Mate choice: From sexual cues to cognitive adaptations
By Geoffrey Miller

Abstract

Evolutionary psychologists have successfully combined sexual selection theory and empirical research to compile lists of sexual attractiveness cues used in human mate choice. But a list of inputs is not the same as a normative or descriptive model of a psychological adaptation. We need to shift from cataloguing sexual cues to modelling cognitive adaptations for mate choice. This theoretical chapter addresses how to make this transition in three parts. The introduction discusses four general problems with cue-cataloguing as an evolutionary psychology research strategy: animals' promiscuous flexibility of cue use, cue use being marginal to cognition, cue use being marginal to the hard game-theoretic aspects of mate choice, and cue use being uninformative about the exact adaptive functions of mate choice. The middle section develops six critiques of current mate choice research: the obsession with sex differences, the over-emphasis on physical rather than behavioural cues, the assumption of weighted-linear models of cue integration, the avoidance of game-theoretical problems of mutual choice and assortative mating, the neglect of co-evolution between mate choice heuristics and the cues that they select, and the failure to understand that mate choice is only worth doing if potential mates show significant genetic variance. The conclusion outlines a new normative and descriptive framework for mate choice, centered on the use of brutally efficient search heuristics that exploit the informational structure of human genotypes, phenotypes, and populations to make good mate choices.

Introduction: Four problems with cataloguing sexual cues

Mate choice has become the flagship domain of evolutionary psychology: the best-known example of how evolutionary theory can guide the study of the human mind and human behaviour. Evolutionary psychologists, inspired by sexual selection theory (Darwin, 1871; Cronin, 1991; Andersson, 1994), have successfully discovered and documented some of the diverse cues used in the selection of sexual partners, such as height, intelligence, walking speed, facial symmetry, sense of humour, waist-to-hip ratio, degree of genetic relatedness, full lips, political status, and sexual foreplay skills (for reviews see Buss, 1994; Ridley, 1993; Wright, 1994). Many such cues are important across a wide range of cultures and historical epochs. This universality is not surprising given that such cues show all the classic symptoms of having been sexually selected during human evolution: they distinguish humans from other apes, men from women, and adults from juveniles; they have high costs and complexity so function as reliable indicators of health and developmental homeostasis; and they have exaggerated aesthetic features that play upon the intrinsic perceptual biases of our nervous systems (see Miller, in press, a). These universal cues of attractiveness are the informational inputs to our psychological adaptations for mate choice.

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However, imagine a software engineer's reaction if one of her programmers, charged with designing an algorithm to solve a difficult artificial intelligence problem, returned with nothing more than a list of potentially relevant input variables. The hard part of cognitive engineering is not identifying the inputs, but knowing how to combine them in context-sensitive ways to yield adaptive behaviour. The same holds in evolutionary psychology. Describing the perceptual cues used by a psychological adaptation is just the first and often easiest step in characterizing the adaptation. I am worried that the evolutionary psychology of mate choice may get stuck at this step, producing an ever-expanding catalogue of cues demonstrated to have a statistically significant effect on attractiveness judgements in laboratory experiments, but never progressing to detailed, testable models of the cognitive adaptations that exploit these cues to make real mate choices.

One could argue that we should wait to find all the sexual cues before we try to combine them in a cognitive model of mate choice: building blocks first, architectural plans later. But this building-block approach will fail for many of the same reasons that evolutionary psychologists believe non-Darwinian psychology has failed. First, there is Brunswik's (1956) problem of "vicarious functioning": animals are notoriously opportunistic in their use of cues. Brunswik argued that "systematic designs", where a single cue's value is varied and its behavioural effects are measured, are a powerful way of finding out what cues *can* affect behaviour in the psychology laboratory, but are an extremely weak way of finding out what cues are most informative and most often used under natural conditions, or how such cues are integrated to guide adaptive behaviour. People almost never admit indifference in mate choice, so almost any cue distinguishing two potential mates in the laboratory can reliably yield an effect on choice behaviour, whether or not the cue has much ecological validity.

Second, the longer and more diverse our cue-catalogue becomes, the easier it will be for critics of evolutionary psychology to claim that general-purpose associative learning mechanisms could account for human mate choice, by correlating pre-processed cues with desired behavioural outcomes. If evolutionary psychology produces nothing more than cue-catalogues, evolved adaptations will continue to be marginalized to the periphery of cognition, in low-level perception and in the motivational systems that guide associative learning. Mate choice reaches deep into the heart of cognition – judgement, decision-making, and reasoning – so gives evolutionary psychology a fertile opportunity for showing why even cognition must be a set of domain-specific adaptations. But so, far, that opportunity has been wasted by obsessing about sexual cues.

Third, cataloguing attractiveness cues makes it easy to avoid modelling the intricacies of mate choice as an interactive social problem of search, assessment, courtship, competition, and mutual choice. The evolutionary psychology of mate choice is mostly, so far, the psychology of what happens in the first five minutes of a single virgin picking favourites from a line-up of passive strangers on a desert island. This Pleistocene tropical fantasy is pleasant for the sexually frustrated graduate student or divorced professor to contemplate precisely because it ignores the horrid game-theoretic interdependency of real-world mate choice.

Fourth, cataloguing cues makes it easy to avoid specifying the adaptive goals of mate choice in much detail. This is because attractiveness cues correlate with virtually every other aspect of an organism's phenotype (for technical reasons of developmental epistasis, physiological condition-dependence, and genetic linkage reinforced by

assortative mating), rendering any cue a pretty good indicator of almost any underlying trait that might be worth selecting.   Only when we investigate combinations of cues that indicate different trade-offs between desirable traits such as parenting ability, current fertility, social status, and immunocompetence, will we be pushed to develop more specific normative and descriptive models of mate choice. These four problems – animals' promiscuous flexibility of cue use, cue use being marginal to cognition, cue use being marginal to the hard game-theoretic aspects of mate choice, and cue use being uninformative about exact adaptive functions – make cue-cataloguing a rather weak method for characterizing our adaptations for mate choice. The next sections describe in more detail some pitfalls of cue-cataloguing compared to cognitive modelling; then the conclusion will outline a normative and descriptive alternative.

Critiques and extensions of current research

There's more to analyzing mate choice than predicting sex differences

Sex differences are easy to investigate because the contrast groups (males and females) come ready-made, predictions from sexual selection theory are often fairly simple, and results attract widespread media interest. But there's much more to mate choice than sex differences. Modern sexual selection theory provides a framework for analyzing one of the most important decision domains faced by all sexually reproducing animals. The theory would be as illuminating if we were hermaphrodites as it is given our two sexes. Although males and females reliably differ in some of the traits they seek and the cues they use, the basic game-theoretic problem of attracting the best mate who will accept you remains very similar for both sexes. I am worried that in the popular media and even in the minds of some evolutionary psychologists, the study of mate choice has become synonymous with the study of sex differences in the relative weights given to certain cues of attractiveness.

While sexual dimorphism usually indicates sexual selection, not all sexual selection produces sexual dimorphism (see Andersson, 1994). If evolutionary psychology assumes that all sexually monomorphic traits (e.g. human language, intelligence, and creativity) evolved without any help from sexual selection, we prematurely rule out one of the most powerful, inventive, and pervasive selection forces in nature (see Miller & Todd, 1995). Also, while mate choice mechanisms may show sexual dimorphism at the level of cue perception, they may not at higher cognitive and strategic levels. Males and females face largely similar problems assessing potentially deceptive cues, integrating cues, searching through a sequence of prospects, and finding the best mate who will accept them. These strategic problems will continue to be overlooked if we equate mate choice with sexual dimorphism in the traditional, rather crude way.

From physical to behavioural cues

An irony of evolutionary psychology is that many mate choice researchers have emphasized the sexual cues that are least psychological: physical attractiveness cues. Faces, breasts, buttocks, muscles, penises, symmetry, height, and other morphological traits have all been subject to intense analysis, while psychological traits such as intelligence, creativity, personality, sense of humour, social skills, kindness, and ideology have received mostly lip service (see Buss, 1994; Ridley, 1993). The reasons are

twofold: the ease of experimentally manipulating stimuli that represent morphological traits, and the importance of physical attractiveness as a convenient, low-cost "filtering cue" early in courtship. Evolutionary psychology's focus on the physical is a reasonable first step if our goal is demonstrating that there exist human universals of attractiveness, contra the claims of some cultural anthropologists and humanities scholars. But if our goal is to analyze our most important and distinctive mating strategies, selection criteria, and courtship traits, then we must analyze how people make mate choices based on psychological features. The payoffs could be significant. Whereas models of mate choice based on physical traits can only explain the evolutionary origins of our bodies, models that include psychological traits may explain the origins of our most distinctive mental capacities (see Miller, in press, a, b). The co-evolution between mate choice mechanisms and the courtship behaviours that they select puts the study of mate choice at the very heart of evolutionary psychology, because we are studying the core psychological adaptations that catalyze the emergence of other psychological adaptations via sexual selection.

Beyond weighted linear models of cue integration

Many mate choice researchers seem to assume that organisms register a set of cues associated with each potential mate, attach some standard weight to each cue, and then add the weights together to arrive at an overall rating of attractiveness. Such "weighted-linear" models of cue integration, derived from Brunswik (1955) and revived in some recent neural network models, seem like the simplest way to start an analysis, and make it easy to interpret subjects' numerical responses on questionnaires about the relative importance of different attractiveness cues (see Buss, 1994). But the apparent cognitive simplicity of weighted linear models may be deceptive. Gigerenzer and Goldstein (in press) have analyzed several alternatives to weighted-linear integration that make better decisions, using less information, operating faster, and better fitting some subjects' think-aloud protocols. Their "Take the Best" heuristic, for example, would be a fast, frugal way to decide which of two prospects has higher mate value. This heuristic checks each prospect on one cue at a time, with the cues ranked in order of their ecological validity (correlation between cue value and mate value). The first cue that distinguishes the prospects would be used to make one's mate choice. If subjects using this Take the Best heuristic were asked for their "cue weights", they would find it a meaningless question, and might report some other quantity (such as ecological validity, discrimination rate, recency of cue use, or cue ranking) on a questionnaire. Use of such heuristics may explain the puzzling finding that in many domains, subjects claim to use more cues than prove significant in post-hoc multiple regression analyses of their decisions. This is exactly what we would expect from Take the Best: the vast majority of decisions many be determined by the few top-ranked cues, but where those cues don't distinguish between prospects, subjects must use lower-ranked cues to decide.

Another reason for questioning weighted-linear models is that the assessment costs of different features used in mate choice are so wildly disparate. Morphological features such as face and body shape can be assessed in a momentary glance, whereas resourcefulness in emergencies, parenting skills, and capacity for avoiding sexual boredom can be assessed only after months of interaction. A depth-first search for all cue values in every prospect you encounter would be an idiotic way to search for a mate. Instead, people use the easily-assessed physical cues as filtering devices to decide who to talk to; they use conversations to decide who to have sex with; and they

use sexual relations and capacity for intimacy to decide who to have children with. What is the relative "weight" then, of facial beauty, versus wit in conversation, versus foreplay skills? The question is meaningless, if people are integrating these cues sequentially, nonlinearly, and intelligently, rather than according to a weighted-linear method that ignores cue assessment costs.

Moreover, this sequential cue-integration heuristic would produce behaviour that could be misinterpreted all too easily as reflecting distinctive cue-weightings for short versus long-term mating (cf. Buss, 1994). People would start relationships with prospects they find physically attractive, but only continue relationships with those they find psychologically compatible. Post-hoc, it would look as if they attached a higher "weight" to physical attractiveness for short-term matings, and a higher "weight" to psychological features for long-term matings. But the apparent correlation between cue weight and relationship duration could be an artefact of some cues taking longer to assess than others, with relationships ending only when someone becomes unhappy with the most recent information they learned about their partner. To investigate sequential cue integration heuristics, we need fewer questionnaire studies and single-cue experiments, and more detailed interviews (we can call them "protocol analyses" if that helps get them published) in which we actually listen to what people say about how they confront the selective, biased, deceptive trickles of information that their would-be partners leak to them.

Mutual choice, two-sided matching, and assortative mating

Although sexual harassment by males is endemic in nature, most matings seem to require mutual consent. This mutual choice constraint complicates matters, because fulfilling two sets of preferences in mating is multiplicatively harder than fulfilling one (for discussion of this problem in sexual selection simulations, see Miller & Todd, 1993). Nevertheless, evolutionary psychologists are fortunate that economists have already done some hard thinking about how mutual choice works in mating markets. This is in the literature of several hundred papers on "two-sided matching" (see Roth & Sotomayor, 1990) which, as far as I know, has never previously been cited or discussed in evolutionary psychology. A prototypical two-sided matching analysis assumes a population of men and women, where each individual has a complete and transitive set of preferences across members of the opposite sex (based on some unspecified assessment process). A "stable matching" is defined as a pairwise assortment of men and women such that no individual would prefer to be paired to someone else, who would also prefer to be paired to them. In game theory terms, a stable matching is a Nash equilibrium in the mating market. One heartening result from this literature is that at least one stable matching exists for every mating market with two sexes (Gale & Shapley, 1962). Further, no stable matching exists for mating markets with one or three sexes (Roth & Sotomayor, 1990).

Moreover, a simple algorithm called the "deferred acceptance procedure" is guaranteed to find a stable matching pretty quickly (Roth & Sotomayor, 1990). In this procedure, one sex proposes, and the other sex accepts or rejects. For example, each man first proposes to his most-favoured women. Each woman rejects any suitors who are unacceptable, and each woman who receives more than one proposal rejects all but her most preferred. Any man not yet rejected is kept "engaged". The procedure then iterates, with any man rejected on a previous step proposing to his next most preferred

woman. Engaged women can switch if a more-preferred man proposes to her. The algorithm stops after any step in which no man is rejected. Women who did not receive any acceptable proposals, and men rejected by all women acceptable to them, stay single. If preferences are strict, then the set of people who remain single is the same for all stable matchings. Surprisingly, if preferences are strict and if there are multiple stable matchings, the deferred acceptance procedure with men proposing will always find the matching that is most preferred by men *and least preferred by women*, while the reverse is true if women propose.

This leads to a strange corollary: although men in mating markets are supposedly competing with each other, once they realize the game-theoretic implications of mutual choice, they can recognize their common interest in devising a matching procedure that attains their most preferred stable matching. This "male-optimal" matching makes men as happy as they could be, given the preferences women actually have, and makes women as miserable as they could be given a stable matching. Whichever sex proposes will reach its most preferred Nash equilibrium in the mating game. Moreover, I suspect that given monogamy, the preferences of the proposing sex could be shown to constitute stronger sexual-selection pressures than the preferences of the other sex. These results also suggest that, if some assortative mating procedures are more efficient than others in attaining stable matchings, then group selection could favour such mating procedures, without having to overcome any individual-level selection (Miller, 1994a). These matching results should be more broadly appreciated by evolutionary psychologists, because they identify confluences and conflicts of interest that would otherwise be overlooked.

Co-evolution of mate choice heuristics and the cues they select

Although mate choice heuristics are selected to exploit the sexual cues available in the environment, those cues themselves are heritable traits that are selected by the choice heuristics. This leads to a particularly fast, capricious, and dynamic form of co-evolution (Miller & Todd, 1995; Todd & Miller, 1993, in press). The diversity of sexually-selected traits and mate preferences across even closely-related species illustrates the speed and power of this co-evolution. Indeed, examination of secondary sexual traits, genitalia, and courtship behaviour is often the only way of distinguishing between sibling species (no surprise, really, since mate preferences are what define species in the first place.)

The co-evolution between sexual traits and mate preferences seems to give evolutionary psychology no logical place to start in analyzing mate choice.   But there are patterns to the co-evolution that run quite deep. For example, Zahavi's original "handicap theory" was essentially a theory about how the reliability of sexual cues as viability-indicators co-evolves with the mate preferences that select them (see Andersson, 1994). His analysis, informed by game theory, suggested that sexual cues will typically evolve to show an intermediate degree of ecological validity (i.e. correlation with the trait they advertise), because only such intermediate degrees of reliability are evolutionarily stable. Also, analysis of some intrinsic perceptual biases that shape the evolution of sexual cues has led Ryan and Keddy-Hector (1992) to discover some aesthetic principles for courtship displays. Likewise, a better understanding of assortative mating should lead to predictions concerning typical levels of genetic linkage and phenotypic intercorrelation between sexual cues, since assortative mating tends to

concentrate heritable high-quality cues in certain offspring. Rather than viewing either sexual cues or mate preferences as givens in our analysis of mate choice, we should view them as co-evolving traits that sometimes reach predictable, evolutionarily stable equilibria, and that other times fly off together in runaway processes that still obey certain evolutionary principles of signalling, advertisement, and assortative mating.

Mate choice and genetic variance

Mate choice research reveals a curious tension within evolutionary psychology concerning within-species genetic variance. On one hand, evolutionary psychologists downplay genetic differences within our species as superficial variants on a species-typical body plan and cognitive architecture. This is because complex adaptations are likely to pervade populations in monomorphic form, lest sexual recombination break apart the co-adapted genes that grow the adaptations (Tooby & Cosmides, 1990). Such arguments have given evolutionary psychology a good pretext for distancing itself from the politically contentious research fields that study genetic variance in modern humans, such as behavioural genetics, psychometrics, and Darwinian anthropology. On the other hand, mate choice is only worth doing if genetic variance is of sufficient *functional* importance to make the benefits of choosing well exceed the substantial search and assessment costs of mate choice (Pomiankowski, 1987). The major reason for mate choice in most sexually-reproducing species is that the genetic quality of your mate determines half the genetic quality of your offspring. Phenotypes are fugitive, but genes are forever. From this perspective, in-species genetic variance is literally the selective environment to which mate choice has adapted. So, how could there be an evolutionary psychology of mate choice, if mate choice requires a level of in-species genetic variance that evolutionary psychology denies could exist?

Three recent developments in sexual selection theory have illuminated this genetic variance issue. First, the gradual recognition that most mutations are harmful has led theorists to propose that this pervasive "biased mutation" is a major reason why mate choice remains worth doing even when adaptations have been under strong stabilizing selection (Pomiankowski, Iwasa, & Nee, 1993). Adaptations are continually eroded by this biased mutation, and mate choice is one of the best ways to counteract such entropy.

Second, whenever sexual selection operates like a "winner-take-all" contest, as in polygyny, evolution favours risk-seeking behaviour – not only risky competitive behaviour as in violent conflict between males (Daly & Wilson, 1988), but also genetic modifiers that maximize genetic and phenotypic variance (Pomiankowski & Moller, 1995). Such modifiers explain why sexually-selected traits typically show much higher coefficients of additive genetic variance than survival traits (Pomiankowski, 1993). I have argued elsewhere that some of our most distinctive psychological adaptations, particularly our capacities for language, art, music, ideology, and creativity, evolved largely under sexual selection (Miller, 1993, in press, a, b). If so, then such capacities would be expected to show quite high genetic variance, especially in males. This may explain why some of our most complex psychological adaptations, such as intelligence measured by IQ tests, are also the most genetically variable and heritable (Miller, 1994b).

Third, sexual selection theorists are recognizing that, while random mating would break apart co-adapted gene complexes to yield monomorphic adaptations within a population, strong assortative mating can maintain relatively complex specializations in polymorphic equilibria. Indeed, speciation itself can be viewed simply as the most extreme form of assortative mating (Miller & Todd, 1993). If species (i.e. self-defining reproductive communities with different mate choice and courtship adaptations) can maintain separate adaptations, then perhaps less extreme forms of assortative mating can maintain less obvious, but still significant, polymorphisms within a species. Also, assortative mating can maintain genetic variance at much higher levels than random mating, so perpetuates its own incentives for mate choice.

Conclusion: Towards a new normative and descriptive framework

Information flows successively from environment through perception, then cognition, decision-making, and action. But selection pressures flow the opposite way, shaping behavioural output most strongly, and trickling back to shape cognition only insofar as it guides adaptive decision-making, and perception only insofar as it guides adaptive cognition (see Miller & Todd, 1990). The fact that information and selection flow in opposite directions through evolving minds puts the study of perception in a curious quandary. From an information-processing viewpoint, low-level perceptual mechanisms, such as those for registering cues of sexual attractiveness, look like the building blocks of cognition. The ease with which experimental psychology can investigate such mechanisms reinforces this impression. But from a selectionist viewpoint, low-level perceptual mechanisms are not the building blocks of psychological adaptation at all, but the last and most indirect products of selection pressures that have already determined an adaptive task, a set of possible behaviours, a decision-making problem, and a requisite set of cognitions.

In my view, evolutionary psychology has become prematurely focused on analyzing sexual cues as perceptual inputs without a sufficient normative and descriptive framework for understanding how these inputs should and could contribute to adaptive mate choices in realistic social contexts. We must remember that mate choice is fundamentally a problem of game-theoretic decision-making given skeptical prospects and hostile competitors, not just a problem of optimal cue-integration and rational social judgement. Animals encounter sexual prospects drawn from a fluid population with unknown statistical distributions of attractiveness, fertility, and viability. Prospects appear in unpredictable and often irrevocable order. Some features of prospects can be assessed instantly, cheaply, and reliably; others can be discovered only after long, expensive, and interactive courtship. Prospects also have unknown deviations from an unknown population-typical set of mate preferences. Typically, one's own attractiveness and mate value can be inferred only indirectly. The strategies and attractions of one's competitors are even less accessible. Lost in this sea of uncertainty, deception, competition, and coyness, you must try to combine your genes with the best genes that you can attract, and combine your parental effort with the most fertile and viable mate you can find.

Task complexities like this seem overwhelming, but evolution has two secret weapons: the adaptations it constructs can ruthlessly exploit any available structure in the environment, and they can shamelessly sacrifice generality, rationality, elegance, simplicity, completeness, and perfection in favour of adaptive efficiency. We must

expect mate choice adaptations that take short-cuts, that use cheap and easily perceived cues first, that put cues together in the order they're available, and that rely on social stereotypes whenever they're more valid than not. Our descriptive models of mate choice should draw not just on some recycled perceptual psychology, but on the full range of information-processing heuristics wherever we can find them: judgement and decision research, social cognition, artificial intelligence, economics, whatever. We must be as inventive in developing models as evolution must have been in designing mechanisms.

We should be equally pragmatic in developing better normative models for understanding what adaptive efficiency means in mate choice, drawing not just from sexual selection theory, but also game theory, decision theory, and statistics. Principally, we must develop better ways of describing the task environment in which mate choice operates: what is the sexual game being played, what are the payoffs, what kinds of strategic decisions must be made, and what information is available for making them? Mate choice mechanisms are adaptations, and adaptations are always adaptations to something: a well-specified task and a well-specified environment. If we try to model mate choice too directly, using little more than some basic sexual selection theory combined with the narrow set of empirical methods favoured by psychology journal editors, we won't be capitalizing on the full power of our Darwinian framework. This framework requires equal attention to analyzing environment structure, analyzing adaptive tasks, and analyzing adaptations themselves. Analyzing environment structure doesn't just mean outlining an impressionistic reconstruction of Pleistocene social dynamics. It means detailed, quantitative analysis of human genotypes, bodies, and behaviours as informational structures on which mate choice mechanisms operate. Analyzing the adaptive task in mate choice doesn't just mean sketching how a despot might maximize offspring number by picking nubile slave girls. It means detailed, explicit analysis of mating games as played by ordinary humans, both ancestral and modern, with all the complexities of mutual choice, assortative mating, affordability, commitment, and deception. If we face these challenges, the technical achievements of mate choice research might finally match its popularity.

Acknowledgements

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