Mate choice turns cognitive

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Evolutionary psychology has revolutionized research on human mate choice and sexual attraction in recent years, combining a rigorous Darwinian framework based on sexual selection theory with a loosely cognitivist orientation to task analysis and mechanism modelling. This hard Darwinian, soft computational approach has been most successful at revealing the adaptive logic behind physical beauty, demonstrating that many sexual cues computed from face and body shape are not arbitrary, but function as reliable indicators of phenotypic and genetic quality. The same approach could be extended from physical to psychological cues if evolutionary psychology built stronger ties with personality psychology, psychometrics and behavioral genetics. A major challenge for mate choice research is to develop more explicit computational models at three levels, specifying: (1) the perceptual adaptations that register sexual cues given sensory input, (2) the judgment adaptations that integrate multiple cues into assessments of overall attractiveness, and (3) the search strategies that people follow in trying to form mutually attracted pairs. We describe both recent efforts and possible extensions in these directions. The resulting confluence between evolutionary principles, cognitive models and game-theoretic insights can put mate choice research at the vanguard of an emerging 'evolutionary cognitive science' more concerned with domain-specific mental adaptations than with domain-general intelligence.

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Why do we fall in love? How do we decide whom to marry? How do we perceive someone as beautiful or exciting? In the last few years, research into these questions has been revolutionized by a surprising marriage of evolutionary and cognitive perspectives. Mate choice research now uses evolutionary theory as the explicit functional framework for understanding human sexual psychology[1–7]. At the same time, it is implicitly guided by the 'computational sufficiency' principle of cognitive science, that psychological models should aim to be computationally specific enough to reproduce the behavior being modelled[8,9]. These Darwinian and cognitive revolutions have produced a renaissance in mate choice research, a topic that now dominates both human evolutionary psychology and animal behavior studies in other species[10].

Until a decade ago, research on human mate choice was limited mostly to social psychology studies on 'interpersonal attraction'[11], sex research interviews and cultural anthropology. Social cognition research in particular tended to view sexual attraction as an outcome of arbitrary, poorly defined factors such as proximity, similarity, salience and stereotypes that distort domain-general social attribution mechanisms[12].

Recently, mate choice has become dominated by evolutionary psychology, which takes a functional, cross-cultural, domain-specific approach to understanding the adaptive goals of mate choice. Evolutionary psychologists search for 'mental adaptations', complex mechanisms that have been shaped over millennia of natural selection and sexual selection to solve the survival and reproduction problems that faced our hunter-gatherer hominid ancestors in Pleistocene Africa[13,14]. Through the influence of cognitive science, these adaptations are typically viewed as intricate software designed by evolution, specialized to process naturally occurring information about biologically important situations in ways that guide adaptive behavior[9]. Thus, evolutionary psychologists tend to analyze mate choice in terms of the structure of the environment outside the decision-maker (including observable cues and hidden traits of potential mates, and features of the local mating system), and the types of perception, computation, inference, search, utility functions, decision policies, strategies and signals that the decision-maker uses[3,4,6,9,15].

The mate choice task

Mate choice is one of the most important decision-making tasks that face sexually reproducing animals. By definition, sexual reproduction entails combining one's own genes with another individual's genes to produce offspring. Through mate choice, animals can influence the quality of

Box 1. The heritability of fitness: does mate choice favor good genes?

A central question in sexual selection theory has been to what extent biological fitness (survival and reproduction ability) remains genetically heritable in most species[a–k]. If fitness is highly heritable, individual variation in survival and reproduction prospects are heavily influenced by genetic differences between individuals, so there would be strong incentives for mate choice to favor sexual cues that advertise 'good genes'. But if fitness is not heritable, it would be determined by a sort of environmental lottery that just influences an individual's phenotype. Mate choice might just favor cues advertising components of that phenotypic quality that are important for reproduction and parenting. Unfortunately, sexual selection theorists often referred to phenotypic quality as a 'direct' benefit of mate choice, and to genotypic quality as an 'indirect' benefit, biasing investigation in favor of the former[b].

Until recently, many biologists and evolutionary psychologists believed that fitness was not heritable in most species most of the time, because natural selection should tend to eliminate any genetic variation in traits that influence survival or reproduction ability[j,l]. However, molecular genetic studies have shown that most species in the wild retain large amounts of genetic variation in fitness-related traits. Also, theorists realized that mutation pressure, spatial and temporal variations in selection and migration tend to maintain heritable fitness[b,d,f]. Finally, every human mental trait ever studied by behavioral geneticists shows significant heritability, even traits that must be strongly fitness related, such as general intelligence and sexual orientation[i].

Many biologists now agree that fitness often remains substantially heritable, in most species most of the time[f,h]. Thus, our mate choice strategies probably evolved to focus on sexual cues that advertise heritable fitness. From a selfish gene's point of view, mate choice is supremely important because it determines whose genes it will have to collaborate with in all succeeding generations.

If a mate's quality is heritable, that genotypic quality can be inferred not just from that prospect's phenotype, but from the phenotypes of all their close genetic relatives, of both sexes and all ages. It would then make sense to pay attention to a prospect's family members, using some kind of intuitive genetics to integrate genotypic quality information across kin. This would be especially valuable in avoiding recessive mutations that may lurk hidden in a sexual prospect (for instance, Uncle Fester's strange degenerative condition). The cognitive mechanisms for doing this kin-based mate choice remain to be established and investigated.

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the genes passed on to their offspring from their sexual partner, and the quality of the parental care those offspring will receive (Box 1). By forming a joint genetic venture with a high-quality mate, one's genes are more likely to end up in healthy, fertile offspring and grand-offspring[16–19]. Individuals carrying genes for bad mate choice mechanisms pick bad mates, so that these genes usually end up in fewer or lower-quality offspring, who take them with them to evolutionary oblivion.

This evolutionary view leads to a rough 'computational theory' of mate choice. The adaptive goal of mate choice is to maximize the reproductive quality (including heritable fitness, health, fertility, status, intelligence, parenting ability, etc.) of one's sexual partners, subject to various constraints such as courtship costs, limited search time and mutual choice (in almost all mammals, both male and female must choose to mate). The inputs to mate choice adaptations are certain observable features of potential sexual partners called 'sexual cues', which indicate valuable information about each partner's quality. The initial outputs of mate choice are decisions to court an individual or not, and to accept or reject courtship offers (later, mate choice also

influences decisions to continue or terminate pregnancies and relationships). Mate choice can then be broken down into three inter-related subtasks: (1) perceiving basic sexual cues that provide reliable, relevant information about potential mates; (2) integrating those cues to estimate underlying trait values such as health, intelligence, fertility and social status, and further using those trait values to judge overall sexual attractiveness; and (3) searching through a series of prospects and deciding which ones to court or accept, based on their attractiveness. We review these in turn.

Identifying sexual cues

So far, the vast majority of mate choice research has focused on the first subtask, identifying sexual cues and investigating what information they reveal about sexual prospects. This research has shown how an evolutionary framework can demystify sexual attraction by identifying specific cues that influence choice of sexual partners universally across different individuals and cultures[20,21]. Well-documented sexual cues now include such diverse items as height, intelligence, facial averageness, kindness, scent, male jaw size, female

Box 2. Indicators and the handicap principle

Biologists such as Alfred Russell Wallace, George Williams and William Hamilton have long argued that mate choice should favor cues that indicate a prospect's quality including health, fertility, parasite resistance, parenting abilities and heritable fitness[a,b]. However, this idea that mate choice favors 'indicators' rather than arbitrary, aesthetic traits was not widely considered until 1975, when Amotz Zahavi[c] initiated intense controversy with his 'handicap principle'. Zahavi proposed that the only way to demonstrate one's quality reliably during courtship is to display a high-cost signal such as a heavy peacock's tail, an exhausting bird-song concert or an expensive sports car. Only these costly 'handicap' signals are evolutionarily stable indicators of their producer's quality, because cheap signals are too easy for low-quality imitators to fake[c].

After much opposition to this counterintuitive idea, evolutionary theory and animal data are increasingly supporting the handicap principle[a]. Sexual cues in many species, both bodily ornaments and courtship behaviors, have been shown to function as reliable quality indicators: they have high growth and maintenance costs, their size and condition correlates with their owner's overall fitness and genetic quality, and they influence mating decisions[a].

Many human facial and bodily features probably function as indicators of health, strength, fertility, youth, disease resistance, parasite resistance, hormone levels and developmental stability, many of which are genetically heritable[d–y]. Many unique human mental adaptations such as language, art, music and humor might also be used in courtship as reliable indicators of important, heritable psychological traits such as intelligence, creativity and learning ability[e,f]. Humans might also use costly displays of culture and technology as handicaps in courtship, with learned behaviors following evolutionary principles of reliable signalling. If so, Thorsten Veblen's venerable theory of 'conspicuous consumption', where expensive, useless products and services function as indicators of wealth and status, can be viewed as a special case of the handicap principle.

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waist-to-hip ratio and political status[2–7,19–24]. Research on cues of facial attractiveness[25–30], body attractiveness[31–34] and social status[20,21,35,36] has been especially fruitful.

From the viewpoint of higher-level cognition, these cues are just potentially relevant input variables for computing overall attractiveness and deciding whom to court[6]. But these cues should also be seen as the outputs of complex, finely tuned perceptual adaptations – as computational achievements that do not come for free from raw sensory input[9]. In this view, identifying sexual cues is synonymous with identifying the basic perceptual adaptations for computing sexual attractiveness.

Cues are usually assumed to be cues of something. Mate choice researchers are arguing vehemently about what information, if any, the various sexual cues reveal[10,37]. There are two basic questions: (1) Are the cues reliable indicators of personal traits relevant to mating, or purely arbitrary, aesthetic displays? (Box 2) (2) Are individual differences in the quality of the cues or the underlying traits genetically heritable? (Box 1) The combined answers to these two independent questions yield four possible hypotheses about the information content of any given sexual cue. Non-evolutionary research on interpersonal attraction[11] assumed that most sexual cues were arbitrary and non-heritable. Sir

Ronald Fisher's 1930 theory of 'runaway sexual selection'[10] suggested that many cues are arbitrary but heritable. Most researchers accept that runaway often happens, but think it is not sufficient to explain why sexually selected traits persist in such extreme and costly forms (cf. Kalick and colleagues[38]). In general, evolutionary psychologists agree that sexual cues indicate some aspect of an individual's reproductive value or fitness[24,39], but disagree about the heritability issue. Until quite recently, most researchers viewed sexual cues as indicators of phenotypic quality but not of heritable genotypic quality. The studied cues of female attractiveness indicated mostly health and fertility, and cues of male attractiveness indicated mostly social status and resource-acquisition ability[3], but researchers often assumed that these had low heritability.

Now, however, a growing number of researchers believe that many fitness-related traits remain at least moderately heritable, and that some sexual cues indicate these heritable trait values[2,5–7,10,16–19,23,28,33,34,39–41]. Research on facial and bodily symmetry has been especially convincing in this regard, as new meta-analyses show that bilateral symmetry not only influences sexual attractiveness[42], but is also heritable[43], and is a good indicator of health, disease resistance and overall fitness[44,45]. Symmetry reveals not just a healthy body, but good genes[46].

This increasingly popular view, that many sexual cues are reliable indicators of heritable traits, represents a true cognitive revolution regarding sexual attraction. It suggests that sexual cues are being used to estimate each prospect's heritable quality, perhaps using some rather sophisticated intuitive understanding of phenotypic correlations between cues and traits, and some intuitive genetics concerning the heritability of those traits. Mate choice can then be seen as a kind of cue-based inference, and human performance in mate choice tasks can be compared with normative models of decision-making. By contrast, older views that sexual cues are arbitrary and non-heritable offered no standards for assessing how good people are at mate choice.

Thus, the best mate choice research tends to resemble Egon Brunswik's[47] venerable strategy of seeing how closely people's subjective cue use reflects the objective ecological validity of the cues. Two main classes of physical sexual cues have been explored recently as indicators of fitness: hormonal markers and cues of symmetry, both of which signal health[23,24,28]. For example, a low female ratio of waist circumference to hip circumference (waist-to-hip ratio, or WHR) of about 0.7 has been shown to be most attractive to men across all cultures examined[31,32]. A low WHR is also a good hormonal marker, a reliable indicator of female health, youth and immediate fertility. Women who are sexually immature, post-menopausal or in the last two trimesters of pregnancy, or women who have an excess of male sexual hormones or who suffer from various diseases, have higher WHRs[31]. Pleistocene men who preferred a higher to a lower WHR left fewer offspring to inherit their maladaptive preference.

Beyond the WHR, several facial features reveal health through their hormone-influenced growth. Male sex hormones produce larger jaws, noses and chins. Furthermore, because these hormones are immunosuppressors, a larger lower face in males functions as a health indicator: only disease-resistant males can afford the immunosuppressing hormones required to grow big jaws[24,28,48]. Conversely, female sex hormones produce smaller female lower faces, which are considered more attractive[4].
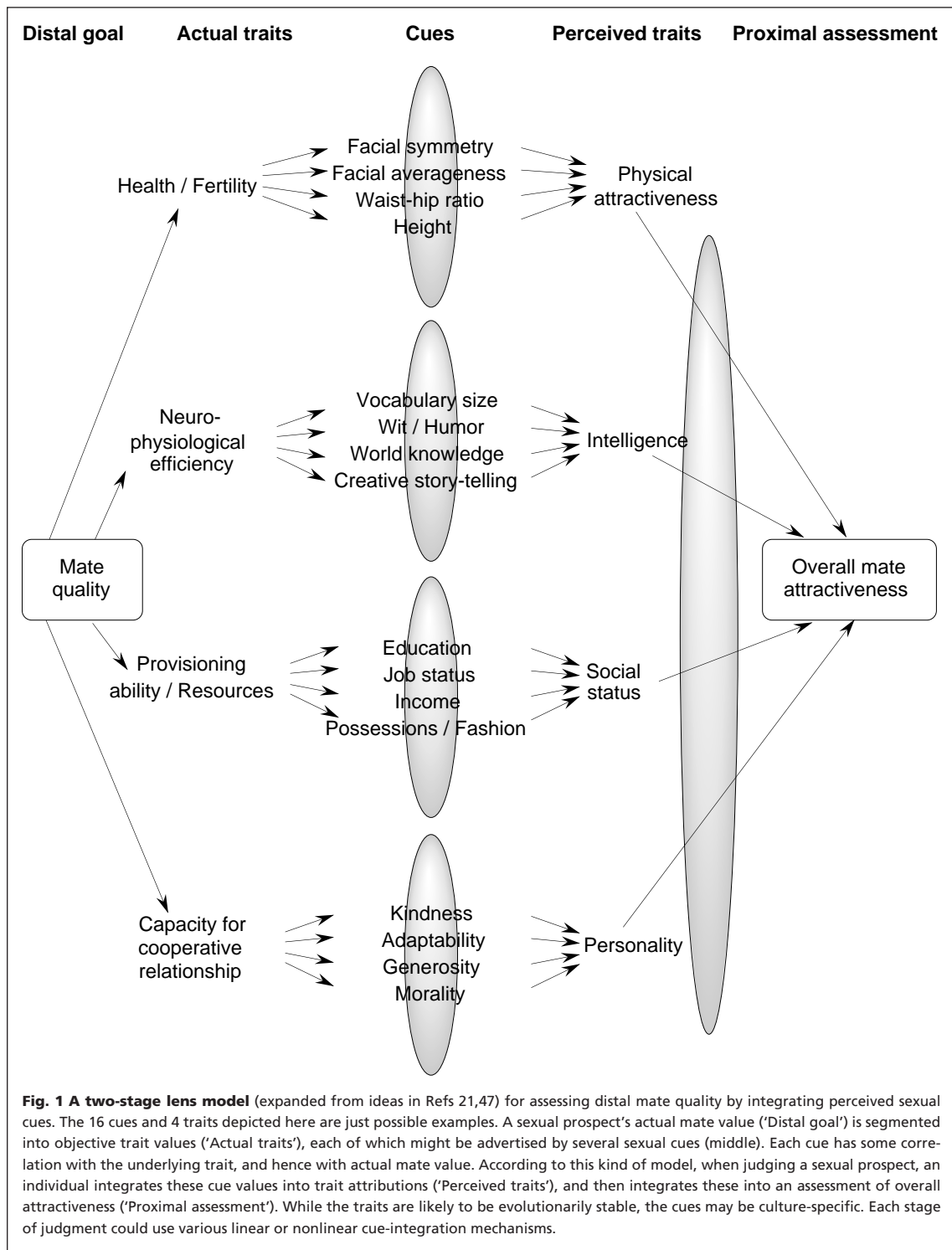
While hormonal markers reveal healthy sex-specific development, other cues such as facial symmetry and averageness seem to reveal the overall stability of development, including heritable resistance against environmental perturbations (pathogens, parasites, poor food, toxins or injuries), and genetic perturbations (inbreeding, homozygosity, deleterious mutations or chromosomal abnormalities)[9,24,28–30,42,46,48] (see also Ref. 38, which suggests the opposite view). Facial symmetry in each sex correlates positively with the expression of the sex-specific hormonal markers: symmetry correlates positively with size of lower face in men but negatively with size of lower face in women[4,19], as one would expect if both symmetry and hormonal-marker cues indicate phenotypic quality.

From physical to psychological attractiveness

So far, mate choice research has focused much more on physical cues of attractiveness than on psychological traits such as intelligence, creativity and kindness. Cross-cultural questionnaires show that psychological traits are important in human mating, with both sexes valuing intelligence and kindness very highly, females valuing wealth and social status more than males do, and males valuing youth and physical attractiveness more than females do[3,20]. However, research on psychological traits typically presents participants with verbal trait descriptions, so little is known about how psychological traits are inferred from observable behavior.

There are methodological reasons for focusing on physical cues, especially visual cues: they are relatively easy to measure, and they can be photographed and manipulated to create precisely controlled experimental stimuli[6,11,25,29–34]. However, there is also some resistance to studying psychological cues in the same way as physical cues, that is, as indicators of phenotypic and genotypic quality. For example, the idea that intelligence might be valued in mate choice as an indicator of neurophysiological efficiency, developmental stability and heritable fitness seems reasonable, given the current state of intelligence research[49,50] and behavioral genetics[51], but has been avoided by many evolutionary psychologists[3,9,14,21,52].

The standard evolutionary psychology view is that human mental adaptations have been subject to such strong selection that they have very little genetic variation left[52]. However, it is hard to reconcile that view with the evidence from behavioral genetics that not a single human psychological trait ever investigated has zero heritability, and most have heritabilities between 0.3 and 0.8 (Ref. 51). It is also hard to reconcile with the evolution of strong mate preferences for psychological traits, which presuppose enough individual variation to have made mate choice worth exercising over recent evolutionary time[1–7,10,15–19,40–46]. Greater cooperation between workers in personality psychology, psychometrics, behavioral genetics and evolutionary psychology will be required to understand mate choice for human psychological traits.

Distal goal	Actual traits	Cues	Perceived traits	Proximal assessment

Health / Fertility → Facial symmetry / Facial averageness / Waist-hip ratio / Height → Physical attractiveness

Neuro-physiological efficiency → Vocabulary size / Wit / Humor / World knowledge / Creative story-telling → Intelligence

Mate quality

Provisioning ability / Resources → Education / Job status / Income / Possessions / Fashion → Social status

Capacity for cooperative relationship → Kindness / Adaptability / Generosity / Morality → Personality

Overall mate attractiveness

Fig. 1 A two-stage lens model (expanded from ideas in Refs 21,47) for assessing distal mate quality by integrating perceived sexual cues. The 16 cues and 4 traits depicted here are just possible examples. A sexual prospect's actual mate value ('Distal goal') is segmented into objective trait values ('Actual traits'), each of which might be advertised by several sexual cues (middle). Each cue has some correlation with the underlying trait, and hence with actual mate value. According to this kind of model, when judging a sexual prospect, an individual integrates these cue values into trait attributions ('Perceived traits'), and then integrates these into an assessment of overall attractiveness ('Proximal assessment'). While the traits are likely to be evolutionarily stable, the cues may be culture-specific. Each stage of judgment could use various linear or nonlinear cue-integration mechanisms.

Cue integration mechanisms

Sexual cues must be integrated somehow to yield overall attractiveness judgments that can guide mate choice. In mate choice, this integration problem is made clear by use of a 'lens model'[21], where a distal variable such as female fertility or male status is indicated by a number of proximal cues, which are then recombined by a receiver into an estimate of the distal variable (see Fig. 1). In Brunswik's[47] original lens model, cues are weighted subjectively in accordance with their objective ecological validity (how strongly they are correlated with the distal variable) and then combined.

Pros and cons of linear cue integration for mate choice

Weighted linear models have been used traditionally in such settings to compute single judgments from multiple cues, by summing up each cue multiplied by a factor representing its importance. As reviewed above, researchers are measuring correlations between sexual cues such as WHR[31] and facial attractiveness[38] and underlying characteristics like health. Linear models of physical attractiveness using these correlations as cue weights (ecological validities) might soon become testable against human judgment.

Linear models might seem crude, but they out-perform expert human judgment in many other personality assessment
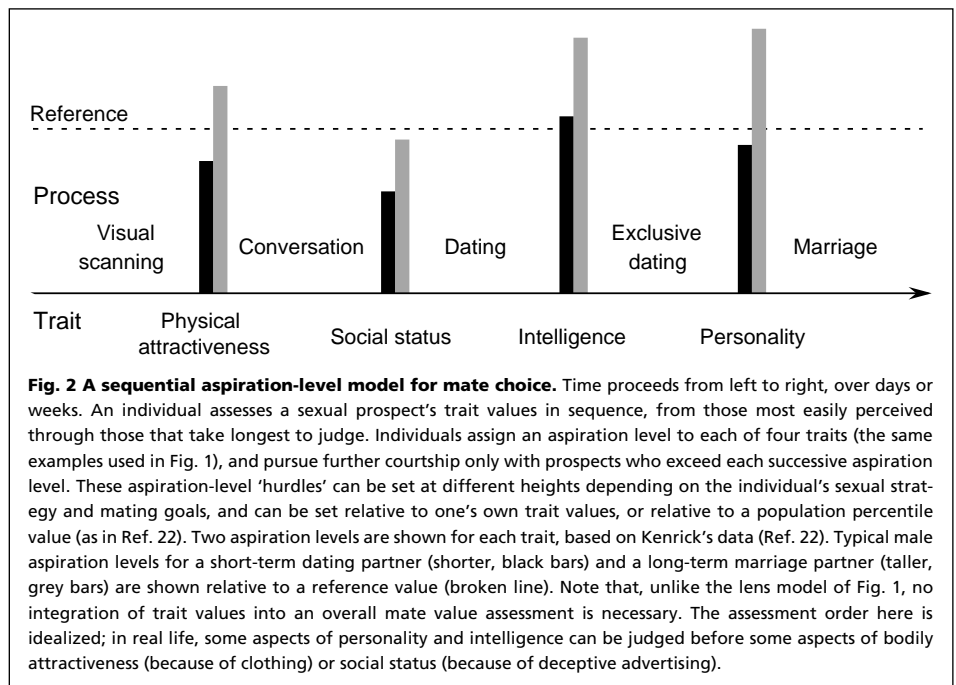
tasks[53]. The performance of linear models is also very robust to (sign-preserving) changes in cue weights[54]. Although linear models are a parsimonious first step in modelling mate choice, they have two problems.

First, some sexual cues interact non-linearly to influence attractiveness. For example, Jensen-Campbell and colleagues[35] used path analysis to show that dominance and agreeableness interact non-linearly to affect women's attractiveness ratings of men: disagreeable, selfish men are seen as undesirable no matter how dominant they are, but for agreeable, prosocial men, dominance increases their attractiveness significantly. Their analysis also suggested that the effect of agreeableness was mediated consciously, but that dominance affected attractiveness unconsciously, suggesting that different cues interact not only non-linearly, but across quite different levels of processing[36]. Perceiving some sexual cues must require non-linear computation (for example, perceiving WHR presumably involves computing a ratio, not a weighted sum). It should be no surprise that integrating cue values into trait assessments might also require non-linear computation.

Second, linear models usually assume all necessary cues will be available simultaneously. However, different sexual cues require different lengths of time to assess: physical beauty can be perceived immediately, assessing intelligence requires at least a few minutes of conversation but recognizing a tendency to philander might take years[6]. Linear models that waited until all cues became known would take too long, but those that integrated only the most accessible cues would make too many mistakes. Also, linear models assume that any cue can be traded off against any other, such that beauty could compensate for infertility, or creativity could compensate for physical cruelty. Such compensatory integration of cues might prove extremely maladaptive in mate choice, because successful reproduction is a complex causal chain, only as strong as the weakest link.

Sequential aspiration levels: an alternative to linear cue integration?

These observations, that sexual cues have different assessment times and minimal thresholds for successful reproduction, suggest an alternative model of integration. It might be adaptive to filter prospects through a series of aspiration levels, using physical appearance to decide whom to talk to, conversation to decide whom to form a short-term relationship with, and psychological compatibility to decide whom to have children with. In this sequential aspiration model, mate choice sets up a series of hurdles, and the courting individual tries to jump over them (see Fig. 2). Sexual cues are used as soon as they are available, rather than being filed away for linear integration once everything is known about a prospect. While Herbert Simon's[8] work on how to mate in chess is better known in cognitive science, his thoughts

Fig. 2 A sequential aspiration-level model for mate choice. Time proceeds from left to right, over days or weeks. An individual assesses a sexual prospect's trait values in sequence, from those most easily perceived through those that take longest to judge. Individuals assign an aspiration level to each of four traits (the same examples used in Fig. 1), and pursue further courtship only with prospects who exceed each successive aspiration level. These aspiration-level 'hurdles' can be set at different heights depending on the individual's sexual strategy and mating goals, and can be set relative to one's own trait values, or relative to a population percentile value (as in Ref. 22). Two aspiration levels are shown for each trait, based on Kenrick's data (Ref. 22). Typical male aspiration levels for a short-term dating partner (shorter, black bars) and a long-term marriage partner (taller, grey bars) are shown relative to a reference value (broken line). Note that, unlike the lens model of Fig. 1, no integration of trait values into an overall mate value assessment is necessary. The assessment order here is idealized; in real life, some aspects of personality and intelligence can be judged before some aspects of bodily attractiveness (because of clothing) or social status (because of deceptive advertising).

about satisficing and aspiration levels in real mating are more relevant here.

The aspiration level for each cue might correspond to some minimal threshold for producing viable, attractive offspring with the prospect. Every interaction with a prospect might bring more information, and each piece of information helps one decide whether to continue or terminate courtship, which has high time, energy, resource and opportunity costs. The type of sexual relationship that is sought influences the aspiration levels for different sexual cues[3]. Kenrick and colleagues[22] found that the minimum acceptable levels for intelligence, kindness, earning capacity and physical attractiveness increased with the length and seriousness of the sexual relationship sought (from dating through short-term sex to long-term dating to marriage), but did so in ways that differed for each trait and for each sex.

This sequential aspiration model resembles other recent models of satisficing, non-compensatory choice[55]. As with other non-compensatory decision processes, this can sometimes lead to intransitive preferences across prospects, but evolution might not mind a bit of intransitivity in mate choice.

Sexual gossip as cue integration across group members

In a group-living species such as humans, one's own assessment of a prospect's value could be influenced by finding out how others rate that prospect. Sexually inexperienced animals often copy the mate choices that older animals make – for instance, females of some fish species tend to pick males that have already been favored by other females[56,57]. Once language evolved in our lineage, this crude strategy for integrating social information about mate values turned into the much more powerful parallel distributed decision-making system known as sexual gossip, a system for integrating diverse views on the sexual cues, traits and qualities of sexual prospects from kin, friends and other
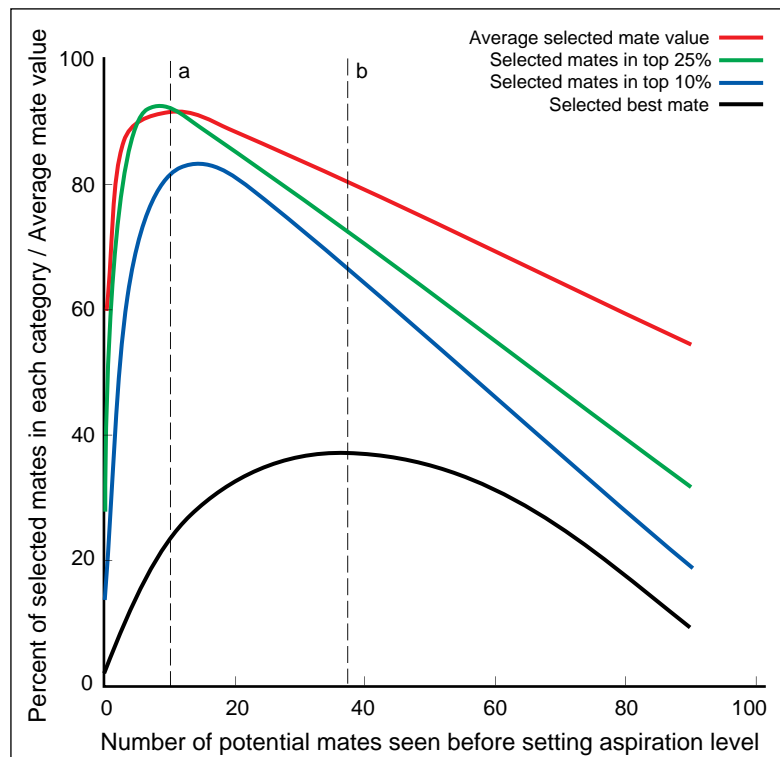
Fig. 3 Search performance based on number of individuals sampled to form an aspiration level for further mate search. Performance on four different criteria is plotted as a function of number of individuals sampled initially (assuming one-sided, non-mutual search), with the highest-value individual from that initial sample used as the aspiration level for future search. These smoothed results are based on simulations (Refs 64,65) with a total mating population of 100, each individual having a mate value between 1 and 100. If the initial sample comprises 10 individuals (x=10, marked a), the average mate value obtained given the resulting aspiration level will be 92 (red curve, top); the chance that the selected mate will be in the top 25% of the population is 92% (green curve, second from top); the chance that the selected mate will be in the top 10% is 82% (blue curve, third from top); and the chance that the very highest-value mate will be selected is 23% (black curve, bottom). Sampling about 10 individuals is also a fast way to form a useful aspiration level for population sizes larger than 100. In contrast, the '37% rule' (x=37, marked b) does better at maximizing the chance of obtaining the very highest-valued mate (to 37%), but has a much higher search cost, and does worse on the other three criteria [average mate value of 81 (red); only a 72% chance of getting a mate in the top 25% (green); only a 67% chance of getting a mate in the top 10% of the population (blue)].

group members. The views of one's parents, who have demonstrable success at producing viable offspring and a strong biological interest in grand-offspring, seem to deserve special weight[40], although they are often ignored in modern societies[58]. Sexual gossip as a distributed decision-making adaptation for mate choice remains almost completely unexplored.

Mate search strategies

Typically, people date a number of individuals in succession before settling down with a long-term partner. Thus, mate choice is a process of sequential search rather than selection from a set of known options. What strategies are appropriate for sequential mate search? Models of optimal search behavior have been developed for decades in statistics, economics, game theory and operations research[58–61]. Such models have only been applied recently to animal and human mate choice[6,15,62–65].

Classic search theory from economics suggests that one should look for a new mate until the costs of further search outweigh the benefits that could be gained by leaving the

current candidate[59]. But in practice, performing a rational cost-benefit analysis of optimal search behavior is not only intractable, but also makes a bad impression on a would-be partner[58,65]. Instead, we might expect a satisficing search strategy[8] to be used, in which individuals search until they find a prospect who exceeds a reasonable aspiration level regarding mate value.

How should that aspiration level be set? Search theory from statistics suggests the '37% rule' derived for the 'secretary search problem': estimate the number of prospects one is likely to meet in life, let the first 37% of them pass by without picking any of them, but use the highest mate value observed in that initial sample as the aspiration level for searching through the rest, until one is found who exceeds that threshold[60,64]. This is a proven optimal way of setting an aspiration level, but only for a search where one receives positive payoff only for picking the very highest-value prospect from a random sequence of prospects with an unknown distribution of values, without any backtracking to previously encountered prospects, without any search or courtship costs and without any possibility of being rejected by the prospect. By sampling a much smaller number of prospects initially, say a dozen, one can actually attain a higher expected mate value than the 37% rule delivers (although a lower chance of finding the very highest-valued prospect), with much lower search costs and a much lower risk of being stuck with a low-value mate[64,65] (Fig. 3).

More importantly, the 'secretary problem' ignores the problem that a prospect you desire may reject you. This mutual choice constraint makes the search much harder[64,65]. Game-theory models of 'two-sided matching' address these complexities[61] directly, and propose various search strategies which guarantee that a population reaches a 'stable matching': a pairwise assortment of individuals where no individual would prefer to be mated with someone else who would also prefer to be mated with them. However, two-sided matching models typically assume strict monogamy (no 'extra-pair copulations'), complete information and exhaustive preferences: everyone has complete, consistent, transitive preferences across all possible prospects that they encounter.

Non-monotonic utility functions for mutual mate choice

A simpler way to take mutual choice into account could be to set one's aspiration level by taking one's own mate value into account, and directing courtship effort at those prospects most likely to reciprocate[15,65]. If there is a utility function that maps from perceived prospect quality onto courtship effort directed at that prospect, it seems obvious that the function should be monotonically increasing. However, evolution might not always favor monotonic preferences in mate choice. Mate choice demands mutual consent, and if courtship has high costs, it would be maladaptive to waste courtship on prospects much higher in quality than oneself, who would be unlikely to reciprocate. Perhaps the courtship–effort function should peak near one's own mate value, not at the maximum possible value. Or there might be two thresholds, a minimum below which courtship is deemed not worthwhile, and a maximum above which courtship would probably be futile. Both monotonic and non-monotonic mate preferences could give rise to the

strong assortative mating (positive correlations between male and female quality for mated pairs) that has been observed for humans[66]. The problem of learning one's own mate value, to take mutual choice into account during mate search, presents a further cognitive challenge[65].

Courtship turns cognitive

Mate choice is a hard problem in domain-specific judgment and decision-making. But it is simple compared with the cognitive demands of courtship, which require advertising all of one's physical and mental traits in maximally appealing ways to a skeptical, intelligent, interactive sexual prospect, and equally motivated, intelligent sexual competitors[2,3,6,7,21]. Mate choice and courtship are locked into an evolutionary arms race. At the physical level, mate choice for bodily and facial traits exerts sexual selection pressures on those traits, changing their form dramatically over evolutionary time[10,18]. The same sexual selection happens at the psychological level: any mate choice in favor of (heritable) mental traits must shape those traits evolutionarily[6]. This effect is obvious to sexual selection theorists, but its implications for cognitive science are poorly appreciated. To the extent that mate choice turned cognitive in the course of human evolution, favoring sexual cues of psychological rather than physical quality, courtship had to turn cognitive too, advertising those qualities. If mate choice favored intelligence, creativity, generosity and linguistic expressiveness, then intelligence, creativity, altruism and language might have evolved partially through sexual selection rather than survival selection[6,7,18,67]. Thus, in studying human cognition, we may be studying the evolutionary products of mate choice.

Conclusion

Mate choice research is thriving because it is rigorously evolutionary but, so far, only loosely computational. However, with the evolutionary origins and functional goals of mate choice reaching firmer agreement, we argue that the time is right for more intimate relations between evolutionary psychology and cognitive modelling at three levels. First, research on adaptations for perceiving sexual cues, both physical and psychological, would benefit from a much tighter feedback loop between computational modelling and human experimentation designed to test competing models. Second, research on adaptations for integrating sexual cues into trait values and attractiveness estimates might prove an excellent arena in which to test supposedly domain-general cognitive science models of cue-based inference, categorization, learning, judgment, social attribution, intuitive statistics and so forth. Third, research on mate search strategies might illustrate how to combine theories of adaptive function (such as sexual selection theory), theories of normative rationality (such as game theory and optimal search models), empirical data (such as sex research) and cognitive models of strategic decision-making.

More generally, a cognitive perspective on mate choice research might open the way towards an evolutionary cognitive science organized around adaptive problems and content-specific domains, rather than supposedly domain-general processes of perception, categorization, inference, learning, judgment and decision-making. Mate choice and courtship demand the seamless integration of all these processes. Cognitive science has been defined as the study of knowledge and intelligence. But knowledge is always knowledge of something, and intelligence is always intelligence for some goal. As mate choice research turns cognitive, it is becoming clearer that, at least in this domain, our knowledge is about each other, and our intelligence is for reproduction.

Outstanding questions

- Do mate search strategies (including assessments of one's own attractiveness) exert any top-down influence on our adaptations for perceiving physical and psychological attractiveness, or are these perceptual adaptations totally modular, automatic and encapsulated?
- How do mate choice strategies vary as a function of one's age, sex, intelligence, physical attractiveness, health, wealth, sexual experience, family circumstances, overall mate value, local demographics and constraints (legal, economic, cultural and moral) of the local mating market?
- Is cue-based judgment of psychological traits in mate choice any better than cue-based judgment of such traits in clinical psychology, which is pretty poor[53]?
- Can romantic love be understood functionally as an adaptive influence on mate choice, perhaps by generating sexual commitment through over-estimating a prospect's mate value, or through construing their unique features as uniquely desirable? Does love act as a satisficing mechanism to stop further mate search?
- How well do our evolved mating strategies work in modern societies with large cities, contraception, legal monogamy, heritable wealth and so forth? Could social institutions be changed to promote happier mating patterns, bearing in mind that sexual competition is often a zero-sum game?
- How do we learn the correlations between evolutionarily novel sexual cues such as monetary wealth, property, media fame, graduate education and fashionable clothing, and underlying traits relevant to mate choice? Can novel cues advertise heritable traits?

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