

Protean primates: The evolution of adaptive unpredictability in competition and courtship

By Geoffrey Miller

Published as:

Miller, G. F. (1997). Protean primates: The evolution of adaptive unpredictability in competition and courtship. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 312-340). Cambridge, UK: Cambridge U. Press.

Abstract

Machiavellian intelligence evolves because it lets primates predict and manipulate each others' behavior. But game theory suggests that evolution will not stop there: predictive capacities tend to select for unpredictability in counter-strategies, just as many competitive games favor "mixed" (stochastic) strategies. For example, prey animals often evolve "protean" (adaptively unpredictable) evasion behavior to foil the predictive pursuit tactics used by their predators. The same adaptive logic should apply to more abstract social tactics, but protean social behavior remains overlooked in primatology and psychology, because complex order rather than useful chaos has been considered the hallmark of evolved adaptations. This chapter reviews the notions of psychological selection from evolutionary theory, mixed strategies from game theory, and protean behavior from behavioral ecology. It then presents six possible types of social proteanism in primates, and develops a model of how sexual selection through mate choice could have elaborated primate social proteanism into human creative intelligence.

1 Introduction: Unpredictability, animacy, and psychology

Nature cloaks herself in many modes of unpredictability. Science advances in part by recognizing and distinguishing these modes (see Kruger, Gigerenzer, & Morgan, 1987). Statistical mechanics modelled the complexity of fluids using stochastic principles. Quantum theory accepted the noisiness of elementary particles. Chaos theory revealed that many dynamical systems show extreme sensitivity to initial conditions. Evolutionary theory showed how random variation plus cumulative selection could yield organic complexity. Such progress in physics and biology has not been matched by psychology. Although unpredictability is a hallmark of animal behavior, it has been the bane of the behavioral sciences. Variation in behavior, whether across species, situation, space, or time, has usually been attributed either to adaptation or to error, with adaptation narrowly defined as systematic (if complex) correspondence between environmental conditions and behavioral tactics, and error narrowly defined as raw behavioral noise. Psychology's favorite statistical shibboleth, analysis of variance, assumes that behavior can be explained by the interaction of environmental determinants and random, nonadaptive noise.

This chapter examines a type of behavior that is both adaptive and noisy, both functional and unpredictable, and that has therefore been overlooked by most behavioral scientists. The difficulty of predicting animal behavior may be much more than a side-effect of the complexity of animal brains. Rather, the unpredictability may result from those brains having been selected over evolutionary history to baffle and surprise all of the would-be psychologists who preceded us. To appreciate why psychology is hard, we have to stop thinking of brains as physical systems full of quantum noise and chaos, or as computational systems full of informational noise and software bugs. We have to start thinking of brains as biological systems that evolved to

generate certain kinds of adaptive unpredictability under certain conditions of competition and courtship.

2 Genuine unpredictability is the best defense against predictive mind-reading

The Machiavellian Intelligence hypothesis suggests that apes and humans have evolved special cognitive adaptations for predicting and manipulating the behavior of other individuals (Humphrey, 1976; Byrne & Whiten, 1988; Whiten & Byrne, 1988). These adaptations are postulated to include a "Theory of Mind" module for attributing beliefs and desires to others, to better predict their behavior. (see Leslie, 1994; Baron-Cohen, 1995; Dennett, 1988). Suppose these hypotheses are right. Would evolution stop there, with everyone able to predict and manipulate each other's behavior, or would counter-strategies also be expected to evolve? In a society of Machiavellian psycho-analysts, individuals that are harder to predict and manipulate must have selective advantages.

In their classic paper on mind-reading and manipulation, Krebs and Dawkins (1984) identified only two defenses an animal might use against having its actions predicted by a hostile "mind-reader": concealment (of telltale intention cues), and active deception (by generating false cues). They overlook the classic third option, familiar to all military strategists, sports coaches, and game theorists, who routinely confront the problem of stopping an enemy from predicting and preparing for their next move: randomness. Genuine unpredictability. The kind that submarine commanders used in World War II when they threw dice to determine their zigzagging paths during dangerous patrols against surface ships. Thus, resistance to mind-reading may take several major forms: (1) hiding intentions (the Poker Face Strategy), (2) disinformation and deceit (the KGB Strategy), and (3) adaptive unpredictability (the Protean Strategy). Because these strategies are useful under different circumstances at different times, we might expect that they will tend to evolve together in a repertoire of social defenses against mind-reading. However, the Protean Strategy has been much neglected compared to the Poker Face and KGB Strategies. And, while the Poker Face and KGB Strategies remain vulnerable to the coevolution of smarter intention-sensing and deception-foiling capacities, there is no real defense against genuine unpredictability. Thus, the Protean Strategy may be the only evolutionarily stable strategy in the arms race against Machiavellian Intelligence.

The Protean Strategy's usefulness has been overlooked because evolution was widely assumed to produce deterministic mechanisms of animal behavior. Descartes wrote of animals as automata; ethologists wrote of sign stimuli and simple releasing mechanisms; sociobiologists wrote of genes for specific behaviors. Such determinism makes sense for behaviors that deal with inanimate objects, but was extended too easily to behaviors subject to mind-reading. For example, Krebs and Dawkins (1984, p. 384) suggest that "Natural selection itself will favour male sea otters whose behavior happens to take advantage of the lawfulness of female behavior. The effect is that the male manipulates the female in much the same way as he manipulates a stone animals respond in mechanical, robot-like fashion to key stimuli." Further, their notion of mind-reading was based on using statistical laws to exploit the supposed predictability of animal behavior: "For an animal, the equivalent of the data-collection and statistical analysis is performed either by natural selection acting on the mind-reader's ancestors over a long period, by some process of learning during its own lifetime" (Krebs & Dawkins, 1984, p. 386).

This view of animals as intuitive statisticians suggests some obvious counter-measures. Anything that psychologists try to eliminate from their laboratory experiments can be useful

against intuitive psychologists in the wild. Skew their distributions. Dehomogenize their variances. Bias their samples. Add confounds. Regress to the mean. Introduce order effects, practice effects, fatigue effects, maturation effects, expectancy effects, prestige biases, interviewer biases, and social desirability biases. Confound their reliability and validity. But these are just ways to delay enemies from discovering the real determinants of your behavior. The best protection is to undermine the determinants themselves to some degree: increase “residual variance” in one’s behavior to erode the validity of an opponent’s correlations, ANOVAs, MANOVAs, and path analyses. Squirt some noise into your behavior and their intuitive statistics will suffer.

This argument may seem silly. The notion of cognition as intuitive statistics, though once popular (e.g. Peterson & Beach, 1967), is problematic (Gigerenzer & Murray, 1987). But the accuracy of perception and cognition should be undermined by noise in the input, whether one models cognition as intuitive statistics, cognitive psychology flowcharts, neural networks, knowledge-based systems, or dynamical systems theory. Genuine unpredictability is an objective, information-theoretic feature of behavior, so would affect any information-processing system that tries to perceive and predict the behavior, no matter what cognitive metaphor one prefers. Thus, the Protean strategy should often prove useful, especially in primate social behavior. But to understand why, in more detail, we must review three things: the notion of psychological selection from evolutionary theory, the notion of mixed strategies from game theory, and the notion of protean behavior from ethology.

3 Psychological selection: How minds guide evolution

One of Darwin’s greatest achievements was to naturalize the role that mind plays in guiding evolution. He discarded grandiose religious ideas about God as Cosmic Designer and philosophical ideas about Reason willing itself into existence (e.g. Hegel, Schopenhauer, Spencer, Lamarck), and explained simply how animal perceptual systems can act as selective forces to shape the fantastic forms and varieties of flowers (Darwin, 1862), domesticated animals (Darwin, 1868), and courtship traits (Darwin, 1871). Particularly in his analysis of female choice, Darwin (1871) started to develop a general theory of ornaments based on regularities of animal perception such as sensitivity to color, symmetry, repetition, and novelty (see Miller, 1993). However, his incipient theory of what I have called “psychological selection” (Miller, 1993) was not taken forward by anyone at first, largely because Wallace (1889) and others proved so skeptical about the possibility of “aesthetic choice” by female animals (see Cronin, 1991). Perception was viewed mainly as a selective force that operates between species to shape morphological adaptations, such as the appearance of fruit, flowers, camouflage, warning coloration, and mimicry (see Wallace, 1870, 1889; Morgan, 1888; Cott, 1940). This hostility towards Darwin’s ideas about the role of minds as selective forces within species, affecting behavior and not just morphology, probably delayed the development of the Machiavellian intelligence hypothesis by about a century, from Darwin (1871) to Humphrey (1976).

Recently though, there has been an explosion of interest in psychological selection — going under a variety of terms such as “sensory drive” (Endler, 1992), “sensory exploitation” (Ryan, 1990), “signal selection” (Zahavi, 1991), and “the influence of receiver psychology on the evolution of animal signals” (Guilford & Dawkins, 1991). However, most such theory continues to emphasize how minds shape bodies, not how minds shape other minds. A few exceptions are some analyses of communication (Dawkins & Krebs, 1978), deception (Krebs & Dawkins,

1984; Byrne & Whiten, 1988), self-deception (Trivers, 1985), and animate motion perception (Miller & Freyd, 1993).

We lack a general theory of how minds can select other minds within a species. This is a major gap in evolutionary theory, because cognition can guide evolution in such powerful and surprising ways. For example, the evolutionary dynamics that arise when mate choice interacts with natural selection may lead to much faster evolutionary innovation, optimization, and diversification (Miller, 1994a; Miller & Todd, 1993, 1995; Todd & Miller, 1993). Developing a useful theory of psychological selection will require identifying fundamental regularities in perception and cognition that emerge repeatedly through convergent evolution, and which could shape the evolution of behavior within or across species. The Machiavellian intelligence hypothesis offers one such regularity: animals living in complex social groups should regularly evolve mental adaptations for social perception, prediction, manipulation, and exploitation. This regularity in turn sets up reliable selective pressures favoring counter-measures such as intention-hiding, tactical deception, and social proteanism. But to understand just how these pressures operate, we must turn to game theory.

4 Differential game theory: Mixed strategies in pursuit and evasion

The idea of a mixed strategy from game theory is best introduced with an example. In the game of *Matching Pennies*, two players each have a coin. Every turn, each player secretly turns her coin heads-up or tails-up. Then the coins are revealed. If the first player, in the role of “matcher,” has turned up the same side as her opponent (e.g. both coins are heads), then she wins a dollar from her opponent. If the coins mismatch (e.g. one is heads, the other tails), then she must pay a dollar to her opponent. Players can repeat this game turn after turn, producing long sequences of heads and tails, until one player goes broke, or, as more often happens, becomes lividly frustrated.

The roles of “matcher” and “non-matcher” seem different, but their goals are fundamentally the same: predict what the opponent will do, and then do whatever is appropriate (matching or not matching) to win the turn. All that matters is to find out the opponent’s intentions. The ideal offensive strategy then is to be the perfect predictor: figure out what the opponent is doing based on her past behavior, extrapolate her strategy to the next move, make the prediction, and win the turn. But there is a remarkably easy way to defeat this prediction strategy, by playing unpredictably:

“In playing Matching Pennies against an at least moderately intelligent opponent, the player will not attempt to find out the opponent’s intentions but will concentrate on avoiding having his own intentions found out, by playing irregularly ‘heads’ and ‘tails’ in successive games” (Von Neumann & Morgenstern, 1944, p. 144).

If a player picks heads with probability 1/2 and tails with probability 1/2, then no opponent, no matter how good a predictor they are, can do better than break even in this game. This half-heads, half-tails strategy is an example of a “mixed strategy,” because it mixes moves unpredictably.

Perhaps the most important and interesting result from Von Neumann and Morgenstern (1944) was that every two-player, zero-sum game of incomplete information with multiple saddle points (which, in technical terms, covers most of the interesting games you could play against someone) has an optimal strategy that is mixed rather than pure. The utility of mixed strategies has also been shown for many situations of pursuit and evasion studied by “differential game

theory” (Isaacs, 1965; Yavin & Pachter, 1987; for review see Miller & Cliff, 1994a). For example, game theorists have designed “electronic jinking” systems to generate unpredictable flight paths for aircraft so they can evade guided missiles, by analogy to gazelles jinking erratically to avoid a predator (Forte & Shinar, 1988).

Evolutionary game theory (Maynard Smith, 1982) has also recognized the optimality of mixed strategies in many contests between animals. But mixed strategies are usually assumed to evolve as behavioral polymorphisms across a population rather than as unpredictable behavior within an individual. Also, evolutionary game theory has focused mostly on single-step games (such as sex-ratio determination or the Hawk-Dove game: see Maynard Smith, 1982) and discrete-step games (such as the iterated prisoner’s dilemma: see Axelrod, 1984). The literature on differential pursuit-evasion games has been strangely overlooked despite its obvious relevance to predator-prey interactions, dominance contests, sexual harassment, and play behavior. Dave Cliff and I have tried to fill this gap by developing simulations of co-evolution between pursuit and evasion strategies, implemented by genetically specified neural networks with noise parameters that evolve to implement proteanism (Miller & Cliff, 1994a, b; Miller & Cliff, submitted; Cliff & Miller, submitted).

5 Protean behavior theory: Unpredictable evasion by animals

A striking historical coincidence: four years after Michael R. A. Chance co-authored one of the foundational papers in Machiavellian intelligence (Chance & Mead, 1953), he became one of the first biologists to recognize the adaptive significance of unpredictable behavior in animals, with a paper titled “The role of convulsions in behavior” (Chance, 1957; see also Chance & Russell, 1959). Researchers had long been puzzled by “audiogenic seizures” in laboratory rats: when lab technicians accidentally jangle their keys, some lab rats go into bizarre convulsions. But Chance (1957) found that if the rats are provided with hiding places (little rat-huts) in their cages, they simply run and hide when keys are jangled; thus, the convulsions may be facultative defensive behaviors rather than pathological oddities. Convulsions would make it much more difficult for a predator to catch and hold the convulsing animal. Shortly after, Roeder (1962) found that moths tumble and loop unpredictably when hit by bat ultrasound (signalling a predator’s approach); Roeder and Treat (1961) found such tumbling much more effective at bat-evasion than passive tumbling or predictable fleeing (see May, 1991, for recent review).

Humphries and Driver (1970) termed this sort of adaptively unpredictable behavior “protean behavior”, after the mythical Greek river-god Proteus, who eluded capture by continually, unpredictably changing form. Their book *Protean behavior: The biology of unpredictability* (Driver & Humphries, 1988) presents a detailed theory and many ethological observations. Though they did not cite game theory, they made analogies between protean behavior in animals, unpredictable feints in human sports, and randomizing methods in military strategy.

The adaptive logic of proteanism is simple. Animals generally evolve perceptual and cognitive capacities to entrain, track, and predict the movements of other biologically-relevant animals such as prey, predators, and potential mates (Camhi, 1984; Freyd, 1992; Miller & Freyd, 1993; Premack, 1990). Such predictive abilities mean that unpredictable behavior will often be favored in many natural pursuit-evasion situations. For example, if a rabbit fleeing from a fox always chose the single apparently shortest escape route, the very consistency of its behavior would make its escape route more predictable to the fox, its body more likely to be eaten, its genes less likely to replicate, and its fitness lower. Predictability is punished by hostile

animals capable of prediction. Thus, the effectiveness of almost any behavioral tactic can be enhanced by endowing it with characteristics that cannot be predicted by an evolutionary opponent (Driver & Humphries, 1988). Evolutionarily recurring pursuit-evasion contests will usually result in arms races between perceptual capacities for predicting animate motion, and motor capacities for generating protean behavior (Miller & Freyd, 1993).

Along with directional fleeing, protean escape behaviors are probably the most widespread and successful of all behavioral anti-predator tactics, being used by virtually all mobile animals on land, under water, and in the air. Driver and Humphries (1988) review ethological observations from hundreds of species, including insects, fish, birds, and mammals. Human proteanism is obvious in any competitive sport: good boxers use unpredictable feints and attacks, and good rugby players use unpredictable jinks. Predators can also exploit unpredictability to confuse prey, as when weasels do “crazy dances” to baffle the voles that they stalk, or when Australian aborigine hunters do wild dances to mesmerize the kangaroos that they hunt (Driver & Humphries, 1988). Of course, proteanism is typically used at one level of behavioral description (e.g. the trajectory through the environment), and is consistent with maintenance of orderly behavior at other levels (e.g. posture, locomotor gait, obstacle avoidance, perceptual scanning). A possible exception is convulsive “death throes,” when prey use wild, desperate, unpredictable movements to escape from the clutches of predators.

Patterns of animal play behavior reveal the importance of proteanism. Most animal play is play-chasing and play-fighting (Fagen, 1981), and includes intense practice in pursuit and evasion, prediction and proteanism, anticipation and violation of expectations. Judging by the relative play time devoted to learning different skills, foraging for plant foods and navigating through space is much easier than catching prey, escaping from predators, and fighting conspecifics. These latter skills are harder because they demand the robust, continuous, dynamic control of one’s own body in competition with the continuous, dynamic movements of a motivated, well-adapted opponent (Miller & Cliff, 1994a, b). Insofar as primates rehearse proteanism in juvenile play, they probably use it as adults to avoid predators, attack prey, and compete for dominance.

Unpredictability can be useful at many levels of biological organization. When threatened, octopi, cuttlefish, and sea pansies use “color convulsions” across the fast-response chromatophores on their skin, quickly going through different color patterns to defeat the search images (perceptual expectations) used by their predators (Driver & Humphries, 1988). Animals in groups use unpredictable movements, complex motion patterns, and confusing coloration (e.g. zebra stripes or shiny fish scales) to confuse predators. Selection for unpredictability can favor the evolution of large differences between individuals, as when animals within a species evolve “aspect diversity” (polymorphic coloration or behavior) through “apostatic selection” (Clarke, 1962) that favors low-frequency traits (e.g. because predators’ use of search images penalizes common appearances).

Co-evolution itself can be viewed as a pursuit-evasion contest between lineages rather than between individuals. From this perspective, sexual recombination makes sense as a protean strategy that unpredictably mixes up genes so as to “confuse” pathogens (Hamilton, Axelrod, & Tanese, 1990). Indeed, this proteanism argument is one of the leading explanations for the evolution of sex itself (Ridley, 1993). Despite proteanism’s importance, it has been long overlooked in biology, because complex order rather than useful chaos was assumed to be the defining feature of Darwinian adaptations (see Miller, 1993).

6 Can animals really randomize?

For decades, experimental psychologists have investigated whether humans can generate sequences of numbers, letters, or motions that obey various tests of mathematical randomness. Dozens of papers suggested that Reichenbach (1934) was correct in suggesting that humans tend to alternate too much (heads-tails-heads-tails) and don't produce enough long runs (heads-heads-heads-heads). Tune's (1964) review concluded that "humans are incapable of generating a random series of selections from a finite number of alternatives", and Wagenaar's (1972) review concluded "Producing a random series of responses is a difficult, if not impossible task for humans, even when they are explicitly instructed". Complex models were advanced to explain the "heuristics", "biases", or "cognitive constraints" underlying these failures of randomization (e.g. G. A. Miller & Frick, 1949; Kahneman & Tversky, 1972; Treisman & Faulkner, 1987).

However, most such studies were artificial in the extreme, typically requiring isolated subjects to write down a series of numbers on paper with instructions like "be as random as possible." Recently though, Amnon Rapoport — a veteran game theorist (see Rapoport, 1966), and submitter of the "Tit for Tat" strategy that won Axelrod's (1984) iterated prisoner's dilemma contest — reasoned that randomization should be best in real social competition against a predictive opponent. Rapoport and Budescu (1992) found that sequences come much closer to genuine mathematical randomness when they are generated by subjects playing a real, face-to-face, strictly competitive game ("Matching Pennies"), than when they are generated by isolated subjects trying to write down "random sequences." Even without explicit competition, other researchers have shown that animal and human subjects can learn to generate almost perfectly random sequences when given good feedback (Lopes & Oden, 1987; Neuringer, 1986; Neuringer & Voss, 1993). The randomization abilities of monkeys and apes could be tested by having them play a variant of the penny-hiding game, used by Baron-Cohen (1992) to show that autistics lacking a Theory of Mind are poor at randomization in two-person zero-sum games.

The recent skepticism about animals' capacities for varied, unpredictable, novel behavior is ironic because such capacities were fundamental to Behaviorist theories of operant conditioning, which drew explicit parallels between learning and evolution. For example, Skinner (1974) and Campbell (1960) saw random exploratory behavior as analogous to genetic mutations, and reinforcement as analogous to natural selection. Without a reasonably unpredictable, varied set of initial behaviors for reinforcement to "shape," the development of complex behavioral repertoires would be impossible. A classic volume titled *Functions of varied experience* (Fiske & Maddi, 1961) demonstrates the sophistication of Behaviorist reasoning about the importance of behavioral variation, before the computer metaphor and cognitive psychology conflated behavioral variation with noisy information and malfunctioning programs.

7 From unpredictable evasion to social proteanism

The strongest arguments about proteanism have come from studies of pursuit-evasion contests, whether in game theory, evolutionary simulation, or behavioral biology. Would unpredictability still prove adaptive if we shift attention from trajectories through physical space to more abstract trajectories through the space of possible social behaviors? When would "social proteanism" be selected?

There are two levels at which social proteanism makes sense: strategic choices, and tactical details. Roughly, social strategies include things like coalition-forming, peacemaking, short-term mating, long-term consorting, and dominance-challenging; tactics include specific implementations of strategies to exploit local, temporary conditions. Many social strategies are subject to frequency-dependent selection. Examples include the balance between aggressiveness and bluffing in the Hawk-Dove game (Maynard Smith, 1982), between deceptive and honest signals in animal signal theory (Zahavi, 1975; Dawkins & Krebs, 1976), and between extroversion and introversion in evolutionary personality psychology (Buss, 1991; Wilson, 1994). As Maynard Smith (1982) pointed out, any frequency-dependent balance can be implemented either between individuals, as a genetic polymorphism, or within an individual, as unpredictable strategic variation over time. Thus, social proteanism can function to make one's strategic choices unpredictable. But every strategy, every social action or reaction, can also vary in its tactical details, including time, space, style, rhythm, movements, signals, targets, and allies. Introducing uncertainty into each of these tactical variables can render the action more unpredictable, more impervious to counter-measures, and hence more effective.

In general, social proteanism can be viewed as the ultimate extension of Trivers' (1985) theory of adaptive self-deception, which postulates that hiding one's intentions from oneself allows one to better hide them from others. Genuine proteanism means that no part of one's nervous system knows what you will do next, because your actions will be generated stochastically. Thus, it would be impossible to leak "intention cues" to others, because there are no specific intentions. Anywhere that adaptive self-deception might be useful, social proteanism might be even more useful. Indeed, the evolution of social proteanism might act as a brake on Machiavellian intelligence arms races, by undermining the possibility of further improvements in social prediction and manipulation: proteanism casts an oily fog over the dark world of mind-reading.

The following sections outline six examples of social proteanism that we might expect to find in primates with high levels of Machiavellian intelligence. These examples are largely speculative, but I have two defenses. First, for methodological and statistical reasons, it would be extremely hard to notice social proteanism if you weren't looking for it, so the absence of relevant primate data — so far — is not surprising (Miller, 1993). Second, it would be strange if the mixed-strategy game theory that applies to rabbits zig-zagging to escape foxes (Driver & Humphries, 1988), simulated robots evolving noisy neural networks for evasion (Miller & Cliff, 1994b), and military aircraft jinking erratically to avoid guided missiles (Forte & Shinar, 1988), did not apply to those craftiest of animals, the primates.

7.1 Example 1: Protean anger thresholds

Suppose alpha males could adopt one of two strategies for setting their "anger threshold" that determines when they will punish insults to their dominance (e.g. encroachments on their resources or females). With the Old Faithful strategy, the anger threshold is set so that aggressive punishment is generated if and only if an insult exceeds a fixed magnitude T . With the Mad Dog strategy though, the anger threshold is probabilistic, so punishment occurs if an insult exceeds a variable magnitude chosen from a normal distribution with mean T and high variance. Which strategy will work better? Subordinates can quickly learn Old Faithful's anger threshold, and can do anything below magnitude T with impunity. If T is set so anger is only incurred by actual copulation with a female, the subordinates could still groom and provision females at will, establishing useful alliances that increase their claim to alpha status. But subordinates face terrible uncertainty with Mad Dog: can they get away with even a minute of

grooming a female this time? Maybe they did last time, but maybe not this time. Against the Mad Dog strategy, any insult, however slight, risks retaliation — but Mad Dog doesn't incur the time, energy, and injury costs of having a fixed low threshold either. The uncertainty does most of the work of intimidating subordinates. As Betzig (1986) emphasized, the definition of despotism is the power of *arbitrary* life and death over subordinates, and many despots have used the Mad Dog strategy to great effect. This argument about protean anger thresholds would also apply to thresholds for sexual jealousy, sexual coercion, aggressive weaning conflict, aggressive sibling rivalry, juvenile temper tantrums, group warfare, etc. However, indiscriminate use of Mad Dog may worry one's allies in addition to unnerving one's opponents, so its expression should be selective and relatively infrequent.

7.2 Example 2: Protean promiscuity and concealed ovulation

The outcome of sperm competition is fairly unpredictable (see Baker & Bellis, 1995). Females can exploit this fact by mating promiscuously with several males during ovulation, so that there is profound uncertainty about paternity: a male will seldom risk infanticide for fear that the infant he's killing may be his own (Hrdy, 1981; Small, 1993). Promiscuity uses proteanism to confuse paternity. Likewise, concealed ovulation introduces uncertainty about the timing of fertility and hence the paternity of offspring. Most female primates in multi-male groups seem to use either protean promiscuity or concealed ovulation to protect against infanticide.

Obviously, proteanism would also help a female in the choice of when and where to arrange a covert copulation with a subordinate male. The more predictable such sneaky acts, the more risk they incur from dominant males who are trying to mate-guard their females and predict sneaky copulations. Protean lust may be a good strategy: if a female does not know herself when she will be overcome with desire for a subordinate, she cannot leak cues of intended deception to other males. The impulsiveness of some human sexual encounters may reflect such a strategy. Of course, protean timing need not imply indiscriminate mate choice, or indiscreet choice of mating place.

7.3 Example 3: Protean grudges, forgiveness, and reciprocity

Nowak (1990; Nowak & Sigmund, 1992) showed that generous tit-for-tat (GTFT), a stochastic strategy, could evolve and thrive in evolutionary simulations of the noisy, iterated prisoner's dilemma. GTFT cooperates even after an opponent's defection at some non-zero probability (e.g. one-third of the time), and its unpredictability is the key to its success. In Nowak's *noisy* prisoner's dilemma, accidental defections can occur even if both players try to cooperate. This means that the traditional tit-for-tat (TFT) strategy can get locked into infinite cycles of defection as a result of a single mistake. GTFT is more forgiving, but it is impossible to predict exactly when it will cooperate after a defection, so its generosity is hard to exploit. Indeed, allowing GTFT to evolve is one of the most powerful ways to catalyze the evolution of reliable cooperation in the iterated prisoner's dilemma. By allowing probabilities of cooperation after defection to evolve slowly and continuously, Nowak and Sigmund (1992) got full cooperation to evolve where it never could have evolved in one big jump.

This simple simulation has profound implications for reciprocity, exchange, and social relationships. Individuals who forgive defectors after a predictable interval can be exploited repeatedly. Those who forgive after an unpredictable interval are much tougher to exploit. One might even speculate that grudges should decay according to a Poisson distribution over time.

Unpredictable grudges also make it harder for potential defectors to estimate the costs of losing a cooperative partner, such that risk-averse would-be defectors may continue cooperating in the face of this uncertainty. Thus, proteanism can even promote the evolution of reciprocity.

7.4 Example 4: Proteanism and group cooperation

Group cooperation may be facilitated by randomizing processes that make it hard to predict the distribution of costs and benefits from cooperation (Miller, 1994b). An analogy to meiosis shows why: just as the gene-randomizing process of meiosis is necessary to promote peaceful cell division during gamete production, and this peace is disrupted by “meiotic drive” that biases gene allocation among gametes (Hurst, 1992), a cost-benefit lottery may help promote group harmony during high-risk, cooperative activity.

Such lotteries work best when cooperation produces individual fitness payoffs with a positive mean value and a high variance, and with positive and negative outcomes that are fast, final, unpredictable, and unshareable (such as successful fertilization or death). These conditions make it stupid to defect before the lottery and impossible to defect after the lottery. The main resource lotteries in human evolution were probably cooperative hunting, cooperative warfare, and cooperative sexual coercion. For example, Tooby and Cosmides (1993) suggested that the development of projectile weapons may have facilitated the evolution of human cooperative warfare, by making the outcome of warfare more unpredictable to the individual but more beneficial to the winning group. A fast hail of projectiles imposes a more unpredictable survival lottery than an afternoon of hand-to-hand combat, so individual defection is less likely. Moreover, warriors or hunters may draw lots at random to decide who will lead a dangerous raid. Cooperative sexual coercion by males can also function as a reproductive lottery, because the outcome of sperm competition among multiple males is not predictable (see Baker & Bellis, 1995).

Randomization has happier uses. When a Hutterite (type of American fundamentalist) community grows too large, it splits into two groups, and ownership of the original home site is assigned by lottery (Wilson & Sober, 1994). Some of the apparently idiotic, essentially random divination methods used by hunters to predict where prey will be found (e.g. throwing stones on maps of the local environment) may function not only to distribute search effort efficiently (under an optimal foraging model), but to allow collective decision-making without individual guilt or recrimination should the day's efforts prove futile (Campbell, 1974). More recently, Britain's adoption of a national lottery could be construed as a convenient way of promoting national unity and an illusion of fairness in the face of apparently indestructible class divisions and economic collapse. Also, Gigerenzer (in press) has emphasized how in-group variation can implement a form of “adaptive coin-flipping” that benefits the group, though it can be maintained by individual-level selection. In sum, if competition between groups has been important in human evolution (Wilson & Sober, 1994), then we would expect to find evidence of cognitive adaptations that facilitate in-group lotteries.

7.5 Example 5: Proteanism, polymorphism, and personality

Unpredictable variation can prove adaptive across individuals as well as within individuals. Clark (1962) postulated that “apostatic selection” in favor of low-frequency body types and behaviors could maintain substantial morphological and behavioral polymorphism in a species. For example, birds have more trouble finding and eating snails in species with high

levels of polymorphism in shell color and pattern, because the birds' perceptual expectations don't work as well. The same argument may apply to polymorphism at other levels: the predictive power of Machiavellian intelligence may favor greater diversity in personality (i.e. stable social strategies). Evolutionary personality psychologists such as Buss (1991) and Wilson (1994) recognize that frequency-dependent selection can maintain genetic variation in personality traits, but they neglect this possible apostatic effect. Consider how much easier social interactions would be if every individual one encountered had exactly the same personality — i.e. the same social-strategic repertoire, the same goals, the same tastes in mates and friends, the same thresholds for anger or gratitude, etc. Social complexity is not just a function of the number and quality of social relationships in a group (cf. Dunbar, 1993), but also of the inter-individual variations in personality that must be perceived, remembering, and strategized about. Given Machiavellian intelligence, apostatic selection may favor a rapid diversification of personality types, and may maintain behavioral polymorphisms at higher levels than they would otherwise attain. Sexual selection through mate choice may exert additional apostatic pressures, insofar as variety-seeking mechanisms like the Coolidge Effect (Dewsbury, 1981) favor individuals with unusual appearances and behaviors. Just as predictive social intelligence can favor social proteanism within individuals, it can favor a greater diversity of personality across individuals.

7.6 Example 6: Proteanism as a learning-inhibitor, cognition-blocker, and stress-inducer

Unpredictability, aside from making short-term prediction hard, also makes learning hard. Section 2 suggested that behavioral noise interferes with intuitive statistics. Behavioral noise will also interfere with almost any type of inductive learning about behavior. It simply becomes more difficult to puzzle out the determinants of another agent's behavior if their behavior is indeterministic in certain ways.

Proteanism has a host of other nasty psychological effects on opponents; these can be characterized using the language of cognitive psychology. Proteanism makes top-down perceptual expectations less useful, so makes perception slower and less accurate. It demands attention by violating expectations, interfering with other “controlled processing” tasks. It interferes with category learning by decreasing the utility of prototypes and blurring boundaries. It undermines schema-based reasoning by reducing the validity of social schemata. It overloads memory, by requiring the storage of heterogeneous ensembles of episodic memories, rather than simple, representative exemplars. It introduces uncertainty, confusion, and conflict at almost every stage of cognition. Research on human judgment and decision-making shows that we are not only risk-averse, but uncertainty-averse (Ellsberg, 1961; Becker & Brownson, 1964; Hogarth & Kunreuther, 1989), and proteanism capitalizes on these aversions.

Proteanism could also induce debilitating levels of physiological stress in opponents. Many studies have shown that lack of control over an unpredictable environment causes stress, depression, disease, and feelings of helplessness (see Seligman, 1975). Sapolsky (1994) notes that “Unpredictability makes stressors much more stressful.” Low-quality predictive information does not help: especially stressful are vague warnings of an upcoming menace that will occur at an unpredictable time, and against which few precautions can be taken. For example, a male primate rising in rank could benefit by “warning” an alpha male that a takeover attempt is imminent, without providing any tactical details; the alpha's resulting worries and stress could make the takeover more likely to succeed. Conversely, the alpha could use the Mad Dog strategy to impose continuous, debilitating stress on potential challengers. Dominants may have evolved a tacit understanding that by using proteanism to induce sufficient long-term

learned helplessness in rivals, their immune systems will be sufficiently compromised that pathogens and predators will finish them off, with little physical risk to the dominant.

8 From social proteanism to creative intelligence?

One rarely-examined assumption of the Machiavellian intelligence hypothesis is that domain-specific social cognition (e.g. a theory of mind module) is uniquely likely to facilitate the evolution of full-blown, human-level intelligence and creativity. The assumption seems plausible at first, but I cannot see its real logical force. It *seems* a short step from the capacity to attribute beliefs and desires to other agents, to the capacities for language, metacognition, episodic memory, and high-level planning. But the same reasoning could predict that it's only a short evolutionary step from beaver dams to Greek architecture, from depth perception to representational painting, from social insect colonies to Marxism, and from echolocation to radar. The formal similarities can hide huge evolutionary gaps. Evolution tends to produce domain-specific cognitive modules tightly adapted to specific, evolutionarily recurring tasks (Cosmides & Tooby, 1994). We do not yet have any theory about which such domain-specific capacities are more likely to have more domain-general spin-offs. And there are good functional arguments for relative domain-generality being a primitive rather than an advanced state for most cognitive capacities: the longer a capacity is under selection, the more automatic, unconscious, domain-specific, encapsulated, and specialized it is expected to become (Cosmides & Tooby, 1994). Thus, the apparent flexibility of social cognition in great apes may reflect its evolutionary recency (i.e. its primitiveness, inconvenience, inefficiency, unreliability, and general looseness). In another 20 million years, perhaps mind-reading in the great apes would become as encapsulated, specialized, and unconscious as web-spinning in the spider. The sloppy boundaries of social cognition in apes may have little direct relation to the evolution of more domain-general human intelligence.

Proteanism is different, because its evolution provides one critical substrate for creative thought: the capacity for rapid, unpredictable generation of highly variable alternatives. Almost every modern theory of learning and cognition relies upon some mechanism of random variation and selective retention (Campbell, 1960, 1974). Studies of human creativity have long stressed the interplay between random generation (e.g. brainstorming, divergent thinking, remote associations) and selective evaluation (see Boden, 1991). The most baffling and poorly explained feature of creative thought is the mechanism of random generation, whether mythologized as the creative muse, deified as divine inspiration, or rationalized as "divergent thinking." The theory of protean behavior (Driver & Humphries, 1988; Miller, 1993) seems to offer the first evolutionary explanation for this crucial randomization mechanism, and thus leads to the first naturalistic account of the evolution of human creativity.

A problem remains: why don't all animals with capacities for protean evasion of predators develop human-level creative thought? One might expect that randomization capacities, plus basic capacities for mentally representing one's environment, plus generic natural selection for intelligence, would produce creative thought in almost all species capable of proteanism. But it hasn't. Even worse, most species with social proteanism (e.g. apes, and maybe some dolphins, whales, and elephants) do not evolve human-style creative intelligence.

The easy way out of this dilemma is to "pull a Steven Jay": invoke historical contingency, genetic drift, epistasis, heterochrony, local optima, or some other dark refuge of anti-adaptationism (Gould, 1989), and suggest that one lineage with social proteanism, social intelligence, social creativity, large brains, and good luck just happened to evolve human

cognition. But we must face the hard facts: full-blown creative cognition is so rare, expensive, and complex that it must have evolved under *direct* selection (Foley, 1992; Miller, 1993) — not through the happy overlap of cognitive capacities selected for other functions. Social proteanism just provides one important mechanism (randomization) that could have been “exapted” for creative intelligence; it doesn’t lead straight to humans up some evolutionary ladder. The next section outlines one possible model of direct selection for creative intelligence; it takes social proteanism as a starting point, but requires sexual selection to do most of the work.

9 From proteanism to creativity: Runaway sexual selection for unpredictability-indicators?

Suppose that capacities for proteanism became an important component of primate social intelligence, especially in apes and early hominids. Insofar as proteanism contributed to competitive success, along with size, strength, health, and social skills, we might expect that mate choice mechanisms would evolve to favor exaggerated displays of proteanism, along with displays of size, strength, health, and social skills. The more important proteanism becomes in social competition and survival, the more likely it is to be advertised and elaborated in courtship. Once proteanism came under the influence of mate choice, three new processes could come into play.

First, Zahavi’s (1975) handicap principle might predict that only proteanism-displays that are costly (e.g. energetically expensive) would be reliable, so proteanism-displays would probably become elaborated and specialized, leading to special “protean courtship displays” that might bear little resemblance to the original social protean tactics. However, skill at proteanism is almost as hard to fake as other features relevant to mate choice (e.g. size, strength, health, status), because proteanism can be directly assessed by capacities for social prediction. So proteanism-displays in courtship may evolve to be quite distinct from social proteanism in competition, and their informational features may become elaborated (e.g. into unpredictability at higher and higher levels of cognitive or strategic performance), but they need not become elaborated in physical magnitude, e.g. through exaggerated movements. Thus, human lovers sometimes whisper creative jokes, metaphors, and stories to each other, using proteanism elaborated at the level of cognitive content, but not at the level of physical size or intensity — unlike most other products of sexual selection, such as 6-foot-long peacock tails, or 120-decibel humpback whale songs.

Second, under Ryan’s (1990) sensory exploitation model, any intrinsic sensory biases that favored unpredictability could exert an influence on mate choice, so could select for proteanism. We know of such a sensory bias already: neophilia (selective attention to the novel and the unexpected). Nervous systems rely heavily on expectations, and usually evolve mechanisms to detect violations of expectations. These novelty-detectors direct attention to environmental features that require deeper, more focused cognitive processing. Thus, neophilia tends to favor proteanism because unpredictability attracts attention. Darwin (1871) attached great importance to neophilia in explaining the diversity and rapid evolutionary turnover of bird plumage: “It would appear that mere novelty, or slight changes for the sake of change, have sometimes acted on female birds as a charm, like changes of fashion with us.” Some female birds have been shown to prefer male birds who have larger song repertoires, allowing greater diversity and novelty of performance (Catchpole, 1987; Podos et al., 1992). Such neophilia probably accounts for the astounding complexity and variety of songs by blackbird, nightingales, mockingbirds, parrots, and mynahs. Moving from birds to primates, Small (1993) emphasized

neophilia in primate mate choice: “The only consistent interest seen among the general primate population is an interest in novelty and variety. Although the possibility of choosing for good genes, good fathers, or good friends remains an option open to female primates, they seem to prefer the unexpected.” Neophilia in humans has been studied most extensively as “sensation-seeking” (Zuckerman, 1984), and “openness”: one of the “Big Five” personality traits (see Buss, 1991). Both sensation-seeking and openness are moderately heritable, as illustrated by the recent discovery of the “novelty-seeking” polymorphism of the D4DR dopamine receptor gene (see Cloninger, Adolfsson, & Svrakic, 1996). Neophilia’s current heritability suggests that it could have driven a Fisherian runaway process in our ancestors. Human neophilia is also the foundation of the art, music, television, film, publishing, drug, travel, pornography, and fashion industries, which account for a substantial proportion of the global economy. Martindale (1990) has documented the importance of neophilia in the development of diverse artistic, literary, and musical styles over history. If birds, primates, and humans show neophilia, early hominids probably did too, and this neophilia in mate choice could have exerted strong, directional selection in favor of human-level creativity.

Third, under Fisher’s (1930) runaway sexual selection model, any initial preference for proteanism, whether due to indicator mechanisms or neophilic biases, can lead to positive-feedback dynamics that elaborate both the mate preference and the preferred trait. The runaway process works because preferences become genetically correlated (“linked”) with the traits they prefer, and this genetic linkage drives the process even in the face of substantial natural selection and biased mutation (Pomiankowski, Iwasa, & Nee, 1991). Runaway is especially likely given a “directional preference” of the more-is-better variety (Kirkpatrick, 1987; Miller & Todd, 1993).

What would such “protean courtship displays” look like? What sort of behaviors could possibly advertise capacities for behavioral unpredictability, variability, and novelty? Any behavior that humans consider “creative” would work: art, music, humor, language, metaphors, stories, concepts, ideologies — in short, almost all of human culture can function to advertise proteanism. Protean sexuality may be manifest in the incredible variety of sexual foreplay and intercourse positions observed in bonobos or “pygmy chimpanzees” (see De Waal, 1989). But full-blown, creative, protean courtship displays seem unique to humans. Creativity strips proteanism down to its bare essentials: the innovative, unpredictable recombination of recognizable perceptual, conceptual, or performative elements. The more abstracted away from real social tactics such creativity becomes, the more accurate and specialized a proteanism-indicator it is. Thus, most of the human mind’s capacities that have baffled evolutionary theorists from Wallace (1889) onwards might be illuminated by considering their functions as protean courtship displays.

Of course, in all such displays we see an interplay between proteanism and ritualization, both of which increase the effectiveness of the display signal (see Krebs & Davies, 1987, chapter 14). Ritualization increases impact through the use of repetition, high intensity, strong contrasts, alerting signals, and stereotyping in basic units (Huxley, 1966; Krebs & Davies, 1987), whereas proteanism attracts attention, creates memorable juxtapositions, and produces humor by violating expectations. Ritualized themes and protean variations, and ritualized units and protean combinations, are common in human culture. Language combines ritualized grammar, phonology, semantics, and conversational norms with protean sentence structure, intonation, word choice, story plot, and expressive content. Music combines ritualized rules of tonality, rhythmicity, melody, and harmony, and protean inventions and variations in particular songs. Art combines ritualized representational and stylistic conventions with protean composition, content, and individual style. Displays without any orderly elements are incomprehensible; those without

protean elements are boring. The optimal cultural courtship display is the virtuosic combination of recognizable semantic elements in novel combinations with new emergent meanings.

This hypothesis adds a new stage to the Machiavellian Intelligence model: here, the transition from monkeys to apes and early hominids may reflect the evolution of new social-competitive skills, but the transition from early hominids to modern humans represents the evolution of new courtship skills. Technological or ecological selection pressures were probably not so important in the evolution of intelligence; tool-making and hunting innovations merely allowed our ancestors to bear the energetic burden of growing such large courtship ornaments, i.e. brains (see Foley, 1992; Aiello & Wheeler, 1995). Still, we need to develop empirical tests that distinguish not only between ecological and social models of encephalization (as in Byrne, 1995), but also, within the social realm, between social-competitive and sexual-selective models.

The Machiavellian intelligence hypothesis has lumped together all possible selection pressures that can emerge from behavioral interactions between conspecifics. Since the vast majority of runaway processes that result in fast elaborations of behavioral capacities probably occur within species, the Machiavellian hypothesis scored an easy win over other, much weaker theories of human mental evolution (e.g. intelligence through tool-making, hunting, gathering, neoteny, drift, or gene-culture coevolution). But it is time to ask about the relative contributions of each distinctive relationship type to hominid and human evolution: though inter-related, we should try to avoid conflating parent-offspring interactions, reciprocity, competition for social status, between-group competition, mate choice, etc. My bets are on mate choice as the mainspring of human mental evolution, because the runaway processes of sexual selection are the best-established and most thoroughly modelled (see Andersson, 1994; Miller, 1993; Miller & Todd, 1995), and result in adaptations like bird song, whale song, and courtship dances that are most similar to the products of human creative intelligence. All social competition is ultimately reproductive competition, and sexual selection through mate choice is at the heart of reproduction competition. My view therefore differs somewhat from that of Whiten and Byrne (1988, p. 3), who downplayed sexual selection in suggesting that “In the earlier paper [Chance & Mead, 1953] an important *misconception* was that sexual relationships represent the essence of primate life, and the key ‘problem’ requiring cleverness” (my italics). Agreed, primatologists used to over-play the centrality of male-male aggressive sexual conflict, but sexual competition more broadly construed is the very heart of primate and human social life.

14 Conclusions

Social behavior in primates and humans shows many regularities, but we must not assume that predictable regularity is always adaptive. Given the predictive capacities postulated by the Machiavellian Intelligence hypothesis, we would expect a coevolutionary arms race to ensue in competitive domains like competition and courtship, between social prediction and social proteanism. Of course, in more cooperative relationships between kin, friends, and lovers, we might expect social intelligence to favor social predictability rather than unpredictability. A general theory of how social intelligence can select for unpredictability under some conditions and predictability under other conditions might account for the evolution not only of social proteanism in competition and creativity in courtship, but also of empathy, reliability, and intimacy. Further research with primates and humans could investigate not only our capacities for mind-reading others, but our capacities for making our own minds harder or easier to read, by switching from unpredictability in some contexts to predictability in others.

This paper has reviewed the psychological selection theory, differential game theory, and protean behavior theory relevant to understanding the adaptive value of unpredictability, and has developed six examples where such unpredictability could prove adaptive in primate behavior. We also saw how runaway sexual selection may tend to elaborate social proteanism into various protean courtship displays such as art, music, humor, and language. The bridge from primate social intelligence to human cultural intelligence was crossed not through social-competitive pressures for Machiavellian Intelligence, but through mate-choice pressures for Protean Intelligence. We humans, and most of what we do — including writing papers for books like this — are the happy result.

Acknowledgments

This research was supported by an NSF-NATO Post-Doctoral Fellowship, RCD-9255323, NSF Research Grant INT-9203229, an NSF Graduate Fellowship, NSF grant BNS90-21684 to Roger Shepard, the University of Sussex, the University of Nottingham, and the Max Planck Society. For helpful discussions, comments, and/or collaboration, thanks to Rosalind Arden, Simon Baron-Cohen, Richard Byrne, Dave Cliff, Donald Campbell, Leda Cosmides, Helena Cronin, Franz De Waal, Dan Dennett, Peter Driver, Robin Dunbar, Robert Foley, Jennifer Freyd, Gerd Gigerenzer, John Maynard Smith, Roger Shepard, Elliot Sober, Peter Todd, John Tooby, and Andy Whiten.

References

- Aiello, L. C., & Wheeler, P. (1995). The expensive tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, 36 (2), 199-221.
- Andersson, M. B. (1994). *Sexual selection*. Princeton U. Press.
- Axelrod, R. (1984). *The evolution of cooperation*. Basic Books.
- Baker, M., & Bellis, M. (1995). *Human sperm competition*. London: Chapman & Hall.
- Baron-Cohen, S. (1992). Out of sight or out of mind? Another look at deception in autism. *J. Child Psychology and Psychiatry*, 33 (7), 1141-1155.
- Baron-Cohen, S. (1995). *Mindblindness*. MIT Press.
- Betzig, L. (1986). *Despotism and differential reproduction: A Darwinian view of history*. Hawthorne, NY: Aldine.
- Boden, M. (1991). *The creative mind*. Basic Books.
- Buss, D. M. (1991). Evolutionary personality psychology. *Annual Review of Psychology*, 42, 459-491.
- Byrne, R. (1995). *The thinking ape: Evolutionary origins of intelligence*. Oxford U. Press.
- Byrne, R. & Whiten, A. (Eds.) (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford U. Press.
- Camhi, J. M. (1984). *Neuroethology: Nerve cells and the natural behavior of animals*. Sinauer.

- Campbell, D. (1960). Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review*, 67, 380-400.
- Campbell, D. (1974). Evolutionary epistemology. In P. A. Schilpp (Ed.), *The philosophy of Karl Popper*. La Salle, IL: Open Court.
- Catchpole, C. K. (1987). Bird song, sexual selection and female choice. *Trends in Evolution and Ecology*, 2, 94-97.
- Chance, M. R. A. (1957). The role of convulsions in behavior. *Behavioral Science*, 2, 30-45.
- Chance, M. R. A., & Mead, A. (1953). Social behavior and primate evolution. Reprinted in R. Byrne & A. Whiten (Eds.) (1988), *Machiavellian intelligence*, pp. 34-49. Oxford U. Press.
- Chance, M. R. A., & Russell, W. M. S. (1959). Protean displays: a form of allaesthetic behavior. *Proc. Zoological Soc. of London*, 132, 65-70.
- Clarke, B. C. (1962). The evidence for apostatic selection. *Heredity*, 24, 347-352.
- Cliff, D., & Miller, G. F. (submitted). Co-evolution of pursuit and evasion, II: Simulation methods, results, and analysis. For *Adaptive Behavior*.
- Cloninger, C. R., Adolfsson, R., & Svrakic, N. M. (1996). Mapping genes for human personality. *Nature Genetics*, 12, 3-4.
- Cosmides, L., & Tooby, J. (1994). Origins of domain specificity: The evolution of functional organization. In L. A. Hirschfeld & S. A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture*, pp. 85-116. Cambridge U. Press.
- Cott, H. B. (1940). *Adaptive coloration in animals*. London: Methuen.
- Darwin, C. (1862). *On the various contrivances by which orchids are fertilized by insects*. London: John Murray.
- Darwin, C. (1868). *On the variation of animals and plants under domestication*. London: John Murray.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex* (2 vols.) London: John Murray.
- Dawkins, R., & Krebs, J. R. (1978). Animal signals: information or manipulation? In J. R. Krebs & N. B. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (2nd Ed.), pp. 282-309. Blackwell Scientific.
- De Waal, F. (1989). *Peacemaking among primates*. Harvard U. Press
- Dennett, D. (1988). The intentional stance in theory and practice. In R. Byrne & A. Whiten (Eds.), *Machiavellian intelligence*, pp. 180-202. Oxford U. Press.

- Dewsbury, D. A. (1981). Effects of novelty on copulatory behavior: The Coolidge effect and related phenomena. *Psychological Bulletin*, 89, 464-482.
- Driver, P. M., and Humphries, N. (1988). *Protean behavior: The biology of unpredictability*. Oxford U. Press.
- Dunbar, R. (1993). Coevolution of neocortical size, group size, and language. *Behavioral and Brain Sciences*, 16(4), 681-735.
- Ellsberg, D. (1961). Risk, ambiguity, and the Savage axioms. *Quarterly J. Economics*, 75, 643-699.
- Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist*, 139, S125-S153.
- Fagen, R. (1981). *Animal play behavior*. Oxford U. Press.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Fiske, D. W., & Maddi, S. R. (1961). *Functions of varied experience*. Homewood, IL: Dorsey Press.
- Foley, R. (1992). Ecology and energetics of encephalization in hominid evolution. In A. Whiten & E. M. Widdowson (Eds.), *Foraging strategies and natural diet of monkeys, apes and humans*. Oxford U. Press.
- Forte, I., & Shinar, J. (1989). Improved guidance law design based on the mixed-strategy concept. *J. Guidance, Control, and Dynamics*, 12 (5), 739-745.
- Freyd, J. J. (1992). Dynamic representations guiding adaptive behavior. In F. Macar, V. Pouthas, & W. J. Friedman (Eds.), *Time, Action and Cognition: Towards Bridging the Gap*, pp. 309-323. Dordrecht: Kluwer Academic Publishers.
- Gigerenzer, G. (in press). Rationality: Why social context matters. In P. B. Baltes & U. Staudinger (Eds.), *Interactive minds: Life-span perspectives on the social foundations of cognition*. Cambridge U. Press.
- Gigerenzer, G., & Murray, J. L. (1987). *Cognition as intuitive statistics*. Erlbaum.
- Gould, S. J. (1989). *Wonderful life*. New York: Norton.
- Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behavior*, 42, 1-14.
- Hamilton, W. D., Axelrod, R., & Tanese, R. (1990). Sexual reproduction as an adaptation to resist parasites: A review. *Proc. Nat'l Acad. Sciences (USA)* 87(9), 3566-3573.
- Hogarth, R. M., & Kunreuther, H. C. (1989). Risk, ambiguity, and insurance. *J. Risk and Uncertainty*, 2, 5-35.
- Hrdy, S. B. (1981). *The woman that never evolved*. Harvard U. Press.

- Humphrey, N. (1976). The social function of intellect. Reprinted in R. Byrne & A. Whiten (Eds.) (1988). *Machiavellian intelligence*, pp. 13-26. Oxford U. Press.
- Humphries, D. A., & Driver, P. M. (1970). Protean defense by prey animals. *Oecologia*, 5, 285-302.
- Hurst, L. D. (1992). Intragenomic conflict as an evolutionary force. *Proc. Royal Soc. London B*, 248, 135-140.
- Huxley, J. (1966). A discussion of ritualisation of behaviour in animals and man: Introduction. *Phil. Trans. Royal Soc. London B*, 251, 247-271.
- Isaacs, R. (1965). *Differential games*. New York: John Wiley.
- Kahneman, D., & Tversky, A. (1972). Subjective probability: A judgment of representativeness. *Cognitive Psychology*, 3, 430-454.
- Kirkpatrick, M. (1987). The evolutionary forces acting on female preferences in polygynous animals. In J. W. Bradbury and M. B. Andersson (Eds.), *Sexual selection: Testing the alternatives* (pp. 67-82). New York: John Wiley.
- Krebs, J. R., & Dawkins, R. (1984). Animal signals: Mindreading and manipulation. In J. R. Krebs & N. B. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (2nd Ed.), pp. 380-402. Oxford: Blackwell Scientific.
- Krebs, J. R., & Davies, N.B. (1987). *An introduction to behavioral ecology* (2nd Ed.). Blackwell Scientific.
- Kruger, L., Gigerenzer, G., & Morgan, M. S. (Eds.). (1987). *The probabilistic revolution. Vol. 2. Ideas in the sciences*. MIT Press.
- Leslie, A. (1994). ToMM, ToBY, and Agency: Core architecture and domain specificity. In L. A. Hirschfeld & S. A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture*, pp. 119-148. Cambridge U. Press.
- Lopes, L. L., & Oden, G. C. (1987). Distinguishing between random and nonrandom events. *J. Experimental Psych.: Learning, memory, and cognition*, 13 (3), 392-400.
- Martindale, C. (1990). *The clockwork muse*. Harper Collins.
- May, M. (1991). Aerial defense tactics of flying insects. *American Scientist*, 79, 316-328.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge U. Press.
- Miller, G. A., & Frick, F. C. (1949). Statistical behavioristics and sequences of responses. *Psychological Review*, 56, 311-324.
- Miller, G. F. (1993). *Evolution of the human brain through runaway sexual selection: The mind as a protean courtship device*. Ph.D. thesis, Stanford University Psychology Department. (Available through UMI microfilms.)

- Miller, G. F. (1994a). Exploiting mate choice in evolutionary computation: Sexual selection as a process of search, optimization, and diversification. In T. C. Fogarty (Ed.), *Evolutionary Computing: Proceedings of the 1994 Artificial Intelligence and Simulation of Behavior (AISB) Society Workshop*, pp. 65-79. Springer-Verlag.
- Miller, G. F. (1994b). Beyond shared fate: Group-selected mechanisms for cooperation and competition in fuzzy, fluid vehicles. *Behavioral and Brain Sciences*, 17 (4), 630-631.
- Miller, G. F. & Cliff, D. (1994a). *Co-evolution of pursuit and evasion: Biological and game-theoretic foundations*. Cognitive Science Research Paper CSRP-311, University of Sussex.
- Miller, G. F., & Cliff, D. (1994b). Protean behavior in dynamic games: Arguments for the co-evolution of pursuit-evasion tactics in simulated robots. In D. Cliff, P. Husbands, J. A. Meyer, & S. Wilson (Eds.), *From Animals to Animats 3: Proceedings of the Third International Conference on Simulation of Adaptive Behavior*, pp. 411-420. MIT Press/Bradford Books.
- Miller, G. F. & Cliff, D. (submitted). Co-evolution of pursuit and evasion, I: Biological and game-theoretic foundations. For *Adaptive Behavior*.
- Miller, G. F., & Freyd, J. J. (1993). *Dynamic mental representations of animate motion: The interplay among evolutionary, cognitive, and behavioral dynamics*. Cognitive Science Research Paper CSRP-290, University of Sussex.
- Miller, G. F., & Todd, P. M. (1993). Evolutionary wanderlust: Sexual selection with directional mate preferences. In J.-A. Meyer, H. L. Roitblat, & S. W. Wilson (Eds.), *From Animals to Animats 2: Proceedings of the Second International Conference on Simulation of Adaptive Behavior*, pp. 21-30. MIT Press.
- Miller, G. F., & Todd, P. M. (1995). The role of mate choice in biocomputation: Sexual selection as a process of search, optimization, and diversification. In W. Banzaf & F. H. Eeckman (Eds.), *Evolution and biocomputation: Computational models of evolution*, pp. 169-204. Springer-Verlag.
- Morgan, C. L. (1888). Natural selection and elimination. *Nature*, Aug. 16, 370.
- Neuringer, A. (1986). Can people behave "randomly"? The role of feedback. *J. Exper. Psych.: General*, 115 (1), 62-75.
- Neuringer, A., & Voss, C. (1993). Approximating chaotic behavior. *Psychological Science*, 4 (2), 113-119.
- Nowak, M. A. (1990). Stochastic strategies in the prisoner's dilemma. *Theoretical population biology*, 47 (1), 93-112.
- Nowak, M. A., & Sigmund, K. (1992). Tit for tat in heterogenous populations. *Nature*, 355 (6357), 250-252.

- Peterson, C. R., & Beach, L. R. (1967). Man as an intuitive statistician. *Psychological Bulletin*, 68, 29-46.
- Podos, J., Peters, S., Rudnicki, T., Marler, P., & Nowicki, S. (1992). The organization of song repertoires in song sparrows: Themes and variations. *Ethology*, 90 (2), 89-106.
- Pomiankowski, A., Iwasa, Y., & Nee, S. (1991). The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution*, 45 (6): 1422-1430.
- Premack, D. (1990). The infant's theory of self-propelled objects. *Cognition*, 36, 1-16.
- Rapoport, A., & Budescu, D. V. (1992). Generation of random series in two-person strictly competitive games. *J. Experimental Psych.: General*, 121 (3), 352-363.
- Reichenbach, H. (1934/1949). *The theory of probability*. (Translated by E. Hutten & M. Reichenbach.) Berkeley: U. California Press.
- Ridley, M. (1993). *The red queen: Sex and the evolution of human nature*. London: Viking.
- Roeder, K. D. & Treat, A. E. (1961). The detection and evasion of bats by moths. *American Scientist*, 49, 135-148.
- Roeder, K. D. (1962). The behavior of free-flying moths in the presence of artificial ultrasonic pulses. *Animal Behavior*, 10, 300-4.
- Ryan, M. J. (1990). Sexual selection, sensory systems, and sensory exploitation. *Oxford Surveys of Evolutionary Biology*, 7, 156-195.
- Sapolsky, R. (1994). *Why zebras don't get ulcers: A guide to stress, stress-related diseases, and coping*. W. H. Freeman.
- Seligman, M. (1975). *Helplessness: On depression, development, and death*. W. H. Freeman.
- Skinner, B. F. (1974). *About behaviorism*. New York: Alfred A. Knopf.
- Small, M. (1993). *Female choices: Sexual behavior of female primates*. Cornell U. Press.
- Tooby, J., & Cosmides, L. (1993). *The evolutionary psychology of coalitional aggression*. Paper presented at the Fifth Annual Meeting of the Human Behavior and Evolutionary Society, Aug 4-8, Binghamton University, 1993.
- Todd, P. M., & Miller, G. F. (1993). Parental guidance suggested: How parental imprinting evolves through sexual selection as an adaptive learning mechanism. *Adaptive Behavior*, 2 (1): 5-47.
- Treisman, M., & Faulkner, A. (1987). Generation of random sequences by human subjects: Cognitive operations or psychological process? *J. Experimental Psychology: General*, 116 (4), 337-355.
- Trivers, R. (1985). *Social evolution*. Benjamin/Cummings.

- Tune, G. S. (1964). Response tendencies: A review of some relevant literature. *Psychological Bulletin*, 61 (4), 286-302.
- Von Neumann, J., & Morgenstern, O. (1944). *Theory of games and economic behavior*. Princeton: Princeton U. Press.
- Wagenaar, W. A. (1972). Generation of random sequences by human subjects: A critical survey of literature. *Psychological Bulletin*, 77, 65-72.
- Wallace, A. R. (1870). *Contributions to the theory of natural selection*. London: Macmillan.
- Wallace, A. R. (1889) *Darwinism: An exposition of the theory of natural selection, with some of its applications*. London: Macmillan.
- Whiten, A., & Byrne, R. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, 11, 233-273.
- Wilson, D. S. (1994). Adaptive genetic variation and human evolutionary psychology. *Ethology and sociobiology*, 15 (4), 219-235.
- Wilson, D. S., & Sober, E. (1994). Re-introducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences*, 17 (4). [pages?]
- Yavin, Y., & Pachter, M. (Eds.). (1987). *Pursuit-evasion differential games*. Pergamon Press.
- Zahavi, A. (1975). Mate selection — a selection of handicap. *J. Theoretical Biology*, 53, 205-214.
- Zahavi, A. (1991). On the definition of sexual selection, Fisher's model, and the evolution of waste and of signals in general. *Animal Behavior*, 42 (3), 501-503.
- Zuckerman, M. (1984). Sensation seeking: A comparative approach to a human trait. *Behavioral and Brain Sciences*, 7, 413-471.