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Through Evolution's Eyes: Extracting Mate Preferences by Linking Visual Attention to Adaptive Design

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Abstract Information is crucial to decision-making, including mate choice decisions. Perceptual systems, such as attention, evolved in part to forage for reproductive information; consequently, these systems can be used to reveal mate preferences. Here, I consider the place of visual information in human mate choice and provide a rationale for pressing into service methods drawn from the attention literature for the study of mate choice decisions. Because visual attention is allocated automatically and selectively, it may be used to complement common methods of mate preference assessment, such as self-report questionnaires and measures of genital arousal, while avoiding some of the pitfalls of these methods. Beyond the utility of increasing confidence in extant research findings by employing relatively unobtrusive methods, visual attention paradigms can also allow researchers to explore a variety of questions that are rarely asked, such as those concerned with signal efficiency and tradeoffs in the assessment of mate value.

Keywords Mate choice · Visual attention · Information · Signals · Human body

Introduction

Like all sexually reproducing species, *Homo sapiens* has been saddled with the problem of choosing a mate. Perceptual systems, although not strictly required, may have proven useful over evolutionary time in identifying and evaluating information about the quality of potential mates. This may be true of complex organisms as well as simpler ones, like plants, that use third parties, like bees, to select mates by fertilizing while foraging for food. Mate choice decisions will almost certainly be influenced by the perception of information about the sex, fertility, and fecundity of a potential mate. In species that exhibit long-term pair bonds and biparental care, as is the case among humans, the expected survivorship of a mate may also be important for the production and ultimate success of offspring. Together, predictors of these characteristics can be used to determine an individual's value on a hypothetical "mating market."

In evolutionary terms, humans face a pair of reproductive problems in which only a small subset of all possible solutions can lead to genetic posterity: how to signal one's value on the mating market and how to evaluate the signals of others (Barber, 1995). For meaningful signals to evolve, selection must prevent the transmission of misinformation. By design, signals are presented honestly when dishonest ones are too costly to produce, when faking is punished by others engaged in "policing," when honesty is in the shared interests of the signaler and receiver, or when signals are intimately tied to other traits and are impossible to fake (Maynard Smith & Harper, 2003). Concomitantly, selection has tailored receiver perceptual systems to improve the accuracy of mate value assessments. Thus, receivers may eventually evolve to disregard misinformation, increasing selection pressure on signal honesty.

The current article reviews the place of visual information and its perception in the design of human sexual psychology. In this endeavor, I am indebted to an influential evolution-minded review of female attractiveness as revealed through physical traits, written by Symons (1995). It is my intention to recast his line of argument and link to it some of the discoveries made since the publication of his review. Here, I am primarily concerned with receiver psychology, and so do not

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require a demonstration that aspects of the body were designed by selection to signal information per se, so long as bodies indeed convey such information, even incidentally. From the premise that individuals are on display, I argue that they are also the subjects of critical evaluation. To begin, I sketch the outline of an evolutionary framework for the use of information in mate choice decisions. I then briefly review some of the literature on visual displays of information by the human body and its assessment by receivers. Following this, I discuss the strengths and weaknesses of two of the most common methods of extracting mate preferences from receiver psychology: self-report questionnaires and physiological measures of genital arousal. Finally, I show how mate preference research can benefit from embracing less obtrusive testing paradigms adopted from the literature on visual attention, and conclude with some suggestions for future research.

Evolution and Information

The design of the decision-making systems underlying mate choice is perhaps best understood in terms of the search for information and its transfer from signaler to receiver. There are a few aspects of this functional perspective that warrant consideration. First, the contemporary human mind is the product of small, cumulative increases in the fit of decision rules to their respective domains over generations of competition among alternative genotypes. This process of adaptation would have been improved by the availability of information in the physical and social environment, especially information that reliably predicted reproductive success, and that was regularly present in the environment.

Decision rules will be sensitive to this sort of information. For instance, age-specific birth rates can be predicted in part by local life expectancy (Wilson & Daly, 1997). Reproductive timing decisions have also been under the purview of selection: they are responsive to the environment and under direct selection in other animals (Nussey, Postma, Gienapp, & Visser, 2005), and humans are probably not an exception in this regard. Undoubtedly, selection built the mind to respond to information that was predictive of reproductive success in past environments, but whether this same information remains equally predictive today is merely a consequence of the continuity of its properties over time and across environments. So, animals (humans included) are not fitness maximizers. Rather, they tend to behave *as if* maximizing fitness, and they can be expected to do so only under circumstances sufficiently similar to those of their ancestors.

To provide an example of the above distinction, consider the well-established finding in sex research (and in the adult entertainment business) that men are readily aroused by pornographic stimuli. It is obviously not adaptive for heterosexual men to respond to two-dimensional images of naked women, but they are aroused nevertheless. Yet, visual pornography contains many of the cues predictive of reproductive opportunities that would have been relevant to our ancestors, such as nudity and proceptive body postures and facial expressions. Since photographs and video did not exist in our ancestral past, these modes of information transfer usurp receiver perceptual systems, which have not been designed to discriminate against fabricated stimuli, thereby producing a sexual response to cues that cannot possibly lead to reproduction. Pornography thus causes a functional error in an otherwise adaptive system.

A second aspect of an evolution-minded perspective on mate choice takes into consideration the costs of mating, including those that follow from the shaping of perceptual systems to selectively attend to relevant information. There may be risks inherent in foraging for some types of information and tradeoffs in the development and rededication of neural substrates and sensory schemes underlying mate choice decisions (Daly, 1978). Thus, the ease by which a signal is observed and processed will also affect the evolution of receiver psychology.

If the signals used to make mate choice decisions are weighted by their ability to deliver quality information, some will produce a larger sexual response than others and a few important signals may reduce or negate the effects of others. When judging physical attractiveness, signals that are relatively unambiguous and assessed at relatively low cost—what I will refer to more generally as "efficient" signals—may be given greatest emphasis, and the compilation of all such signals may lead to maximum response. Furthermore, the weighting of a signal does not need to be invariant across individuals or over time. Assessment processes may depend on characteristics determined by normal variation in development, such as one's own quality and consequent ability to attract a mate. They may also depend on context, as in the choice between the pursuit of a short- and a long-term mate: what receivers are designed to value in the short run (e.g., present likelihood of conception) may be quite different from what they value in the long run (e.g., committed parenting).

Human Visual Displays

In support of the above framework, the human body is expected to convey reliable information about reproductive characteristics, and this information ought to be perceptible to observers. For the sake of brevity, I will review only a few examples of the visual display and assessment of reproductive information. Interested readers are referred to Symons (1995) and Thornhill and Gangestad (1997) for more in-depth reviews.

Among individuals of reproductive age, a time in which secondary sex characteristics are most pronounced, biological sex may be signaled by many traits. Observers are able to rapidly infer from the structure of the face and walking gait both the biological sex and the degree of masculinity/femininity of individuals, and preferences for these traits vary in corresponding ways (e.g., Perrett et al., 1998; Troje, 2002). Women's preferences for masculine and feminine male faces vary as a function of the attractiveness of the individual making the assessment, the type of assessment being made (e.g., short- versus long-term relationship), menstrual cycle phase, and current involvement in a romantic relationship (Little, Burt, Penton-Voak, & Perrett, 2001; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Penton-Voak et al., 1999, 2003; Penton-Voak & Perrett, 2000). Many of these differences in perception and evaluation reflect known differences in underlying traits. For instance, the perceived masculinity of male faces is positively associated with circulating levels of the rated males' testosterone, a hormone central to the development and maintenance of masculine traits (Penton-Voak & Chen, 2004). Likewise, estrogen, a hormone fundamental to female reproductive capability, is positively associated with the perceived femininity, attractiveness, and health of women's faces (Law Smith et al., 2006).

The distribution of body fat also signals biological sex and, among women, further signals fertility status. The waist-to-hip ratio (the circumference of the waist divided by the circumference of the hips) and breast tissues undergo dramatic sex-dependent changes at puberty, resulting in sexually dimorphic body shapes (Laurence, Monaghan, & Gusterson, 1991; Singh, 2002). The size of a woman's breasts and waist-to-hip ratio are associated with estrogen and progesterone profiles, predicting the probability of conception and, hence, fertility status (Jasieńska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). As expected, men prefer women with low waist-to-hip ratios, those tending to signal high fertility (reviewed in Singh, 2002).

Health is another facet of mate value that can be signaled by the body and face. In a landmark study, Hamilton and Zuk (1982) proposed that there might be permanent genetic variation within sexually reproducing species in response to coevolving parasites and other pathogens. An important corollary is that populations encountering high pathogen prevalence would be under increased pressure to signal and assess health, via phenotypic markers of "good genes" (additive genetic effects that lead to an increase in robustness to environmental disturbances; Neff & Pitcher, 2005), in order to produce pathogen-resistant offspring. If variability in phenotypic quality among individuals is due to variability at the genetic level, then members of a pathogen-stressed population may accordingly enhance their ability to discriminate potential mates by placing greater emphasis on signals of health when making mate choice decisions (Gangestad & Buss, 1993; Low, 1990).

There are many possible signals of health. A simple one is fluctuating asymmetry (FA), which is the random deviation in bilateral symmetry of a trait (e.g., ear location) tending to be symmetrical at the population level. FA is typically used as a measure of developmental instability—the resilience of an organism to perturbations, such as infection by pathogens, deleterious mutations, or injuries, over the lifespan. In theory, an increase in developmental instability leads to an increase in FA, because perturbations will rarely have symmetrical effects on the body. FA accounts for a small but consistent proportion of the variance in male reproductive success and in women's mate preferences (especially in the short run); its low predictive power may be due to the noisiness of the measure as an index of developmental instability (Gangestad 2000). Other signals of health, such as the shape, color and texture of the face, also have effects on mate preferences (Jones et al., 2005a, b). Notably, many of these preferences were predicted by evolution-minded hypotheses about the benefits a healthy mate can deliver to an individual as well as to their shared offspring.

Finally, work on kinship (reviewed by DeBruine, Jones, Little, & Perrett, 2008) raises a different set of signals that have been surprisingly neglected. A good deal of empirical work has focused on psychological adaptations to avoid incestuous mating (DeBruine, 2005; Lieberman, Tooby, & Cosmides, 2003; Shepher, 1971; Wolf, 1995), but little research has been devoted to the information that parents may provide about the quality of their own offspring to interested parties. Heredity implies that individuals will tend to resemble their biological parents more than they will other individuals drawn at random from the population. Thus, where heritable variation in a trait exists, parental and offspring phenotypes will be correlated. Human generations substantially overlap, so characteristics such as fertility, developmental stability, parenting skill, and relationship fidelity might all be predictable from information about a potential mate's parents. Whether and how these cues are used may be of great interest to sex researchers.

A Darwinian perspective sheds light on information signaled by the body. Likewise, it helps to reveal the design of psychological systems that forage for and make use of this information. To do so, however, researchers need tools to study the functional goals that mate choice psychology is designed to achieve. The next section deals with some common methods of extracting sexual interests in order to make inferences about mate choice decisions, and provides some reasons why we might wish to look elsewhere for novel methods.

Extracting Interests

Sexual interests are not always easily observed. As such, researchers have relied heavily on the methodological staple of social psychology: the survey questionnaire. Questionnaires have the virtue of being cheap as well as easy to construct and disseminate, but the validity of the method rests on the assumption that it taps into participants' interests rather than *expectations* of what their interests ought to be. In the case of mate preferences, this assumption is tenuous, because they are normatively prescribed. Sex offenders, for instance, often have reasons to conceal their preferences. Moreover, mate preferences may not be readily accessed by conscious introspection, so people may unwittingly report false preferences.

To remedy some of the problems of questionnaire methods, measures of genital arousal have been developed to assay sexual preferences. Unfortunately, these measures pose their own problems. Measuring genital response can be embarrassing for participants, possibly biasing both sample recruitment and subsequent reactions to stimuli: individuals willing to undergo such testing procedures may not be representative members of the population at large, and may be more or less inclined to respond to *verboten* stimuli (such as pre- or circumpubertal children) during testing. Moreover, despite being among the best measures of sexual interests (Lalumière, Quinsey, Harris, Rice, & Trautrimas, 2003), these techniques are not universally regarded as ethical and are unlikely to be sanctioned for use with children (Quinsey, Rice, Harris, & Reid, 1993).

Recent work suggests a more serious concern with measures of genital arousal, specifically with regard to women, and perhaps with regard to bisexual men as well. In these measures, strength of preference is inferred by degree of vasocongestive response. Yet, self-reported hetero- and homosexual, but not post-operative transsexual, women show non-specific genital arousal patterns to videos of male–female, male–male, and female–female sexual stimuli, despite simultaneously reporting specific introspective ("subjective") arousal to these stimuli (Chivers, Rieger, Latty, & Bailey, 2004). Perhaps more puzzling is women's significant genital, but not introspective, arousal to videos of copulating male and female bonobo chimpanzees (Chivers & Bailey, 2005). Although these findings are curious, the vasocongestive method does appear to be measuring sexual arousal (Suschinsky, Lalumière, & Chivers, in press). In contrast, hetero- and homosexual men in these studies show specific genital responses that correspond to their introspective preferences, and show no response to chimpanzee sex. Yet, bisexual men, who would be expected to display non-specific genital arousal patterns for the aforementioned stimulus types (based on their stated introspective preferences), instead show specific arousal patterns (Rieger, Chivers, & Bailey, 2005). These discrepancies between genital and self-reported arousal hint at an important distinction between introspective measures of mate preference and other measures that do not rely on conscious elicitation (Chivers, 2005; Rieger et al., 2005).

What is needed is a complementary measure of mate preferences that circumvents the problems discussed above. In the next section, I put forth the argument that visual attention measures are suited to this purpose, for the following reasons: visual information is central to human mate choice; attention is designed to facilitate information foraging; and attention is allocated automatically and selectively.

The Eyes Have It

Thus far, I have tried to make a case for the relevance of visual information in mate choice decisions. Of course, humans can use information gathered from the olfactory, auditory, tactile, and gustatory senses in mate choice decisions. Nevertheless, we are remarkably visual creatures, and there is no shortage of studies finding effects of subtle alterations in visual information on preferences. Nor are we alone, in this regard, within the primate order: male Rhesus macaques are willing to pay, in the currency of fruit juice, to view pictures of sexually receptive female macaques' perinea (sexual swellings that signal fertility status; Deaner, Khera, & Platt, 2005). For these reasons, I will focus on visual attention paradigms as methods of extracting sexual interests. In principle, however, attentional paradigms tuned to other sensory channels can be used for the same purpose.

Attention can be characterized as a mechanism designed to guide information foraging. Given a problem, attention can be used to pick out from a large array those pieces of information that will help provide a solution. Attention serves this purpose by limiting the flow of information into the brain, because individuals tend to encounter information in the environment at rates that far exceed their ability to process it (Dukas, 1998). The upshot of this sort of selective allocation of attention is that it can elucidate mate preferences. Moreover, visual attention is allocated automatically and without need for conscious processing (Hayhoe & Ballard, 2005), so it can be observed fairly unobtrusively.

Perhaps the simplest attentional method to extract mate preferences is to measure the length of time an individual voluntarily examines a visual stimulus before shifting attention to a new one. This "dwell time" measure correlates with genital arousal and predicts self-reported preferences for biological sex and age (Quinsey, Ketsetzis, Earls, & Karamanoukian, 1996; Quinsey et al., 1993; Silverthorne & Quinsey, 2000). It can also be used to discriminate among certain sex offender subgroups (e.g., offenders with child versus adult victims; Abel, Jordan, Hand, Holland, & Phipps, 2001; Abel, Lawry, Karlstrom, Osborn, & Gillespie, 1994; Harris, Rice, Quinsey, & Chaplin, 1996).

Methods that track eye movements ("saccades") can record search patterns, dwell time, and the frequency of visual fixations to a small target within a larger scene, providing a more nuanced measure of visual attention. Two recent studies used eye-tracking methods to test a pair of hypotheses generated from the notion that visual attention serves to direct information foraging activity: (1) individuals should selectively attend to signals that provide information most relevant to the viewer and the task, and (2) especially attend to those signals that provide such information most efficiently (that is, with the least ambiguity and cost). In support of the first hypothesis, Rupp and Wallen (2007) showed heterosexual male and female participants a series of sexually explicit images of heterosexual couples engaged in oral sex and intercourse; during viewing, participants' eye movements were recorded. After testing, the dwell time of visual fixations to particular regions of interest of the stimuli were analyzed for selective allocation of attention. In support of the first prediction, male and female participants selectively attended to the male face, female face, and genital regions and selectively avoided the image backgrounds. Interestingly, women using oral contraceptives were significantly more likely to attend to clothing and background information than other participants in the study.

Suschinsky, Elias, and Krupp (2007) provide a test of the second hypothesis. Heterosexual men were presented with three images of the same woman simultaneously, over six 20-s trials (each trial representing a different woman). The images of each woman were identical in every respect, except for the waist-to-hip ratio, which had been digitally manipulated as a control feature. Suschinsky et al. (2007) found that regions known from previous research to provide valuable information about health, age, and fertility (i.e., the head, chest, and waist and hip regions) were attended to, as measured by dwell time and frequency of fixations, more often and for longer than regions that may be highly redundant and provide lower quality information upon which to make useful discriminations (i.e., the legs).

Admittedly, these are very limited investigations of the involvement of attentional systems in mate choice decisions, and they leave us with more questions than they can answer. For instance, although Suschinsky et al. (2007, in press) supported their hypotheses, they observed that the head and chest regions were attended to almost equally and that the waist and hips region less so, even though the only manipulated body characteristic was the latter region. Does the waist-to-hip ratio provide less information, or information of lower quality, than the face and breasts? Is it more computationally difficult to process, creating higher assessment costs than these other regions? Although these are interesting theoretical questions that should be answered, they need not deter us from using attentional paradigms to study preferences in the meantime. As stated in the preceding section, the point of this exercise is to find a measure of mate preferences that avoids conscious elicitation of sexual interests and is resilient to attempts to conceal actual preferences. Yet, the methods just described are not entirely robust to these concerns: a savvy participant can mislead researchers by biasing his attention to non-preferred stimuli. Below, I provide one further attentional method, in which it is impossible for participants to systematically bias their responses to mislead researchers (or themselves).

The current model of attention championed in the literature is analogous to a computer processing information in parallel. In this way, attention can be divided and used for concurrent tasks. But cognitive resources are limited, so divided attention comes at the cost of efficiency: the more tasks being attended to, the more interference among them. Thus, the search for and identification of an object in a visual scene can in some circumstances be impeded by the introduction of a second object that may or may not be relevant to the original identification task (Ambinder & Simons, 2005; Duncan, Ward, & Shapiro, 1994; Theeuwes, Kramer, Hahn, & Irwin, 1998); this is known as attentional "capture." A recent study by Jiang, Costello, Fang, Huang, and He (2006) exploits this phenomenon in order to investigate the effects of participant sex and sexual-orientation on the allocation of spatial attention. Viewing through a mirror stereoscope, participants were briefly shown two pairs of stimuli on-screen simultaneously: presented to the dominant eye were two patches of visual "noise" and presented to the other eye was a nude image (of either a man or a woman) and a scrambled version of the same image. Because of a phenomenon known as interocular suppression, the noise patches override conscious perception of the nude image, so the nude image is effectively rendered invisible to participant awareness. Immediately after presenting the images and noise patches, a "probe" tilted 1° clockwise or 1° counterclockwise was briefly presented on one of the two sides of visual fixation (and nothing was presented on the other side). Participants were simply asked at the end of each trial whether the probe was oriented clockwise or counterclockwise. Heterosexual male, heterosexual female, and homosexual male participants all performed more accurately on this task when the probe appeared on the same side of fixation as a nude image of their preferred sex (female images for heterosexual men, male images for heterosexual women and homosexual men) than when it appeared on the opposite side of fixation, suggesting that their attention was captured by images of their preferred sex. A mixed group of homosexual and bisexual women were intermediate to heterosexual men and heterosexual women with regard to this attentional effect, but this is likely due to the fact that this group was heterogeneous for their preferred sex. Since the images in this method are "invisible" to the viewer, and the extraction of preferences requires no articulated statement of preferences of any sort, it would be very difficult for participants to intentionally or unintentionally bias their responses to mislead researchers. In theory, the same sort of unobtrusive methodology could be employed to investigate preferences for any visual feature.

In the following section, I conclude this review by considering a few other aspects of information and attention that may be relevant to future research.

Paying Attention to Attention

If receiver psychology is designed to favor efficient signals, it is possible to predict which signals will be most important in a given mate choice task. However, in the pursuit of this goal, researchers should be careful not to perpetrate a common error. Mate choice is typically studied with an implicitly or explicitly narrowed set of prospective mates, having been pre-selected by researchers or through the assumptions of the participant. However, real-world mate choice requires decision-makers to select a subset of candidates from a much larger set: every single person in the local environment (of both sexes, of any age, and of any relation to the decision-maker) is a potential mate until they are relegated to the "inappropriate" subset, inappropriate meaning here a choice that would reduce, rather than have improved, one's opportunities for reproduction in ancestral environments. Logically, one might even extend this larger set to include all objects, animate or inanimate, as they must also be excluded from the narrowed choice set before a decision can be reached and a mate pursued.

Decision-making systems should work rather quickly to exclude the vast majority of individuals (or other objects) in the larger set, by using features that are unique to "appropriate" choices. For instance, individuals drawn from a moderately homogeneous subset of potential mates (e.g., young women attending a university in New York) will differ in appearance, on average, in particular ways from individuals drawn from a substantially more heterogeneous set (e.g., male and female New Yorkers ranging from 6 to 80 years of age) that encompasses the former subset. Certain signals may be very useful in narrowing down the list, and so may act as "gatekeepers." These are signals that rapidly remove patently inappropriate options (such as young children) from consideration, so that decision-makers can gather information on more appropriate options. But gatekeeping signals may no longer be informative when making a decision about the quality of individuals in an already-narrowed subset. This fact may go some way in explaining the finding by Suschinsky et al. (2007, in press) that the waist-to-hip ratio was attended to less than the face and chest regions of the images in their eye-tracking task: the study made use of a very homogenous stimulus set (young, attractive women), where the waist-to-hip ratio may play a much smaller part than other signals in mate choice decisions. Signals that discriminate between and within subsets are equally important, but between-subset signals tend to be ignored, with rare exception (e.g., Quinsey & Lalumière, 1995).

Gatekeeping signals can be studied by monitoring attentional allocation to specific signals and varying the heterogeneity of the stimulus set. To make finer distinctions about the importance of particular signals, one can evaluate how an individual prioritizes some features over others by examining attentional allocation while simultaneously imposing processing costs—by manipulating stimulus exposure times and cognitive load, for example. By increasing the computational difficulty of the task, individuals may be obliged to rely on the most efficient signals. From this, one can also study how mate choice decisions suffer when attention becomes increasingly limited to fewer signals.

Attention is essential to information foraging and, hence, to decision-making. It is allocated automatically and can be measured unobtrusively, making it an attractive method to reveal mate preferences. There remain many unanswered questions worth pursuing, aside from the ones already raised, about tradeoffs in visual assessment, the efficiency and redundancy of visual signals, the co-evolution of physical signals and receiver psychology, and the differential effects of conscious and unconscious processing on mate choice decisions. The psychology underlying mate choice decisions has undoubtedly undergone chronic selection, and so should evidence an unambiguous appearance of design. Attention can offer a unique window on this design.

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