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Original Article

Generalization in mate-choice copying in humans

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There is much evidence that humans, as other species, are affected by social information when making mate-choice decisions. Witnessing a rival show interest in a member of the opposite sex tends to lead human observers of both sexes to thereafter rate that person as more appealing as a potential mate. However, how this occurs is not well understood. We investigate whether this effect is specific to the individual witnessed or will generalize to other potential mates with shared characteristics—that is, whether humans exhibit trait-based or just individual-based mate-choice copying. We found that whereas this kind of generalization did occur with some traits, it appeared to depend on age, and conspicuously, it did not occur with (inner) facial traits. We discuss possible explanations for the age specificity and cue specificity in terms of informational benefits and how people attend to unfamiliar faces. *Key words:* cultural transmission, generalization, mate choice, mate-choice copying, sexual selection, social learning. *[Behav Ecol 23:112–124 (2012)]*

Milan Kundera (1978) describes it as "one of life's great secrets: women don't look for handsome men, they look for men with beautiful women" (p.12). Hogan-Warburg (1966), describing ruff hens, said it somewhat differently: "It has been observed several times that a crouching or copulating female especially attracts other females and stimulates them to crouch also" (p.196). These are expressions of violations of the assumption that mate-choice decisions are made independently of each other (Gibson and Langen 1996). Mate-choice copying (Losey et al. 1986; Höglund et al. 1990; Pomiankowski 1990) is one way in which this happens, where having been chosen as a mate heightens one's subsequent appeal as a mate among observing rivals. Females of several species have been shown to utilize the mate choice of conspecific females to inform their own mate search, preferring chosen males over others. Kundera's (1978) observation that humans are among the species that exhibit mate-choice copying has recently received experimental substantiation (Eva and Wood 2006; Jones et al. 2007; Waynforth 2007; Little et al. 2008; Parker and Burkley 2009; but see Uller and Johansson 2003), for both males and females (Place et al. 2010).

Whether a potential mate has already succeeded in acquiring a mate or not is readily visible in many species. In a competitive mating environment, the mate choices of rivals may contain valuable information about the quality of potential mates (Gibson and Höglund 1992; Nordell and Valone 1998), information that may otherwise be costly to attain (Gibson et al. 1991; Briggs et al. 1996; Dugatkin and Godin 1998), unreliable (Sirot 2001; Brennan et al. 2008), difficult to ascertain (Goulet 1998; Nordell and Valone 1998), or require specific experience (Dugatkin and Godin 1993; Amlacher and Dugatkin 2005; Vukomanovic and Rodd 2007). Furthermore, time for mate choice may be heavily constrained, putting pressure on quicker decisions (Höglund et al. 1995). These considerations lead to the expectation that animals may come to exploit social information as a quick, low cost indication of mate quality (Pomiankowski 1990; Wade and Pruett-Jones 1990; Höglund et al. 1995), either as an alternative to assessing mates independently (Briggs et al. 1996), or as a source of additional information (Gibson and Bachman 1992; Mery et al. 2009).

If mate-choice copying is a domain-specific adaptation, we expect the manner in which the information is utilized to match the problem. However, there is more that may constrain the evolution of copying than function. The form of extant mechanisms in which context copying appears will also have consequences. The constraints that phylogeny and function separately place on the evolution of copying both require consideration. Though evolutionary history is difficult to know, 1 viable possibility is that mate-choice copying is serially homologous to other forms of learning. The underlying mechanism may hold much in common with other forms of learning. Alternatively, mate-choice copying may be a manifestation of a general learning mechanism applied in this specific domain. In either case, the prediction is that mate-choice copying will behave similarly to other forms of learning. One common feature of learning mechanisms is generalization. Is generalization a quality of mate-choice copying in humans? That is, when we are affected by social information in mate-choice copying, and assess someone more favorably after witnessing them receiving sexual attention, have we learned something not only about that individual but also about other, similar individuals as well?

To illustrate the question, suppose we change our assessment of Snow White when we see her courted by Prince Charming. Have we learned something just about her? Or have we incidentally also learned something about other similar individuals,

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say Snow Grey, who holds observable traits in common with Snow White, such as pale skin or a red bow in her hair? If an instance of human mate-choice copying generalizes in this way between individuals who are similar in terms of their features or traits, it can be termed "trait-based"; if specific to the person observed, it is "individual-based".

The distinction between individual-based and trait-based mate-choice copying is not always drawn. Mate-choice copying has sometimes been assumed to be trait-based (in discussions: Brown and Fawcett 2005; Laland and Janik 2006; in models: Kirkpatrick and Dugatkin 1994; Agrawal 2001), despite that the bulk of the empirical work had exclusively studied choice for the particular individuals observed with the model mate chooser. The possibility and significance of trait-based copying was discussed (Brooks 1998) before it was observed (White and Galef 2000a). Brooks (1998) pointed out that mate-choice copying results in "cultural inheritance" of preference only if it goes beyond the individual, to a lasting change in the types of mates subsequently preferred, that is, only if mate-choice copying is trait based. Thus, whether copying is trait based or exclusively individual based can have important consequences regarding cultural evolution and sexual selection.

Both individual-based and trait-based mate-choice copying have been demonstrated among animals of several species (see next section). In humans, individual-based copying has been shown using multiple methods (e.g., Jones et al. 2007; Waynforth 2007; Place et al. 2010). Given the prevalence of cultural learning in humans, including for features used in mate selection (Meskó and Bereczkei 2004; Wohlrab et al. 2007), we may also expect human mate-choice copying to generalize to those with similar traits. Generalized change of attractiveness ratings has since been found with artificial manipulations of eye-spacing (Little et al. 2011; see DISCUSSION) and shirt color (Place 2010), traits selected to be arbitrary. Here, through a series of experiments, we demonstrate that, given the distribution of traits within an actual population of mate seekers, both males and females fail to exhibit trait-based mate-choice copying for facial traits, yet exhibit it for hair and clothing traits. Meanwhile, the same participants, with the same stimuli, consistently showed individual-based mate-choice copying, replicating earlier findings (Place et al. 2010). Furthermore, age-related individual differences appear in trait-based, but not individual-based copying. We find that this pattern of social information use suits how and when the information will be most useful. We begin by reviewing work on trait-based mate-choice copying in other species and functional considerations, from which our predictions derive, before describing the manipulations of mate-choice information we use to elicit copying in humans.

PHYLOGENY AND TRAIT-BASED MATE-CHOICE COPYING

The question of whether mate-choice copying generalizes has been addressed in 5 previous studies of 5 different species. Female quail, *Coturnix coturnix japonica*, show sexual preferences for males seen consorting with other females (Galef and White 1998).White and Galef (2000) marked males with a penny-sized red or blue dot of dyed chest feathers, or with the addition of white feathers to the brown plumage of the crest. The colored dot was conspicuous on a cryptic ground bird like the quail, but the few white feathers in the crest was chosen as a variant that, though unusual, occurs in wild populations. In both experiments, females witnessing a male with the added marking successfully courting other hens, subsequently showed a preference for novel but similarly marked males.

Comparable demonstrations were made independently with 2 species from the same genus: sailfin mollies (*Poecilia latipinna*) and guppies (*Poecilia reticulata*). Witte and Noltemeier (2002) began with the observation that female sailfin mollies show mating preferences for larger males (Witte and Ryan 1998). Females were allowed to observe a rival affiliating with a smaller male, while a larger male remained alone. Such social information has been shown to affect mating preferences when the choice is between males of similar size, but between males of substantially different size, the typical preference for larger males in this species overrides the influence of copying (Witte and Ryan 1998). Witte and Noltemeier (2002) found, however, that by lengthening the observation period (to 20 minutes vs. 10 minutes in previous studies), the influence of copying strengthened, such that social information was heeded, even in conflict with native preferences: When thereafter allowed to choose between the 2 males, their subjects more often chose the smaller. Of especial relevance to the present question, when the same females were subsequently given similar mate-choice dilemmas between 2 novel males that differed in size, even after a delay of some weeks, they again tended to choose the smaller male. Similarly, female guppies show initial preferences for males with bright coloring (replicated in Godin et al. 2005, Experiment 1). Females observed relatively drably colored males affiliating with females and more brightly colored males alone. This procedure has been shown to be capable of reversing initial species-typical preferences (Dugatkin and Godin 1992). When tested with different males a day later, these females showed a preference for drabber males over brighter males. In both the mollies and the guppies, an initial preference was overshadowed by conflicting social information, and the social information manipulation had affected not only preferences for individual mates but also for characteristics of mates.

Zebra finch, *Taeniopygia guttata*, females exposed to paired and unpaired males subsequently preferred novel males with leg bands (Swaddle et al. 2005) or artificial crest adornments (Kniel et al. 2011) of the color of the paired males. Female fruit flies, *Drosophila melanogaster*, exhibit both individual-based (Mery et al. 2009, Experiment 1) and trait-based (Experiment 2) copying. Given the choice between 2 males dusted with different colors, females preferred those of the color of a similarly dusted male they had previously witnessed being chosen by another female. In all the above species, mate-choice copying appears to be trait based, generalizing to individuals with perceptible characteristics similar to those whose mating successes had been observed. We believe this to be an exhaustive list of published studies that address this matter; to our knowledge, no examples of the converse, where generalization to similar others is lacking, have been documented.

Like the larger list of species that evidence individual-based mate-choice copying, the above 5 species comprise a diverse selection of animals in terms of phylogeny, ecology, and mating behavior. There is no apparent commonality among them in terms of mating system or parental investment. Guppies are polygynous; zebra finch are socially monogamous. Parental investment in the fly is limited to choice of egg laying site; guppies and mollies are viviparous and invest no parental care; both bird species nest and hatch their eggs, but with quail only females care for hatchlings (Mills et al. 1997), whereas, among zebra finch, care for young is provided by both parents (Swaddle et al. 2005) and for considerably longer. So far, ecology appears to be a poor predictor of trait-based copying. That all 5 species that have been tested, so different from each other, show the same pattern may suggest that trait-based mate-choice copying is adaptive use of social information across a broad range of mating contexts. Alternatively, the apparent ubiquity of trait-based copying may be due

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not to functional but phylogenetic constraints, a broad commonality in underlying cognition: All these animals learn by association, and as noted above, a common quality of learning is generalization. Note that trait-based copying may be a consequence of general associative processes whether or not individual-based copying is associative in nature. Hence, phylogenetic considerations suggest that trait-based copying may be a feature of human mate choice as well.

FUNCTION AND TRAIT-BASED MATE-CHOICE COPYING

Individual-based mate-choice copying carries a possibly costly consequence: It places mate seekers especially in the thick of competition (Brennan et al. 2008), specifically leading them to choose mates that have already been chosen by others. Whether this imparts a substantial cost, and to what extent, depends on many factors of the mate-choice environment. In many species, competition often leads to intrasexual conflict, which can have serious survival costs. Furthermore, particularly among monogamous species, the taken mate may often be content with the current situation and resist the new suitor, leading to wasted mating effort. Trait-based copying does not necessarily bear these costs so squarely as it leads the mate seeker to the broader category of the taken plus those similar to the taken, many of whom may be available. Thus, it allows the benefits of copying, the usage of social information, without the hardships of a bias that steers mate seekers so discriminately to the taken. This suggests that trait-based mate-choice copying may be specifically better suited to monogamous species than individual-based copying. Beyond humans, the only other socially monogamous species for which there is currently good evidence of mate-choice copying is the zebra finch—one of the species that showed trait-based copying as well as individual-based (Swaddle et al. 2005).

A convincing case has been made that individual-based mate-choice copying is good usage of social information in a variety of mating environments (Wade and Pruett-Jones 1990; Gibson and Höglund 1992; Nordell and Valone 1998). Is generalization of the effect to similar individuals, trait-based mate-choice copying, likewise adaptive? It may be so if there are perceptible traits that correlate with both mate choice and mate quality (Bradbury 1981): That is, there must be something to be able to generalize with respect to. Though individual-based copying exploits whatever direct correlation may exist between mate quality and mate choice, trait-based copying relies on perceptible intervening traits correlating with both. Given the expectations that mate choice and mate quality may often correlate and that there may be perceptible traits that correlate with each, the conditions for adaptive trait-based copying appear likely to be met in some cases. But not always: If these correlations with traits are low, an indicator of mating success may be a poor cue to mate quality. Consequently, choices made through copying may correspond little with indicators of mate quality. That outward characteristics may poorly predict mate choice is a point that has been made through observation of actual mate-choice patterns (e.g. Gibson et al. 1991). Furthermore, the choice reversal experiments, in which copying disrupts preference for independently assessed mates (Dugatkin and Godin 1992; Coolen et al. 2005; Mery et al. 2009), accentuate that copied preferences may counteract even native mate-choice criteria, putative indicators of mate quality.

Furthermore, if the correlations among mate choice, mate quality, and perceptible traits are appreciable, non-social mechanisms for recognizing the indicator (e.g. innate recognition or individual learning) may constitute better use of available information (Sirot 2001). Indeed, one of the conditions for mate-choice copying, individual-based or otherwise, being adaptive usage of information is that relationship status provides mate quality information that is not fully captured by outward indicators. This may be because outward indicators of mate quality are lacking, unreliable or difficult to discern, or because the information gained concerns qualities of the candidate not readily apparent in physical characteristics, such as parenting ability, sociability, attachment style, fidelity, supportiveness, or intelligence. Such behavioral characteristics are important to mate choice in many animals and specifically in humans (Buss and Barnes 1986; Howard et al. 1987; Penke et al. 2007).

Thus, the functional significance of trait-based copying appears caught between 2 exclusive alternatives. If perceptible cues exist that are good indicators of mate quality, the information is public, and social information about others' mate choices will be superfluous. If mate-choice copying is to give mate seekers information about traits that otherwise require extended interaction to assess, such as behavioral or personality characteristics, then, although individual-based mate-choice copying makes good functional sense, generalizing to others on the basis of perceptible traits may mislead. Hence, functional considerations give reason to not expect trait-based copying.

THE QUESTION

It appears that phylogenetic and functional considerations give differing predictions on the question of whether mate-choice copying will generalize. Phylogenetically, incidence of mate-choice copying appears to be spotty, with more distant species behaving very similarly, whereas nearer species differ. Given that all 5 species in which trait-based copying has been studied have evidenced it, considerations of phylogeny suggest trait-based copying where there is individual-based copying. As humans share with these animals associative learning processes that exhibit generalization in other domains, our beginning hypothesis was that humans will similarly exhibit trait-based mate-choice copying. In contrast, considerations of function suggest that, although individual-based mate-choice copying appears to be good usage of social cues for informing human mate choice, generalizing to others with similar traits—trait-based copying—may be inappropriate usage of social information. Thus, mate-choice copying in humans may have evolved to be specifically individual based. Does such generalization occur when humans copy the mate choices of others? Our results reveal specificity in the circumstances under which it does.

EXPERIMENTS

We tested whether human observers' judgments of appeal or attractiveness of stimulus faces would be affected by perceptions of others' apparent sexual interest, to evince mate-choice copying, and further, whether these observers would generalize this change in assessment to other people expressing shared physical traits, trait-based copying. Videos of people on real speed-dates provided naturalistic mate-choice information (see Place 2010 for additional control experiments). We varied 2 kinds of trait that play a role in natural mating circumstances: facial characteristics and culturally acquired characteristics, clothing, and hair styles. Comparable experiments were conducted with each class of trait with female participants assessing male stimuli and male participants assessing female stimuli.

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Materials

Stimuli for all experiments were taken from the Berlin Speed Dating Study (BSDS) (Asendorpf et al. 2011), an effort that involved systematically running and recording a series of real speed-dating sessions among single daters. All participating daters were individually photographed at the start of the session with neutral expressions and standardized lighting conditions, and then all 3-minute speed-dating interactions were videotaped, start to end. After each interaction, each dater decided whether they wanted to see that person again, indicated discretely on a "score card" returned to the organizers at the end of the event, and in cases where interest was mutual, contact information would be released. Thus, this decision had the real consequence of allowing or disallowing the development of a relationship. The prospect of finding a partner was the sole motivation offered to participants, assuring that they were sincere mate seekers and their decisions were sincere mate choices. This has since received validation: One year after the BSDS sessions, a number of romantic and sexual relationships had developed among the participants (Asendorpf et al. 2011).

Each experiment reported below used forty-eight 20-second, silent video segments of BSDS speed-dating interactions. Each video presentation showed both daters simultaneously. In the experiments, female subjects watched 24 videos, each featuring a different male dater (the "target" stimulus) interacting with a different female dater (the "model"). Each target dater appeared in 1 positive interaction (i.e., where the model dater had subsequently indicated interest in the target) and 1 negative interaction, for a total of 48 videos. Each female subject would see 1 of the 2 videos of each of the 24 male daters, either the positive or the negative interaction, counterbalanced between subjects, for a total of 24 videos. Likewise, male subjects each saw 12 (of 24) videos of target female daters in positive interactions with male model daters and 12 (of 24) in negative interactions. Positive interactions are interpreted as instances of mate choice, and negative interactions, as not.

Frontal facial photographs of BSDS daters were also used, including those appearing in the videos, other BSDS participants that appear in none of the videos shown, and some composites of 2 faces from the same stimulus set. Composites were created using Adobe Photoshop software. This involved replacing some portion of 1 facial photograph with the corresponding portion of another, as expounded below. All photographs were centered frontal images from the crest of the head to the base of the neck, taken on a plain light background. Facial expressions were neutral. All stimuli were presented using DirectRT software on a desktop computer. All stimuli were prepared specifically for this study and were not used elsewhere.

General subject characteristics

Heterosexual students of psychology courses at Indiana University, Bloomington, participated in return for course credit. Subjects were given the opportunity to comment on the experiment in a text box at the end of the session. Roughly 10% of subjects left a comment. Data of 4 subjects were omitted on account of these comments: 2 women who noted that the men appeared too old for them to be interested (from Experiment 2), and in Experiment 1, one subject who had noticed that the images had been manipulated and another who felt "tricked". These were the only 2 indications that people sensed any incongruity in the stimuli. Human subjects were treated in accordance with the standards of the Institutional Review Board for treatment of human subjects in research at Indiana University (Protocol 06-11601).

General design and procedure

All experiments described below follow the same basic within-subjects design, to simultaneously answer 2 questions: Is there individual-based mate-choice copying? Is there trait-based mate-choice copying? Both questions are answered by comparing the change in observers' ratings of stimulus faces, before and after observing a speed-date, as a consequence of the apparent success or failure of the dater in the interaction they observed. If the change in ratings of the target faces shown receiving interest in the video is higher than that of target faces shown in negative interactions, individual-based mate-choice copying is evidenced. If the same holds for the similar-to-target faces, trait-based mate-choice copying is evidenced.

Subjects are first shown a series of opposite-sex facial photographs, one at a time in (simulated) random order. These are from 3 categories: 24 target faces that will be associated directly with mating success information in the videos, faces that are similar to the target faces, and control faces (of other BSDS daters). Subjects are asked to rate each photo on two 9-point Likert-type scales: attractiveness ("How attractive do you find this person?") and appeal as a long-term partner ("How interested would you be in this person for a committed, long-term relationship?"). Next, a series of demographic and personal questions were asked. These questions were placed after the initial ratings in order to lessen interference between initial and ultimate ratings. Subjects were asked to report their age, current relationship status, sexual orientation, ethnicity, and to complete a 9-item scale of self-attractiveness (using 9-point Likert-type responses), comprising the 8-item Self-Perceived Mating Success Scale (Landolt et al. 1995) and an overall rating of their own attractiveness ("How attractive do you think you are?").

After this, subjects were shown a 20-second video clip of the speed-dating interaction for each of 24 pairs of daters. Half of the daters were shown in positive interactions, half in negative, counterbalanced between subjects. On the screen below the video were displayed the facial images of the man and woman in the video (one of which was manipulated in Experiment 1, described below). After viewing the video, female subjects were asked: "Based on the video you just watched, do you think the woman was interested in/attracted to the man?" Male subjects were asked the corresponding question about the man's interest in the woman. Then, the image of the man shown with the video was presented by itself (for female subjects; the woman's image for male subjects), labeled (in blue): "The person you just saw in the previous screen", and subjects were asked to rate it again just as before. Then, one of the control faces was shown, pseudo-randomly selected, labeled (in red): "Not seen in any of the videos shown", and subjects similarly rated it, followed by the 'similar-to target' face, similarly labeled, which subjects also rated. (The labels were included with the photos, along with a similar indication of the photo uniqueness in the instructions for the subjects, to minimize confusion about whom the subjects were rating in each instance.) This procedure was followed for all 24 stimulus videos. The primary difference among the experiments reported here is how similarity is manipulated between the target and similar-to-target faces.

Analyses

In Place et al. (2010), the analyzed variable was the subject's perception of interest between the speed daters, which is dependent on the subjects. Although the perception of interest may be necessary for copying, analyzing our data solely on the basis of subjects' perceptions would make our design quasi-experimental. However, we can also compare observer ratings based on the actual interest that the daters themselves reported, which is varied experimentally. For all of the experiments reported here, we conducted separate analyses treating

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Table 1

Change in ratings (long-term interest and attractiveness) for target faces, similar-to-target faces, and control faces, depending on actual or perceived, positive versus negative interest of model daters, from subjects of both sexes in all experiments

	Perceived interest			Actual interest		
	Negative mean (SD)	Positive mean (SD)	*F* (df)	Negative mean (SD)	Positive mean (SD)	*F* (df)
Experiment 1 (female subjects, *N* = 40)						
Target						
Long term	0.12 (1.27)	0.48 (1.36)	18.04 (1,958)***	0.18 (1.33)	0.41 (1.31)	7.48 (1,958)**
Attractiveness	0.25 (1.37)	0.63 (1.39)	17.76 (1,958)***	0.32 (1.45)	0.55 (1.32)	6.53 (1,958)*
Similar-to-target						
Long term	0.02 (0.80)	−0.05 (0.97)	1.46 (1,958)	0.05 (0.80)	−0.07 (0.96)	4.04 (1,958)
Attractiveness	−0.06 (0.97)	−0.08 (1.00)	0.08 (1,958)	−0.06 (0.94)	−0.09 (1.03)	0.15 (1,958)
Control						
Long term	−0.33 (1.26)	−0.28 (1.22)	0.42 (1,958)	−0.30 (1.27)	−0.30 (1.21)	0.003 (1,958)
Attractiveness	−0.33 (1.27)	−0.34 (1.23)	0.01 (1,958)	−0.34 (1.27)	−0.33 (1.23)	0.01 (1,958)
Experiment 1 (male subjects, *N* = 40)						
Target						
Long term	0.23 (1.44)	0.45 (1.60)	4.88 (1,957)*	0.26 (1.43)	0.45 (1.64)	3.55 (1,957), $P = 0.060$
Attractiveness	0.29 (1.58)	0.54 (1.66)	5.34 (1,958)*	0.34 (1.60)	0.54 (1.66)	3.69 (1,958), $P = 0.055$
Similar-to-target						
Long term	0.09 (1.25)	0.05 (1.16)	0.20 (1,954)	0.03 (1.15)	0.11 (1.24)	1.03 (1,954)
Attractiveness	−0.04 (1.24)	0.01 (1.18)	0.45 (1,958)	−0.06 (1.13)	0.05 (1.28)	2.01 (1,958)
Control						
Long-term	−0.12 (1.42)	−0.07 (1.47)	0.31 (1,958)	−0.13 (1.45)	−0.05 (1.45)	0.83 (1,958)
Attractiveness	−0.21 (1.34)	−0.20 (1.23)	0.006 (1,954)	−0.23 (1.27)	−0.17 (1.28)	0.59 (1,954)
Experiment 2 (female subject, *N* = 40)						
Target						
Long term	0.14 (1.38)	0.46 (1.54)	11.59 (1,958)**	0.19 (1.40)	0.44 (1.54)	7.30 (1,958)**
Attractiveness	0.30 (1.58)	0.68 (1.49)	14.08 (1,958)***	0.36 (1.51)	0.65 (1.57)	8.52 (1,958)**
Similar-to-target						
Long-term	−0.09 (1.25)	−0.08 (1.26)	0.004 (1,958)	−0.10 (1.23)	−0.07 (1.29)	0.19 (1,958)
Attractiveness	−0.17 (1.48)	−0.03 (1.45)	2.27 (1,958)	−0.07 (1.46)	−0.12 (1.47)	0.24 (1,958)
Control						
Long term	−0.08 (1.16)	−0.05 (1.22)	0.13 (1,958)	−0.10 (1.15)	−0.03 (1.23)	0.90 (1,958)
Attractiveness	−0.03 (1.25)	−0.12 (1.31)	1.06 (1,958)	−0.06 (1.28)	−0.10 (1.29)	0.21 (1,958)
Experiment 2 (male subject, *N* = 40)						
Target						
Long term	0.00 (1.57)	0.42 (1.58)	16.84 (1,956)***	0.14 (1.58)	0.36 (1.59)	4.61 (1,956)*
Attractiveness	0.27 (1.62)	0.59 (1.69)	8.43 (1,958)**	0.40 (1.69)	0.53 (1.65)	1.30 (1,958)
Similar-to-target						
Long term	−0.23 (1.53)	−0.01 (1.48)	4.81 (1,958)*	−0.15 (1.48)	−0.05 (1.52)	1.11 (1,958)
Attractiveness	−0.12 (1.57)	0.04 (1.69)	2.35 (1,958)	−0.03 (1.65)	−0.01 (1.65)	0.03 (1,958)
Control						
Long term	−0.09 (1.49)	0.04 (1.37)	1.59 (1,742)	0.00 (1.42)	−0.02 (1.42)	0.07 (1,742)
Attractiveness	0.07 (1.54)	0.04 (1.48)	0.06 (1,742)	0.10 (1.56)	0.00 (1.44)	0.86 (1,742)
Experiment 3 (female subjects, *N* = 40)						
Target						
Long term	0.03 (1.21)	0.33 (1.30)	13.59 (1,958)***	0.08 (1.20)	0.30 (1.32)	7.65 (1,958)**
Attractiveness	0.13 (1.32)	0.44 (1.30)	13.86 (1,958)***	0.15 (1.30)	0.42 (1.33)	10.22 (1,958)**
Similar-to-target						
Long term	−0.17 (1.10)	−0.02 (1.04)	4.60 (1,958)*	−0.11 (1.09)	−0.08 (1.06)	0.20 (1,958)
Attractiveness	−0.19 (1.17)	−0.05 (1.08)	3.69 (1,958), $P = 0.055$	−0.10 (1.15)	−0.13 (1.10)	0.08 (1,958)
Control						
Long term	−0.13 (1.00)	−0.17 (1.06)	0.49 (1,958)	−0.17 (1.06)	−0.14 (1.00)	0.19 (1,958)
Attractiveness	−0.17 (0.96)	−0.17 (1.00)	0.004 (1,958)	−0.18 (1.00)	−0.16 (0.96)	0.04 (1,958)

Mate-choice copying is evidenced where the change in ratings is higher following positive interactions than negative interactions. Significant increases are indicated by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

one or the other of these variables as independent: the perceived interest in order to replicate Place et al. (2010) and the actual interest to bolster that analysis with an experimental design (reported in Table 1).

Mixed-linear modeling was used for all analyses reported, with measures of multiple stimuli as fixed effect and subjects as random effect. Each dependent datum in these tests is the difference between initial and ultimate ratings of a stimulus face. We

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Figure 1
Depiction of the design of Experiment 1 with an example of stimuli presented to female subjects. The 3 faces along the bottom are, left to right, the target face, a control face, and the similar-to-target face, as described in the text.

test whether these differences are more positive following our manipulation, the presentation of positive social information, relative to the analogous presentation of negative social information. Male and female samples are tested separately.

EXPERIMENT 1: GENERALIZATION OF COPYING TO THE FACIALLY SIMILAR

As our question was whether the mate-choice copying effect would generalize to similar others, we needed to show our subjects one person's mating success and test them on a different but similar looking person. But what constitutes similar looking? When one says that 2 people appear similar to each other, this is often referring to their facial characteristics: nose, eyes, mouth, and the space between, the way these features are configured with respect to each other. Thus, we began with manipulations of facial similarity.

Methods

A sample of 40 women (18–22 years, mean age: 19.8, SD: 1.0) and a sample of 40 men (18–23 years, mean: 19.5, SD: 1.1) were each subjected to a sex-specific version of Experiment 1. After rating the initial set of opposite-sex faces and completing the questionnaire, as described above, subjects were presented with the following sequence of stimuli for each of the 24 stimulus dating interactions. They were first shown a 20-second video of a man and woman on a speed date and then asked to rate the same-sex (model) dater's interest in the opposite-sex (target) dater. Subjects then rated 3 opposite-sex faces, presented sequentially: 1) the target dater, 2) a random selection from among the control faces, who appeared in none of the videos, and 3) the similar-to-target face.

The target and similar-to-target faces were manipulated to resemble each other by placing the 'inner face'—forehead to chin; cheek to cheek—of the similar-to-target face onto the photograph of the dater shown in the video. Manipulating the target face to resemble the similar-to-target face, rather than the converse, afforded 2 important advantages. The primary motive was to allow us to imbue multiple daters with the same inner facial characters. Thus, a set of facial characters could be associated with multiple instances of dating success, and this could be compared with corresponding characters associated with multiple instances of dating failure. One association of a face with success or failure may not be enough, so our design, which associates each set of facial

Figure 2
An example of the facial similarity manipulation in Experiment 1. The dater's face (panel 1; not shown to subjects in Experiment 1) is modified to create the "target" face (panel 2) by superimposing onto it the inner-face oval region (panel 3) taken from the "similar-to-target" face (panel 4).

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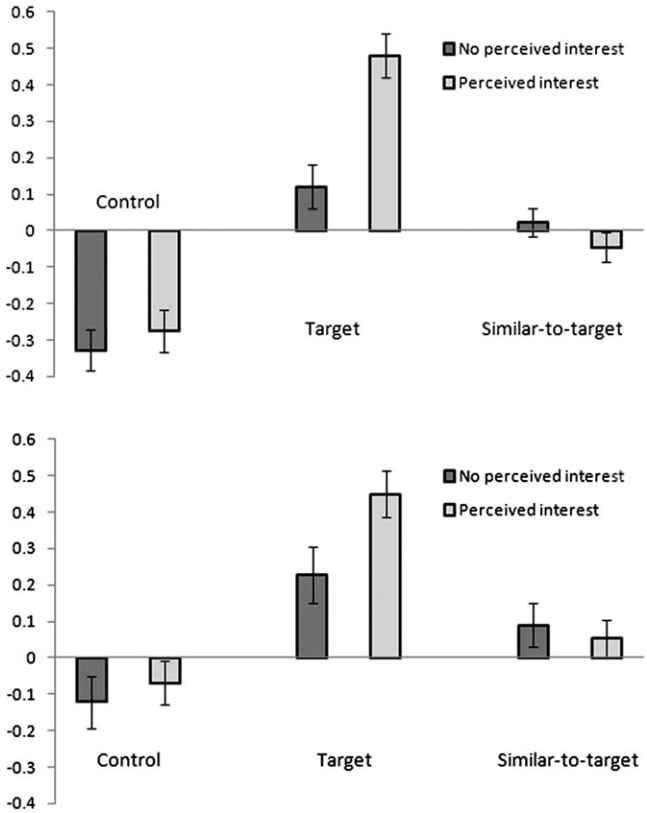

Figure 3
Results from Experiment 1 for female subjects (upper panel) and male subjects (lower panel). Bars show average (±1 SEM) change in rating of the 3 classes of stimuli ("target", "similar-to-target", or "control") in terms of appeal as a potential long-term partner, separately for whether the subject had perceived the interaction as positive (light bars) or negative (dark bars). Mate-choice copying is evidenced where the change in ratings is higher when interest is perceived—here, for target stimuli only.

characters with 4 dating successes or 4 dating failures (see next paragraph), is a more sensitive test of the hypothesis that people generalize the mate-choice copying effect to facially similar others. Second, it meant that each similar-to-target face, which was our primary interest, was an unaltered face of a real person.

The 24 speed-dating interactions used were divided into 6 groups of 4. All 4 targets in 3 of these 6 groups (i.e. 12 target faces) were always shown in positive interactions for a given subject (counterbalanced); the 4 target faces of the other 3 groups were always in negative interactions. All 4 target daters in each group were associated with the same similar-to-target face. Thus, each similar-to-target face was similar to targets in either 4 positive or 4 negative dating interactions.

Experiment 1 was designed to be a sensitive test of the hypothesis that, if subjects assess daters higher when seen in positive interactions, they will likewise increase their assessments of faces with qualities similar to the successful daters. First, our manipulation of similarity was extreme, the target and similar-to-target faces having identical eyes, nose, mouth, and configuration. Second, each similar-to-target face is given multiple doses of concordant social information. Both these qualities should increase the likelihood of a trait-based copying effect appearing if one exists.

As a manipulation check, we verified that attractiveness ratings of composite images used were concordant with ratings of the original images from which they were created. This shows that subjects attended to the facial characteristics of the stimuli presented.

Results

For both sexes, the faces associated directly with mating success information showed individual-based mate-choice copying, replicating Place et al. (2010)—see Table 1 for all statistics. That is, for both male and female observers, ratings of the 12 target faces shown in positive speed-dating interactions (i.e. videos in which the same-sex target dater was perceived as showing interest in the opposite-sex stimulus) increased more than did ratings of the 12 shown in negative interactions. This was true for both dependent measures, ratings of long-term romantic interest and attractiveness. Similar results were obtained when analyzed in terms of the model daters' actual, reported interest (as opposed to the subject's perception of this interest).

The question of primary interest was whether subjects would generalize their increased ratings to similar others, evidencing trait-based mate-choice copying. Despite identical facial features, neither sex showed systematic increases in assessment of the similar-to-target faces, neither for the subjects' perceptions of daters' interest, nor for the daters' actual stated interest.

Notice that ratings of target stimuli shown with the videos, even those shown with negative interactions, tend to increase between the first and last phases of the experiment, whereas the ratings for the control faces, which appear in no videos, tend to decrease (equally after both positive and negative interactions), despite no negative (nor positive) social information. The increase in the target ratings appears to be due to exposure to the behaving person in the video; negative change may occur for stimuli that appear only in a single, repeated photograph. The appropriate comparison when assessing mate-choice copying, thus, is between positive and negative interactions of a given stimulus type, not how either of these relate to the zero line, which cannot be interpreted as no effect. The control faces, therefore, are an important inclusion, putting into perspective the changes of ratings of the similar-to-target faces, which also do not appear in the videos.

EXPERIMENT 2: GENERALIZATION OF COPYING TO THE SIMILARLY STYLED

Facial similarity is not the only way people can resemble each other. People vary in manner of dress and in their hair styles and these qualities appear to be important to mate choice in humans. Such manners of similarity, however, differ from facial similarity in 4 important respects. First, while not wanting to imply a strong dichotomy, the primary mode of transmission through populations is different: Facial qualities are inherited vertically, parent to child; qualities of style can spread horizontally, within generational cohorts. Second, such conventional aspects are much more mutable. On a whim, one can dress like Lena Lovich or Lady Gaga or whoever is the season's pop sensation. Therefore, third, such qualities can potentially spread through populations much more rapidly. This may have implications for the ability of evolutionary change to keep pace with changing pressures. Fourth, although facial qualities indicate a specific individual uniquely, clothing and hair styles do not. People may notice that the enthusiastic fan is sporting the style of her idol, but no one would confuse her for the star on account of it. Her hemline may be advertising membership in a current cultural group but not genetic similarity or kin membership. Hence, styles of dress and hair warrant separate consideration from facial characteristics on the matter of generalization of social information.

In the head and shoulders stimulus photographs used in our experiments, there are thus 2 separable realms of traits we can consider: 1) the inner face, forehead to chin, cheek to cheek, and 2) the rest of the photograph, which includes the hair, clothes, and neck. Experiment 1 showed that subjects, while mate-choice copying, did not generalize this effect to other

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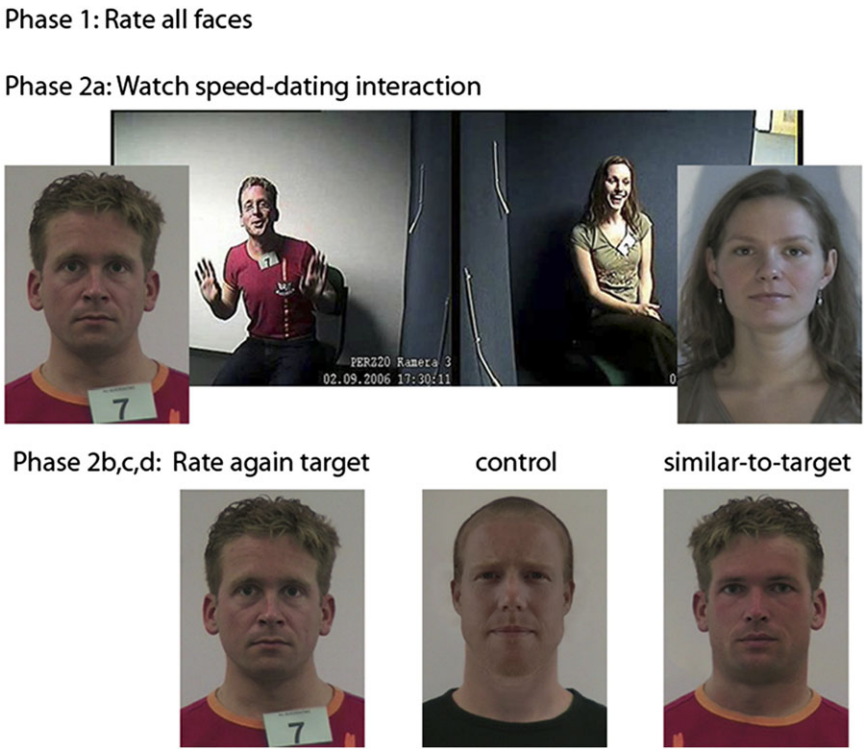

Figure 4
Depiction of the design of Experiment 2 with an example of stimuli seen by female subjects.

people with common inner facial cues. Would our subjects show trait-based copying with nonfacial cues?

Methods

A sample of 40 women (18–23 years, mean age: 19.6, SD: 1.4) and a sample of 40 men (18–25 years, mean: 20.1, SD 1.5) were each subjected to a sex-specific version of Experiment 2. A similar design to Experiment 1 was used, with the key difference being that similar-to-target faces now had no cues taken from the target's inner face but were manipulated to share all cues external to this region. The hair and clothes of each similar-to-target face were the mirror image of the target dater's face. Unlike in Experiment 1, it was not possible to show an altered target stimulus because we needed the clothes/hair in the target photo to match that shown in the video. For this reason, the target photo shown with the video was the unaltered face of the dater in the video, and there was a unique similar-to-target face created for each of the 24 daters. Thus, each similar-to-target face was associated with only one dater's success or failure, making these experiments less sensitive than Experiment 1. An additional set of 6 faces was presented at the beginning of the experiment, with the express function to ground the scale, to start everyone calibrating to the same few faces, and these are not seen again.

Results

Again, as shown in Figure 5 (see Table 1 for statistics), both sexes showed individual-based copying, replicating Place et al. (2010). In both experiments, the change in ratings for faces shown in speed-dating interactions perceived to be positive were higher than for those perceived to be in negative interactions. No differences appeared among the control faces. Similar results were obtained with analogous tests when analyzed in terms of the daters' actual interest.

Unlike in Experiment 1, however, here, there was evidence of trait-based copying as well. Male subjects increased their relationship interest ratings, not only of the faces of successful individuals, but also of the similar-to-target faces associated with successful daters compared with those associated with unsuccessful daters. These effects were significant ($P = 0.029$) for long-term interest and in the predicted direction ($P = 0.126$) for attractiveness ratings (see Table 1). The analogous test for the female subjects, however, did not show a significant difference, obliging further investigation.

EXPERIMENT 3: TESTING FOR AGE EFFECTS AMONG FEMALES

In Experiment 2, evidence of trait-based copying appeared among male subjects but not females. Such a sex difference had not been predicted. Post hoc analyses suggested female subjects' age to be a mediating factor. The 16 female subjects above the median age of our sample (19 years) did not show the predicted difference among ratings of the similar-to-target photos following positive interactions versus negative. Indeed, for both dependent variables, mean change in ratings for these subjects was slightly higher for the negative interactions than positive. However, results from the 24 younger subjects were suggestive of trait-based copying. The change of ratings among these younger subjects was higher for the similar-to-target stimuli following positive interactions than negative [long-term interest: mean (SD) = −0.11 (1.32) versus −0.21 (1.15), respectively], and for attractiveness, the difference would have been significant [0.03 (1.42) versus −0.22 (1.26), $P < 0.05$], had our hypothesis been age-specific. The younger and older females differed substantially from each other on these measures (for attractiveness ratings, $P < 0.05$).

Age is an especially relevant factor to consider in the context of copying. This is because copying is potentially useful as a way for younger individuals to learn socially from more experienced individuals who themselves have the benefit of

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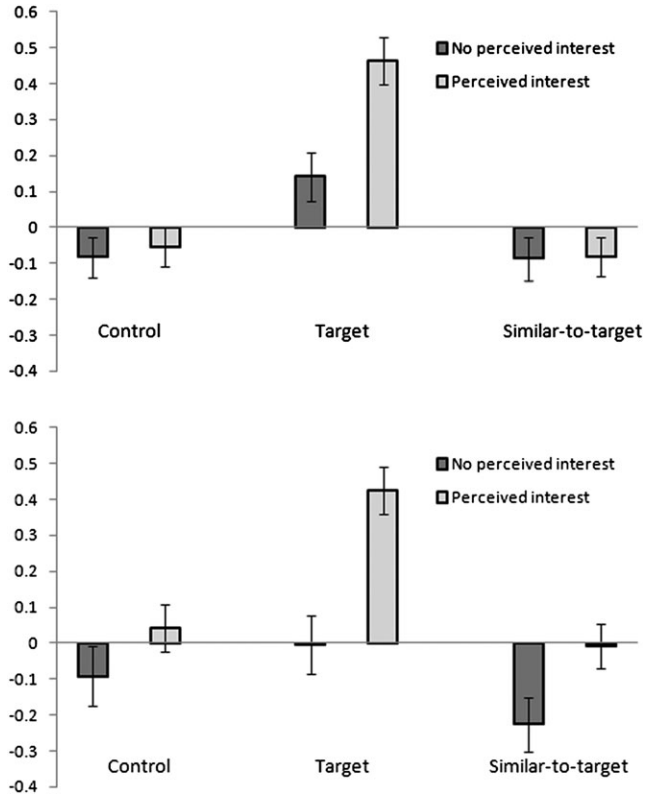

Figure 5
Results from Experiment 2 for female subjects (upper panel) and male subjects (lower panel). Bars show average (±1 SEM) change in rating of the 3 classes of stimuli ("target", "similar-to-target", or "control") in terms of appeal as a potential long-term partner, separately for whether the subject had perceived the interaction as positive (light bars) or negative (dark bars). Mate-choice copying is evidenced where the change in ratings is higher when interest is perceived—here, for target stimuli and for similar-to-target faces for male subjects.

hindsight, having learned through a combination of experience and social learning (Pomiankowski 1990). Some decisions improve with experience and so with age. In such cases, younger individuals are expected to discriminately copy older, whereas the converse is not necessarily good policy and potentially misleading (Dugatkin and Godin 1993; Ophir and Galef 2004; Amlacher and Dugatkin 2005; Vukomanovic and Rodd 2007). Thus, age-specificity is predicted of social copying in general and potentially of mate-choice copying in particular. The prediction that age or experience affect mate-choice copying has been investigated in other species: Experience appears not to affect mate-choice copying in Coturnix quail (Ophir and Galef 2004). Female guppies appear to discriminately copy older females (Dugatkin and Godin 1993; Amlacher and Dugatkin 2005; Vukomanovic and Rodd 2007). Though previous studies of mate-choice copying in humans have not reported age-specific effects, Waynforth (2007) found an analogous association with experience: Less sexually experienced females showed clearer evidence of individual-based copying. However, trait-based copying may behave differently. As it is a way of learning about kinds of mates rather than the quality of an individual mate as with individual-based copying, it is a solution to a different sort of problem. Mate seekers of any age may benefit from social information about particular mates, but perhaps not from copying general preferences from their younger rivals.

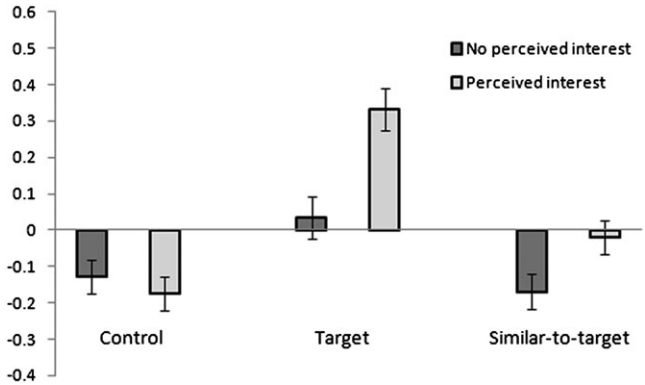

Figure 6
Results from female subjects in Experiment 3. Bars show average (±1 SEM) change in rating of the 3 classes of stimuli ("target", "similar-to-target", or "control") in terms of appeal as a potential long-term partner, separately for whether the subject had perceived the interaction as positive (light bars) or negative (dark bars). Mate-choice copying is evidenced where the change in ratings is higher when interest is perceived—here, for target stimuli and for similar-to-target faces.

Thus, Experiment 3 was conducted to test the hypothesis that human females on the cusp of adulthood will show trait-based copying, with the only difference from Experiment 2 being the age of participants.

Methods

Forty female participants, aged 18–19 years (mean: 18.6, SD: 0.5), were recruited as in the above experiments. The upper age criterion was set at the median of Experiment 2′s sample; the lower age criterion was enforced by our restriction to use of adult participants. The design and stimuli were the same as in Experiment 2.

Results

As in all the above experiments, individual-based copying was observed, whereas control faces showed no differences, and analogous results were obtained whether perceived or actual interest was used to define positive and negative cases (Table 1). Furthermore, ratings of similar-to-target faces were also higher after viewing target males in positive interactions than in negative, for long-term interest ($P = 0.032$) and showing a suggestive analogous trend for attractiveness ratings ($P = 0.055$), evidencing trait-based copying in young females.

The younger subjects here differed not only in absolute age compared with previous subjects, but also in age relative to the models observed in the videos. Is it that trait-based copying fades with copier's age, or that it is specific to copying models older than oneself? As the speed-dating models were, on average, substantially older (18–29 years; mean 24.9; SD 2.7) than the subject samples of both Experiment 2 (18–23 years) and Experiment 3 (18–19 years), the difference in trait-based copying between the samples is difficult to attribute to differences in the relative age between samples and models. Thus, the age-specificity observed appears not to be about the models' age, but the observers'.

The age-specificity observed in trait-based copying of the culturally acquired traits for females was not seen among male subjects. However, all subject samples were from a similarly narrow range of ages (18–25 years). Though a similar range of ages was apparently sufficient to show age differences among females, an analogous change may develop in males at a later

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age. Thus, males may also have shown a developmental course in trait-based copying if a broader range of ages were considered. These facts oblige us to be tentative about drawing conclusions regarding the ontogenetic course of trait-based copying, whether the age-dependence is specific to females or whether it matures at different ages in males and females.

Though these results do not directly show that the teen females differ from their slightly older peers, they do show trait-based copying among the younger females. In the context of Experiment 2, in which the same age range showed very similar results, whereas our older subjects showed no indication of trait-based copying at all, we tentatively conclude that trait-based copying is specific to the youngest adult females. Further research specifically on the age course of this effect is necessary for the drawing of stronger conclusions.

DISCUSSION

Each of the above experiments replicates earlier findings (Place et al. 2010) that one's assessment of another's appeal is heightened upon acquiring social information indicating that person as a successful mate. This is individual-based mate-choice copying. Seeing someone succeed in winning some sexual interest of a potential mate makes that person more attractive to observing third parties. But when we acquire such information, have we learned something exclusively about the observed individual or something more general, applicable also to other potential mates with shared characteristics? The present results suggest that this kind of generalization—trait-based mate-choice copying—occurs in humans but that it is specific to culturally malleable cues, conspicuously not facial traits. We discuss possible explanations for these findings in terms of informational benefits and cue salience.

Though clothing, body decorations, and ways of keeping one's hair are tangible traits important to human mate choice, such traits are inherited primarily culturally (Meskó and Bereczkei 2004; Wohlrab et al. 2007—though not wholly, e.g. hair styles depend in part on the natural color and texture of the hair). For such traits, the evolution of non-social recognition mechanisms is unlikely, so our rationale for not expecting trait-based copying may not apply with respect to such traits. Yet, the informational benefits may still accrue, so long as the cultural trappings of successful mates are indicative of mate quality in others, which may be true. Thus, trait-based copying may be appropriate with respect to culturally acquired characteristics, while not to immediately observable and highly heritable traits, such as facial characteristics. Shared cultural tastes may indicate commonalities relevant to mate quality that shared physiognomy does not. Hence, trait-based copying in humans appears specific to categories of cues in a manner that matches the availability of useful social information for mate choice.

Experiment 1 was the last of a series of experiments (not reported here) designed to get at the same question, all with the same basic design described above but with varying levels of facial similarity of the similar-to-target faces. Our first attempt relied on 'morphing' software, which allows the creation of the average of 2 photographs. Thus, our similarity manipulation in that case was to create and show the midpoint between the target person seen in the video interaction and some other face, and this functioned as our similar-to-target face for each target. Subjectively, this succeeded in producing a face that was similar to the person seen in the video. In other experiments, the similar-to-target face was created by giving a novel face the eyes, or nose and mouth, of the target. In all cases, the results were the same: Individual-based copying was observed, but there appeared to be no generalization to similar faces. In each of these earlier experiments, one could question whether our similar faces were really similar enough, or similar in the right ways, to elicit the effect, hence our multiple attempts. Experiment 1, however, dealt with that concern by making the manipulated facial traits of the similar-to-target the very same as the target's. Taken together, these experiments provide compelling evidence that humans do not readily show trait-based mate-choice copying based on natural inner facial cues.

Our claim is specific to what we manipulated. We note that facial and hair/clothing qualities differ in the manner in which they are inherited and that this may account for the conspicuous observed dissociation between trait-based copying on the basis of these 2 kinds of traits. However, our results do not permit us to draw general conclusions regarding other culturally or genetically inherited traits (e.g. nose rings or skin tones), facial features external to those we varied, such as the jawline (implicated as a mate-choice criterion—Cunningham et al. 1990) or more extreme manipulations of specific features, beyond the natural variation of a racially and culturally homogeneous population with which we are concerned here. To determine whether or how such traits may generalize when copying would oblige further experiments. Already Little et al. (2011) have shown that manipulations mimicking between-population variation can produce analogous effects. They created sets of exaggerated images of faces of 2 artificial morphs (inner faces with very widely-spaced eyes versus very narrowly-spaced) and paired each set with images of attractive or unattractive opposite-sex (inner) faces. Subjects showed generalized changes in preference for similarly altered novel inner faces. However, the systematic manipulation, exaggerated stimuli, and dichotomous distribution of traits are methodological contrivances that may enhance generalization, leaving in question how Little et al. (2011) results pertain to natural, human, within-population mating. Though it is perhaps not surprising that particular manipulations can produce generalization, this makes an interesting comparison with our findings. Between populations, particularly between races, facial traits might fall in distinguishable clusters, as in Little et al. (2011), whereas within-populations, which is our focus, variation will be largely continuous. These very different distributions of facial traits may strongly impact patterns of social information use. Testing the boundaries of trait-based copying in theoretically meaningful ways is one useful direction for future research. For the current study, however, we have limited ourselves to real inner and outer faces from an actual population of daters to assure relevance to natural human mate choice. We conclude that trait-based mate-choice copying for inner facial qualities is conspicuously absent given the naturally occurring variation in a homogeneous human population, while demonstrably present for hair and clothing cues given the same degree of variation.

It remains a viable possibility that our results can be understood in terms of attentional biases in a manner that converges with findings from face recognition research. Whereas inner facial traits are more heavily relied upon for the recognition of familiar faces, for unfamiliar faces people rely equally (Ellis et al. 1979) or preferentially (Haig 1986; Bruce et al. 1999) on head shape and hair. Though not a question our study was designed to address, our results are consistent with the possibility that trait-based copying relies on such attentional biases, and the dissociation observed between generalizing with respect to inner facial cues and cues external to this region may be meaningfully linked to how humans attend to unfamiliar faces. Agreement of attractiveness ratings shows that our subjects attended to inner-facial characteristics but does not convey the relative salience of these to other cues. This view leads to the prediction that manipulations of attention will influence the occurrence of trait-based copying. Attention can be varied experimentally in many ways, such as with timing, movement, boldness of cues (e.g. Little et al.

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2011), as well as aspects of the circumstance or observer that have been associated specifically with differences in how people attend to faces [e.g. familiarity (Ellis et al. 1979) or image resolution (Jarudi and Sinha 2005)], including aspects of relevance to mate choice. Perhaps, the sex and age differences we found, for instance, can be understood in such terms. It is not obvious that the same cues will be similarly salient in face recognition and mate choice. In reviewing what cues people find salient in faces, Shepherd et al. (1981) concludes that "different parts of the face are attended to according to the task" (p. 131). It will be important to ask what causes different cues to be salient in different situations, and whether and why the cues that are salient for individual recognition may also be salient for mate choice. Exploring how the mechanisms underlying generalization of social information usage may interact with biases involved in the recognition of faces is an interesting avenue for future research.

In all 5 previous studies assessing trait-based copying empirically, each with a different species, such copying was observed, but in none of these studies was the effect seen to be specific to certain categories of cues. In quail, trait-based copying occurred with both naturally occurring cues (white feathers on the crown) and arbitrary cues (colored dot on the chest) (White and Galef 2000a). In zebra finch, it was an artificial red crest adornment (Kniel et al. 2011) or colored leg bands (Swaddle et al. 2005), which were reported to be neutral with respect to mate preferences (though the particular colors used in Swaddle et al. 2005, white and orange, are the very colors of the sexual dimorphisms in zebra finch, which may have had an influence on the results obtained). Female fruit flies generalized to painted males (Mery et al. 2009), which appears to be a wholly arbitrarily imposed trait. Mollies (Witte and Noltemeier 2002) and guppies (Godin et al. 2005) showed trait-based copying with respect to size and extent of body coloring, respectively, traits that are important mate-choice criteria in these species.

Individual-based and trait-based mate-choice copying appears to provide solutions to 2 separate kinds of problem. The benefit of the individual-based effect appears specific to the individual, and it remains good usage of information whatever the mate seeker's age or experience level. Though it can be argued that less experienced mate seekers get an extra benefit with copying (Waynforth 2007), we find individual-based copying independent of the ages we tested (see also Place 2010, for the same result across a wider age range). As trait-based copying does appear to depend on age, with only the youngest women generalizing copying to the similarly styled, and shows specificity to particular kinds of cues, it appears to be a separable effect, with a separate function. The information value in trait-based copying in humans appears to be in young mate seekers learning more generally about the culturally acquired qualities of successful mates from the choices of rivals.

If indiscriminate, social learning can pull the learner into maladaptive 'informational cascades' (Bikhchandani et al. 1992), in which the modal spreads, for better or for worse. As misinformation can spread socially as readily as veridical information, social learning must be selective to be useful (Laland 2004). Trait-based mate-choice copying in humans shows selectivity of cue use as well as observer specificity ("copy when young") in ways that make functional sense. The limited cases in which generalization is found across our studies is an interesting and surprising outcome, suggestive of selective pressures at work rather than a broadly applied general learning mechanism.

General versus specific mechanism

Is mate-choice copying in humans the workings of a general or specific mechanism? If copying in humans abides the functional prescription to limit trait-based copying, despite the phylogenetic inertia for generalization, a specific, ad hoc mechanism is suggested. This prediction appears to be supported by our results: Though mate-choice copying appears in both sexes, the patterns with which it generalizes to similar others varies by cue and age, in ways consistent with functional considerations.

These results put pressure on claims that mate-choice copying is an associative process involving association with the model. Witte and Godin (2010) recently concluded that "considerable empirical evidence supports the general view that mate-choice copying best corresponds to an associative learning mechanism, wherein a focal (observer) female associates a cue from the model female with the accepted or rejected male involved" (p. 193). Whether this is the general view is debatable. There is compelling evidence against a general association account of mate-choice copying among some species. For instance, Coturnix quail show striking and ecologically understandable sex differences in the ways in which they are affected by mate-choice information, in both direction (Galef and White 1998; White and Galef 1999) and duration (White and Galef 2000b). We present evidence that mate-choice copying in humans specifically behaves unlike the proposed 'model cue to target' association would predict, failing to generalize in a cue-specific, age-specific manner. This is not to deny that associative learning processes may have some involvement. It is not obvious whether the lack of generalization to the facial characteristics we manipulated indicates an adapted repression of a general tendency for trait-based copying, or whether the generalization of learning seen toward people with similar hair and clothing is itself a specific adaptation. However, the absence of generalization to certain cues bolsters the view that the learning involved in mate-choice copying relies on specific processes that are not well described in terms of association with the model.

It is intriguing that culturally transmitted traits, and not facial characteristics, turned out to be subject to trait-based mate-choice copying, meaning that the attraction to them is likewise subject to "cultural inheritance" (Brooks 1998). The form of learning mirrored the thing learned about: Our subjects learned generalizations about culturally acquired characteristics, and individually about qualities that are specific to individuals.

Sexual selection

The question of trait-based mate-choice copying first emerged in the context of sexual selection (Brooks 1998). It was realized early that mate-choice copying would impact sexual selection (Wade and Pruett-Jones 1990; Dugatkin 1992; Gibson and Höglund 1992), as had been acknowledged for other forms of social learning (e.g. sexual imprinting: ten Cate and Bateson 1988). Mate-choice copying leads to a further favoring of the favored, which will influence sexual selection. However, there are many factors that may determine the form of this influence, notably whether copying is trait-based or exclusively individual based.

Trait-based copying favors not only the favored but also the traits of the favored. It creates preference for the traits of successful individuals and so will focus selection on those traits specifically. This may have 2 conflicting effects on sexual selection. As it concentrates selection specifically on traits associated with reproductive success, it may exacerbate skews in reproductive variance associated with heritable traits. As a consequence, directional sexual selection will receive a distinct boost (Brooks 1998; White and Galef 2000a). However, in a large enough mating pool, because copiers will more often witness modal phenotypes succeeding than rarer phenotypes, trait-based copying may also focus selection differentially on prevalent characters and so have a conservative, stabilizing influence on sexual selection (Kirkpatrick and Dugatkin

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1994). The relative weight of these conflicting selection pressures will depend, potentially very strongly, on the sort of trait generalized. The former, directional influence assumes that the traits showing such generalization are heritable, for example facial traits; the latter, stabilizing influence will operate similarly upon either sort of trait.

What can we now say about how we expect copying to be impacting human evolution? To understand the systematic impact that individual-based copying may have on sexual selection, we would need to be able to quantify how closely mate-choice decisions correlate with heritable characteristics. However, for trait-based copying, the connection is now somewhat clearer. If, as our results suggest for humans, mate-choice copying generalizes particularly readily to hair and clothing styles, which are primarily culturally acquired traits, then the influence of copying on sexual selection will most likely be stabilizing, favoring selection of modal characters. The study of trait-based copying in other animals has not considered the copying of preferences for traits that are themselves culturally transmitted.

CONCLUSION

Mate-choice copying in humans has now been reproduced in several laboratories, using as many variants of method. Here, we have provided evidence not only for individual-based copying but for trait-based copying as well, showing that this is specific to certain types of traits and that the use of trait-based copying changes in early adulthood. This behavior has apparent functional significance and understandable impact on sexual selection. Though mate-choice copying has most often been approached as a specific learning mechanism, there have been proposals that the available evidence suggests reliance on general associative learning mechanisms. Our finding of cue-specific generalization in human mate-choice copying, particularly the resistance to generalize with respect to facial cues, puts pressure on such claims. However, the tentative nature of some of our findings, particularly with regard to the possible developmental course of different forms of mate-choice copying, calls for further studies with larger and broader populations (including other age ranges and cultures), in the laboratory and in the field, additional testing of the generality of the observed effects, and isolation of possible causal factors and the mechanisms through which they act. As we refine our specific knowledge of these patterns of behavior, considerations of phylogeny, function, mechanism (Huxley 1942), development (Tinbergen 1963), and subjectivity (Burghardt 1997) coalesce in a fuller understanding of the animal, evolution, and cognition.

To Kundera's (1978) revelation that, when assessing men, women utilize information about the mate choices of other women, we add that humans of both sexes appear to generalize their use of these social cues to inform their assessments of the similarly styled, but conspicuously show no hint of such generalization to the facially similar.

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