard, Glickman and his co-workers have speculated that it may have been advantageous for females to become dominant over males if this allowed them to help their offspring get enough to eat in the melee around a carcass (Glickman *et al*., 1993). In order to achieve dominance, however, females had to become "androgenized," hence produce testosterone and androstenedione, which they do profusely. In this evolutionary scenario, the penis-like genitals of the female hyena are an extremely costly byproduct of a hormonal shift that has benefited female reproduction overall. This particular trait is definitely not good for the species, but as we realize now, this is never how evolution works: the success of individual reproducers comes first, and big and strong females were favored.

Thus, the hyena's peculiar genitals are part of a bigger picture. Some traits of a species are costly, others beneficial: all that matters is that taken together the traits do a better job for an individual's reproduction than alternative sets of inheritable traits. The lesson is that one cannot fragment the organism. One cannot single out a trait for an adaptive story, as often done in EP: one needs to consider the trait in the context of the entire phenotype.

A Return to *Instinktlehre*?

To move this observation to the human situation, I cannot get around the EP book that has raised most eyebrows. In *A Natural History of Rape*, Randy Thornhill and Craig Palmer (2000) postulate that rape may be an adaptation – that rape may be good for the men who show it. They extrapolate straight from Thornhill's insect studies, in which there are indeed species with male anatomical features that seem designed to force females into sexual contact. But these are flies, and I have argued that, in humans, rape is part of a far bigger picture (de Waal, 2000a). There is human sexuality, a seriously underfunded research area, and there are human power relationships, a feature of human sociality traditionally neglected by psychologists. I won't go into this here (see de Waal, 2001), but ours is a power-hungry, hierarchical species, and I am baffled that social psychology textbooks are still being written as if we are born democrats and egalitarians. The point is that here we have two very rich areas of human behavior—sex and power—which are obviously interconnected. Rape occurs at their interface, having roots in both the sexual and dominance realms, and I don't see how it can be ripped from this larger context to be explained as an isolated behavior, as Thornhill and Palmer try to do.

To be called an adaptation, rape would need to have its own genetic basis relatively separate from other sexual tendencies as well as from personality characteristics, offer special reproductive advantages, and have been favored by selection for this very reason. This is a rather heavy set of requirements that raises a number of pressing questions. Do we know if rapists are genetically unique? I don't think we do. What are the advantages of rape in terms of reproduction? We know noth-

ing about this. Are there costs associated with rape? If you imagine an ancestral small community in which a man raped the wives and daughters of other men, I don't think he would live very long, or else he'd be expelled. Hence raping may not be such a good strategy, at least not within one's own community. And why do humans so often rape individuals with whom they cannot reproduce, such as men raping men, or men raping women who are too young or too old to be fertilized. Why do they rape partners perfectly willing to have consensual sex? There are lots of questions that come up if rape is declared an adaptation, questions that Thornhill and Palmer have failed to answer.

What bothers me most about the strategy of singling out one behavior for evolutionary explanation in this particular case is that the behavior is shown by only a small minority, a fact that is hardly acknowledged yet has serious repercussions. The same applies, by the way, to Martin Daly and Margaret Wilson's (1988) well-known work on infanticide by step-parents. They explain this category of infanticide out of a lack of shared genes with adoptive offspring. But I would argue that in seeking to understand rare behavior we should never forget the norm. As explained in my review of the book by Thornhill and Palmer:

> Even common behavior, like smoking or masturbation, isn't necessarily adaptive - let alone uncommon behavior. If child abuse by stepfathers is evolutionarily explained, or if rape is such a smart reproductive strategy, why do so many *more* stepfathers lovingly care for their children? And why are there so many *more* men who don't rape? Let me call this the dilemma of the rarely exercised option: a Darwinian account for an atypical behavioral choice is incomplete without at least an equally good account for the typical choice (de Waal, 2000a).

To summarize, my problem with adaptationism as it is applied today—and I'm not saying people should not try, but as done today—is that EP has an unfortunate tendency to fragment the organism, the genome, and the brain. Its followers talk about a gene for this or a brain module for that, and look at separate bits of behavior as if we can dissect the organism and its behavior to inspect each part on its own and guess its separate *raison d'être*. If this cannot be done with the components of a watch spread out on the table, it most certainly cannot be done with human behavior.

As for the brain, the current trend within EP to divide brain function into modules reminds me of early ethology, in the 1950s, when there was no limit to the number of instincts one could propose, from self-preservation to aggression, and from sex to motherhood. In those days, each species-typical tendency had its own instinct, and Konrad Lorenz's *Instinktlehre* (German for "instinct doctrine") even included a "parliament" of instincts to tie all components together. Similarly, EP proponents have compared the brain with a Swiss army knife to which evolution has added modules for everything from face recognition, to tool-use, kin-preference, child-care, friendship, cheater detection, and theory of mind (Tooby & Cosmides, 1992).

One problem—apart from the fact that brain modules at any behavioral task level have yet to be demonstrated—is that this would make for an incredibly unwieldy brain, much like a computer to which a chip would need to be added each time we install a new program: one chip for word-processing, one for games, one for our spreadsheet, and so on. Instead, a computer is a multi-purpose device that allows each application to draw on its full potential. A highly integrated,

multi-purpose brain means that every behavioral tendency and capacity can build upon and use the circuitry of existing tendencies and capacities. This view—which again suggests "tinkering" by evolution with the old to achieve the new—is far more complex than the proposal that brain evolution proceeds in discrete steps, producing new brain circuits to control separate pieces of behavior. Instead, evolution gradually transforms the massive machinery of the brain to handle new challenges. Thus, nothing in the human brain is really new: it is always an expansion of, or elaboration upon what existed before.

This is not to say the brain is a blank slate. It seems "prepared" to acquire certain tasks or skills, and to absorb certain kinds of information more easily than others. The studies by Tooby and Cosmides (1992) do indeed suggest such preparation, as do many animal studies, going back to the early work on imprinting, according to which ducks and geese are preprogrammed to pick up information about their species in the first days of life. What makes this happen is unclear, however, and the various labels now in use, from biogrammar, to biological algorithm, brain module, epigenetic rule, or learning predisposition are not really much better at solving the mystery than the concept of instinct was. The term module, in particular, carries the connotation of a part of the brain that is self-contained, encapsulated, and localized, which makes the idea hard to swallow (Panksepp & Panksepp, 2000). The challenge is to find out at which level possible predispositions, such as cheater detection, differ from other kinds of problem solving: could it simply be that certain emotions are attached to social contracts that are not attached to abstract rules? Similarly, it has been argued that face recognition is not a special adaptation but that we learn to pay better attention to faces than to other categories of stimuli (Gauthier & Tarr, 1997). If so, the issue would boil down to motivation and attention rather than to cognition and specialized brain circuitry.

In short, Williams was right to warn that adaptation is an onerous concept that should be applied parsimoniously. In biology, we are used to an integrated view, even if at the same time we consider it useful to analyze capacities separately so as to better understand them. We accept tension between the whole and its parts, or at least between our understanding of the whole and of its parts. What EP needs to develop is a taste for multi-level thinking in which attention freely shifts between immediate ("proximate") explanations of behavior and evolutionary ("ultimate") explanations. The first level is the traditional domain of psychology, the second considers how behavioral tendencies have come into existence over the course of evolution. One cannot jump directly from evolutionary pressures to specific behavioral outcomes, because the intermediate level features a complex psychology that weighs many options and is subject to a variety of influences, such as learning, culture, and motivation. Hence the need for EP to put a little less evolution and a little more psychology in its explanations.

The Inevitability of EP

One of the problems is that when social scientists turn to evolution for answers—as they should!—they often receive the recommendation to read Richard Dawkins' *The Selfish Gene*. Provocative when published, in 1976, this book remains immensely popular. It presents evolution from a gene-centric perspective, however, as if each gene has followed its own evolutionary trajectory, which is of

course not the case. In addition, right in its metaphorical title, the book promulgates the idiosyncratic views of Thomas Henry Huxley, the public defender of Darwin. Huxley saw an amoral nature, “red in tooth and claw,” brutish and selfish without room for kindness and morality. In contrast, Darwin himself regarded human morality as a natural outcome of the evolutionary process. Huxley thus deviated fundamentally from Darwin in being far more pessimistic about human nature, or, as his biographer complained, Huxley ended up “forcing his ethical Ark against the Darwinian current which had brought him so far” (Desmond, 1994, p. 599).

In my writings on the evolution of morality, I have characterized Dawkins as a reincarnation of Huxley (de Waal, 1996, 2001). I feel that it is time for social scientists interested in evolution to return to Darwin and his more balanced perspective. A good place to start would be one of the most respected evolutionary biologist of our time, Ernst Mayr, who, as most biologists, rejects a gene-centric perspective. In his latest book, *What Evolution Is*, Mayr observes:

> … most treatments of evolution are written in a reductionist manner in which all evolutionary phenomena are reduced to the level of the gene. An attempt is then made to explain the higher level evolutionary process by "upward" reasoning. This approach invariably fails. Evolution deals with phenotypes of individuals, with populations, with species; it is not "a change in gene frequencies." The two most important units in evolution are the individual, the principal object of selection, and the population, the stage of diversifying evolution. (Mayr, 2001, p. xiv)

Here, again, one recognizes a voice against fragmentation, which by now must be a familiar theme. I should add, though, that despite my concerns about its excessive adaptationism and sometimes plain misunderstanding of evolutionary theory, I consider EP an inevitable and, in fact, desirable development. The Darwinian framework addresses not just the natural world; it also has the potential to tie together the myriad hypotheses about human behavior now out there. Looking as a relative outsider at the social sciences, I see thousands of little theories that are barely interconnected, even though attempts are sometimes made. One may argue that they do not need to connect, but this amounts to an admission that every area within the larger discipline is free to come up with its own explanations. Consequently, there is a serious lack of mooring to the thinking in psychology, a lack of an overarching idea within which everything must make sense. Every little theory stands by itself, neither competing nor connecting with any others.

Evolutionary theory has the power to bring order to this bewildering forest. First of all, we are animals—some of you may want to argue with that, but we do have DNA, livers, brains, and hearts like every other mammal, and for all intents and purposes we are really not that different from other animals. Human behavior is, up to a point, a product of natural selection. And so, I consider EP as being on the right track, however much I may complain about its current shortcomings. The optimistic view is that these are growing pains, so that those worried about them, should join EP and try to improve it, rather than reject it. As you know, a younger generation of psychologists, anthropologists, and even economists and political scientists is now leaning towards Darwinian approaches, and my hope is that they will turn EP into a serious and rigorous science by being critical of its premises without abandoning the core idea that important aspects of human behavior have been naturally selected. EP has the potential of being as empirically rigorous as

any other part of psychology: evolutionary theory can produce new and interesting ideas, which—and this is critical—are as testable as any other ideas in your discipline. In the end evolutionary theory can serve as the umbrella idea so desperately needed in the social sciences (Wilson, 1998).

Psychology is at the crossroads. The discipline is at the forefront in the social sciences in moving closer to the life sciences but has not yet abandoned its ties to Western philosophy, which ultimately came out of the Christian tradition. And so, psychology is still stuck with a number of ancient Western dualisms. The mind-body divide is one, human-animal dualism another, and then there is the nature-culture dualism that is presently being questioned by students of animal culture (reviewed in de Waal, 2001). Psychology will have to get rid of these dualisms before it can become a unified, empirical science that is a respected part of the life sciences and its non-Christian, Aristotelian tradition. Whereas we can safely leave it to cognitive neuroscience to do away with any lingering mind-body dualism, EP will eventually need to do the same with the human-animal dualism.

Before EP will be effective in this regard, it will need to acknowledge more fully where all of those wonderful concepts and theories that is adopting came from. They came from scientists, such as Darwin, who first of all were naturalists. If EP embraces Edward Wilson it cannot help but get covered in ants, and if it embraces William Hamilton it cannot overlook the beetles and parasites that fascinated this brilliant biologist. As neuroscientist Jaak Panksepp noticed in a recent article on the seven "sins" of EP (one of which is "massive modularity" of the brain), EP would do well to abandon its exclusive focus on the human species. Many of the ideas to be tested should, if true, also hold for other animals (Panksepp & Panksepp, 2000).

It could be argued that comparative psychology (CP) stresses the connections between human and animal behavior, hence that this issue has already been taken care of within the discipline. This is only partially true, though. As its name indicates, CP has traditionally been more interested in *comparing* humans with other animals, and vice versa, than in questions of how and why certain behavioral tendencies evolved. Most of its attention has been directed at learned behavior, thus actually hindering the development of an evolutionary perspective. Also, a distinct resistance to so-called "anthropomorphism" remains, despite the fact that in relation to our closest relatives, the anthropoid apes, the assumption of continuity with human psychology is safer than the assumption of discontinuity (de Waal, 1999).

Possibly, these are just the outdated reservations of a European ethologist about the traditional rival school from across the Atlantic. There is lots of common ground. Since the debunking within CP of the *scala naturae* view of "lower" versus "higher" animals (Hodos & Campbell, 1969), and the synthesis between ethology and CP (Hinde, 1966), CP has grown considerably more open to and interested in evolutionary issues. As such, it can be an ally, helping to turn around the tendency within psychology, including EP, to set us, brainy bipedal apes, apart from the rest of nature.

What can we learn from evolutionary approaches to the behavior of our closest relatives? Primatology faces the same dilemma as EP, namely that the behavior of our subjects is incredibly variable. Primates are not little gene machines: they are not programmed robots who always show the same behavior under the

same circumstances. This is obviously not just the case for nonhuman primates, but behavioral flexibility is most noticeable in the members of this order. Explanations of behavior need to take into account a complex psychology and cognition, variable motivations, individual variability, and the pervasive effects of learning, and even culture. Amidst this "noise," it is hard to make informed guesses about which behavioral tendencies were selected for which reasons over the course of evolution. The reverse is also true when we move, not from existing behavior to evolutionary explanations, but from evolutionary theory to behavioral prediction. The observed behavior is often far more variable than anticipated, suggesting decision-making by the actors based on experience and conflicting tendencies, not all of which are necessarily accounted for by the original theories.

The topics I wish to go over here are politics, peacemaking, and reciprocity, because those are my research interests. They illustrate a range of evolutionary approaches. Primate politics was initially an entirely descriptive project in which the great intelligence of chimpanzees was documented within the social domain. Peacemaking started out the same, but soon this field grew and developed its own theoretical framework of conflict resolution that successfully placed the observed phenomena in an evolutionary context. Studies of reciprocity and cooperation, finally, were from the start influenced and guided by existing evolutionary theory, which inspired the data collection. All three topics have implications for the study and interpretation of human behavior, and all three topics can be studied with rigorous, quantitative methods. Instead of presenting data here, however, I refer readers to the technical papers published in abundance on these phenomena.

Political Primates

Let me start with a 1651 quote from Thomas Hobbes (1991, p. 70), who postulated a general drive for power: "I put for a generall inclination of all mankind, a perpetuall and restlesse desire of Power after power, that ceaseth onely in Death." As I said, this point has been worked under the table by much of social psychology, but did you know that initially Abraham Maslow was very interested in the dominance drive? The whole idea of self-actualization, so popular in American psychology, comes straight out of the early work of Maslow on the dominance hierarchy of monkeys at the same zoo where I used to work, in Madison, Wisconsin (Maslow, 1936). Maslow was, in my mind, initially closer to the truth when he openly postulated a dominance drive, than later when he watered it down to a the more politically correct concept of self-esteem (de Waal, 2001).

Following Hobbes and the early Maslow, I agree that the human species, particularly the human male, has a pronounced dominance drive, a characteristic shared with a host of other social animals. And don't think that dominance always depends on some blind fighting instinct. In chimpanzees, just as in our species, it rather depends on calculated strategies and deal-making. *Chimpanzee Politics* (de Waal, 1982) reports in detail how two adult males of different age fostered an alliance, which for the old male meant a partial return to power and for his younger partner meant the top position, but with the draw-back that he was fully depended on the kingmaker. The two allies entered into an unwritten transaction where the young alpha male had to allow his partner certain sexual privileges. He was in power for four years; but after four years his tolerance began to wear thin and he

tried to claim the privileges all for himself. He began to object to his partner's sexual adventures, breaking them up, and, from one day to the next, his partner ceased supporting him. It really looked as if both males had been monitoring their side of the transaction and a breaking point had been reached.

The next day, the young male had lost his position, because a common rival who was stronger than either one of them immediately stepped into the power vacuum when the ruling coalition collapsed. It shows that chimpanzees have real politics in the sense that their power relationships are not determined by individual abilities, but rather by deals that they close to mutual advantage. And if the benefits run out, new deals will come in their place. Not only do chimpanzees form such alliances, they are also aware of the danger of alliances involving others. Thus, an effective alpha male will break up contacts between other males who together might pose a threat to his position. If the alpha sees one of his partners associate with a rival, he will disrupt this contact immediately, hence follow the same Machiavellian divide-and-rule strategy familiar from Washington politics, the corporate environment, and yes, faculty meetings. So, they're very astute politicians in many ways.

One more aspect of the leadership role, especially for older males, over 25, involves breaking up fights in the group. You have a fight between two females, and the male steps in to stop it. He stands there between them with his arms spread and restores the peace. Known as the *control role*, this behavior is very well developed in some alpha males. We have hard data on this, showing how a particular male who achieved alpha status for a couple of years turned from a winner supporter into a loser supporter. If you support the winners, you are basically exacerbating the conflict by helping aggressors. If you support the losers, you play a protective role. The fact that this male turned from winner to loser supporter precisely in the limited period that he was the leader of the group, and later reverted to his old ways, illustrates behavioral plasticity. Perhaps he was playing a "role," that is, following a behavioral mode based on expectations. We don't know this last part for sure, but it seems clear that his behavior is not following a simple program.

That's what I mean with behavioral flexibility. These animals adjust their social behavior to the situation in which they live and the position that they occupy. When they do not occupy the top spot, they gain from disturbing the peace, stirring things up, and creating trouble for the current alpha male, which is why they support winners. When they become alpha, on the other hand, they become the protector of the downtrodden, the populist, and help everyone against those nasty other males. This makes them popular, and may help them ward off challenges with the help of the entire group. Massive support for popular leaders has indeed been observed in chimpanzees. These males thus make tactical choices. The aspect that evolutionary explanations can address is why the dominance drive exists and why certain choices are advantageous, but they cannot tell us how they are made. For this, we will need cognitive psychology.

Peacemaking

Reconciliation and peacemaking are areas of research that are getting big at the moment (reviewed in Aureli & de Waal, 2000; de Waal, 2000b). In the summer of 2002, various national European behavioral biology societies will get

together for an entire international conference on conflict resolution. This is a field that started out with simple descriptive work, but that is now rapidly moving towards a theoretical framework that is well-supported by observational as well as experimental research.

The discovery of reconciliation in chimpanzees was made in the 1970s. At the time people would tell me, well, chimpanzees do many of the things people do, so we're not surprised that they reconcile; yet other animals would never do such a thing. Now we know that about thirty different primate species do it, and we also have hard evidence for hyenas, dolphins, and domestic goats. Cats, which are solitary hunters, are thus far the only studied species that apparently doesn't reconcile – you may appreciate this, if you have one at home. So, we think that reconciliation is an extremely basic process that will be found in many social species. The reason for it being so widespread is that it restores relationships that have been disturbed by aggression but that are necessary for survival. Since many animals establish cooperative relationships within which conflict occasionally arises, many need mechanisms of repair.

Observations usually start with a spontaneous aggressive interaction. In chimpanzees, such interactions are so uncommon, even in captivity, that it takes an enormous amount of patience to arrive at a decent sample for statistical treatment. Ironically, if we have a species that is "too" peaceful, or a group that is "too" harmonious, we have trouble studying peacemaking. To show you how the behavior looks, let me provide a typical example of two male chimpanzees who have been chasing each other, yelling and screaming, and afterwards rest in a tree. Ten minutes later, one holds out his hand, inviting the other for an embrace (Figure 1). Seconds later they will hug and kiss, and climb down to the ground to groom each other. That's a so-called *reconciliation*, a process that can easily be defined empirically: it is a friendly contact not long after a conflict between two parties. A kiss is the most typical way for chimpanzees to reconcile. Other animals have different styles, however. Bonobos do it with sex, for example, which chimpanzees rarely do. So, each species has a different way of doing things, but the basic principle is still that they reunite after a fight.

One of the standard research methods is the PC/MC method. We look for a period of time, say ten minutes, to see what happens between two opponents who had a fight. That's the PC or post-conflict observation. In Figure 2, which concerns stumptail macaques, you can see that about 60% of the pairs of opponents come together. This needs to be compared with control observations that tell us how these monkeys normally act when they had no fight. Control observations are done at a different observation day but matched to the PC observation for the time of the day and the individuals observed, hence it is called an MC or matched control observation. There is always a comparison between these two measures, PC and MC, when we study reconciliation. Notice that there is far more contact after fights than in control observations, which is exactly the opposite picture than that presented by the old textbooks that I read when I was a student. In those days, Konrad Lorenz's (1966) *On Aggression* was influential. The popular idea was that aggression is a dispersive behavior, which serves to space out individuals. This idea was developed on territorial species, which were the first studied. But with social animals, things are different. We see the opposite happening: aggression brings individuals together.

Figure 1. Chimpanzees invite reconciliation by means of eye-contact and hand gestures. This photograph shows the situation ten minutes after a protracted, noisy conflict between two adult males at the Arnhem Zoo. The challenged male (left) fled into the tree. He is now being approached by his opponent, who stretches out a hand. Within seconds, the two males have a physical reunion and climb down together to groom each other on the ground. Photograph by the author.

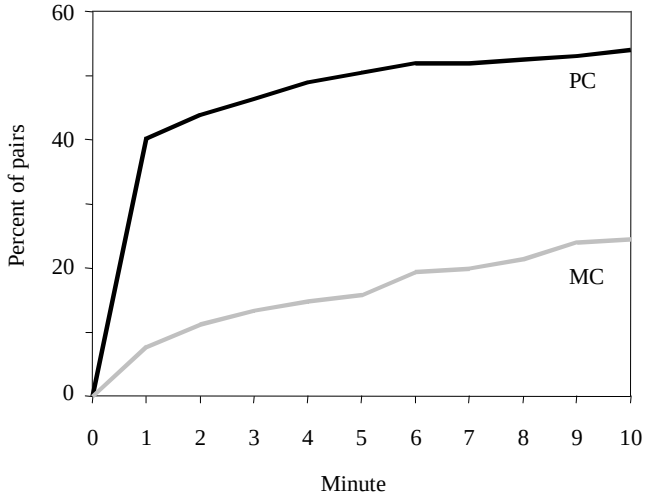

Figure 2. Most primates show a dramatic increase in body contact between former opponents during Post-Conflict (PC) as compared to Matched-Control (MC) observations. Earlier notions about aggression would have predicted the exact opposite (i.e., distancing between previous antagonists). The graph provides the cumulative percentage of opponent-pairs seeking friendly contact during a 10-min time window following 670 spontaneous aggressive incidents in a zoo group of stumptail macaques (after de Waal & Ren, 1988).

If you do the same observations and analyses on human children, as a coworker and I did at a school near Emory, you will find basically the same pattern (Verbeek & de Waal, 2001). The post-conflict data look the same for children, chimpanzees, monkeys, or goats, for that matter. It's the same basic principle. After fights, individuals come together, and they do so especially with partners whom they need for one reason or another. This is known as the valuable-relationship hypothesis, and there's good evidence for it, also from experimental studies.

I always argue that the European community is based on that same principle: the reasoning there was that if you increase the value of relationships, you will get a greater tendency to preserve the peace. And that's what the Europeans have worked on since World War II, now culminating in the adoption of a common currency. They decided instead of fighting all the time, it would be better to foster economic ties. It's an efficient way to get rid of warfare between countries.

We conducted an experiment to see how flexible primate behavior is with regard to reconciliation. This is relevant to determine to what degree evolutionary explanations apply to animal behavior. People have a tendency when they look at other primates to speculate about their "instincts," whereas they immediately assume learning and culture in our own case. Now, I don't even know what an instinct is anymore, and certainly believe that nonhuman primates have lots of skills, meaning that they have acquired behavioral strategies. Our experiment was inspired by the work of Harry Harlow, but done in quite a different way. We took young rhesus monkeys and presented them with stumptail monkeys. Stumptail monkeys will normally reconcile three or four times more often than rhesus monkeys. Rhesus monkeys are sort of the New Yorkers of the primate world, and stumptails the Californians. They are more laid back. So, the rhesus are not good at reconciliation, whereas the stumptails are extremely good at it. We put juveniles of these two species together and compared them with a control procedure for another set of rhesus monkeys who were housed only with other rhesus. The cohousing lasted for five months.

When we put juveniles of the two monkey species in one cage, they were initially segregated: the stumptails would sleep in one corner, the rhesus in another corner. By the end of the five months, however, they were fully integrated. They played together, groomed together, even mated together. But they were juveniles. We selected stumptails slightly older than the rhesus monkeys, so that they would be dominant, assuming that such models would have a greater effect. We found that over the period of cohousing the rhesus monkeys began to reconcile more and more often, until they reached levels very similar to those shown by the stumptails. Interestingly, when we removed the stumptails and tested the rhesus separately, they maintained a conciliatory tendency that was much higher than that of the control rhesus monkeys (de Waal & Johanowicz, 1993).

So, we created a "New & Improved" rhesus monkey. We don't know how long the effect might have lasted because we measured it for only six weeks; but during this period it was dramatic enough to speak of a change in social culture. We changed the behavioral tendencies of rhesus monkey by exposing them to subjects that are more conciliatory, more easygoing than they are. And it shows an enormous amount of flexibility in their behavior. This is why I am almost allergic to terms such as "instinct," because I don't think the behavior of other mammals is

any more instinctive than that of humans: in many ways, they're just as flexible as we are.

Reciprocity

Reciprocal exchange is one of the most promising areas coming out of modern evolutionary approaches, with regards to both animal and human behavior. The above example of political deal-making was not merely anecdotal, because alliances in chimpanzees can be measured and quantified, and we have done so on a large scale in the past, recording literally thousands of them. At present, we have moved to more experimental projects on reciprocity, not unlike the new field of experimental economics that focuses on human behavior. Needless to say, reciprocal help and exchange are absolutely fundamental features of our societies and economies. This field arose as a result of a single theoretical paper published by Robert Trivers (1971): it is a good example of how expectations formulated on the basis of evolutionary considerations can be tested, and have proven helpful in guiding our attention.

Chimpanzees and capuchin monkeys—the two species I work with the most—are special because they are among the very few primates that share food outside the mother-offspring context. I'm very interested in why and how they do so. The capuchin is a small, easy animal to work with, as opposed to the chimpanzee, which is many times stronger than we are. But chimpanzees, too, are interested in each others' food and will share food on occasion—sometimes even hand over a piece of food to another. Most sharing, however, is passive, where one individual will reach for food owned by another, who will let go. But even such passive sharing is very special compared to most animals, in which such a situation might result in a fight or assertion by the dominant, without sharing.

One series of experiments we recently completed concerned the idea that monkeys cooperate on the basis of mental record-keeping of favors. We set up a situation to study tit-for-tat: I do something for you and, a while later, you do something for me. We have strong evidence that such tit-for-tat exists in chimpanzees (de Waal, 1997), but this experiment was done on capuchin monkeys (de Waal & Berger, 2000). Inspired by a classic 1930's study at the Yerkes Primate Center, we confronted a pair of monkeys with a tray with two pull bars attached to it. The two monkeys sat in a test chamber with mesh between them, so that they could see each other and share food through the mesh. The tray was counterweighed such that a single monkey couldn't pull it: they needed to coordinate their pulling. And only one side was baited, meaning that only one of the two monkeys would get a food reward. After successful pulls we measured how much food the possessor shared with its helper. It's very interesting that while they could easily monopolize the food, by sitting in the corner and eating alone, they didn't do this. What we found is that food-sharing after cooperative efforts was higher than after solo efforts. That is, the possessor of food shared more with the monkey on the other side of the mesh if this partner had played a role in getting the food than if the possessor had acquired the food on its own. Capuchins thus seem to reward helpers for their efforts, which is also how they keep the assistant motivated. It is a basic economy.

Conclusions

Studies such as those described above illustrate how in nonhuman primates we face the same sort of dilemmas as in EP: we witness great behavioral plasticity based on development and learning, and even cultural conditioning. As you may have heard, there are increasing speculations about the origins of culture, that is, how one primate group may differ from another of the same species based on socially transmitted habits and knowledge (de Waal, 2001). Animal behavior cannot be understood purely on the basis of natural selection and inborn tendencies any more than human behavior, even though in both cases it obviously helps to think in evolutionary terms.

The examples I have given of political struggles, conflict resolution, and reciprocal altruism all have sound evolutionary thinking attached to them. In the case of political strategies we believe that the male dominance drive and tendency to form coalitions are inborn in both chimpanzees and humans, and that both species apply similar social intelligence to these situations. In the case of peacemaking, we now have a developing theoretical framework that seems applicable in general to conflict among cooperating parties—a framework that is being tested on animals but also increasingly on humans. In the domain of reciprocity, finally, we started out with a solid theoretical framework from which specific hypotheses could be derived. Apart from the testing of tit-for-tat predictions on primate behavior described above, there are excellent studies on human behavior that greatly enlighten the way we look at our own psychology. Some of the best evolutionary psychology (even if it is not called that) now occurs in the field of economic decision-making (e.g., Fehr & Gächter, 2002).

Evolutionary approaches have the potential for bringing an all-encompassing conceptual framework that accommodates and/or replaces the proliferation of disconnected theories in the study of human behavior. The same theories that apply to animal behavior will be applied to human behavior. A unified framework at last! I therefore predict that 50 years from now every psychology department will have Darwin's bearded portrait hanging on the wall. Darwin is really the first evolutionary psychologist. If you read *The Descent of Man* or *Expression of Emotions in Man and Animals*, you will see that these works are directly relevant to human psychology. Indeed, well-known contemporary work, such as that of Paul Ekman (1982) on human facial expressions, has received direct inspiration from Darwin's observations.

Even if the questions asked by evolutionary psychologists, and certainly their answers, may strike some as simplistic, the questions are here to stay. The question of why we choose particular mates, why we avoid incest, why we favor kin over nonkin, what modes of cooperation exist, and so on, are not the traditional questions of psychology, yet they emerge naturally from an evolutionary perspective. These basic questions are central to any evolutionary approach and if you don't like the simplicity of the answers currently coming out of EP, please make an effort to improve them, to broaden the view, because we desperately need a more enlightened EP. I disagree with the accusation, so often leveled against EP, of genetic determinism, yet do feel that the adaptive framework is often applied too quickly and loosely.

The critical point I have tried to make here is that natural selection applies to the whole. It works with the phenotype that is the product of both genetic and nongenetic factors, and so to fragment an organism and its behavior, and talk about the adaptive value of an isolated behavior without considering the larger picture seems useless. The same is true for the splitting of the brain into modules or of the genome into separate genes. I consider this a naïve sort of evolutionary framework that has serious limitations. Exactly the same concerns apply in primatology since primate behavior also develops in interaction with the environment, is flexible, and needs to be seen as an integrated whole.

What this means is that EP can learn from primatology, since we have struggled with these issues for a while longer. Evolutionary approaches began to be applied on a large scale to primate behavior in the 1970s, and, even though we think they have great heuristic power and have often put us on track of many interesting phenomena, we also have learned to be wary of quick adaptationist speculations.

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