

Original Article

Attracting Interest: Dynamic Displays of Proceptivity Increase the Attractiveness of Men and Women

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Abstract: Proceptive signals may influence judgments of opposite-sex attractiveness because these signals indicate high mate quality and/or non-threatening behavior but they may also signal high probable rate of return for mating effort. If so, individuals observing these signals may be sensitive to where the signals are directed to; signals directed toward other individuals may not predict what signals would be directed toward the observer. To explore these possibilities I made use of video stimuli composed of mock interviews with actors. Each actor did one proceptive and one unreceptive interview. Each interview was presented as being directed toward participants or toward an opposite sex interviewer. Proceptivity enhanced the attractiveness of opposite-sex actors and an interaction between proceptive state and signal direction was found, with this pattern varying substantially between actors. The possibility that this variation is mediated by the physical attractiveness and sex of the actors will be discussed.

Keywords: Attractiveness, proceptivity, mating effort, mate choice

Introduction

Mate competition complicates mate choice because there is no assurance that one will secure a mating with one's first choice. In effect, mate choice is a form of mating effort allocation (i.e. toward whom should one devote it?). Sexual attraction may function to facilitate adaptive allocations of mating effort.

Accordingly, it is not surprising that physical/structural features in humans signaling fecundity, health, "good genes" and genetic compatibility provoke sexual attraction among the opposite sex (e.g., Singh, 1993; Fink and Penton-Voak, 2002; Gangestad and Scheyd, 2005; DeBruine, 2004; Jones et al., 2004). However, behavior also has informational value for potential mates. For instance, people's dancing ability is associated with body symmetry, a measure of developmental stability and hence disease resistance (Brown et al., 2005). It is likely that such dynamic signals provide a wide range

of information about potential benefits, both direct and indirect. Dynamic stimuli may be both more information-laden and more ecologically valid than the static stimuli used in the vast majority of facial attractiveness research; dynamic stimuli incorporate behavioral and structural signals of mate value and more closely approximate the encounters with potential mates that ancestral humans experienced. Furthermore, although it would be reasonable to expect attractiveness ratings of static and dynamic presentations of faces to be correlated, these correlations may not even reach statistical significance (Rubenstein, 2005). However, despite their likely importance, dynamic behavioral signals have generally received less attention from researchers, and proceptivity offers one such example.

Proceptive behavior is produced by the signaler to initiate or encourage further sexual interaction with the intended receiver (Beach, 1976; Givens, 1978). Unreceptivity is the polar opposite; behavior produced to discourage further interaction. Beach (1976) coined proceptivity to describe solicitation behavior of female mammals during estrus, such as presenting genitalia to males, well documented in rats (Madlafousek and Hlinak, 1977) and various primates (e.g., Thompson-Handler et al., 1984; Chambers and Phoenix, 1987; Hausfater and Takacs, 1987; Fedigan, 1992). However, the term could also encompass behaviors produced by males, such as the nuptial bow of lekking Lesser Prairie Chickens (Johnsgard, 1994), or by both sexes, such as the complex courtship displays that take place between Wandering Albatross mates (Jouventin and Lequette, 1990). Presenting may sometimes be part of a human female's proceptive repertoire, but more subtle signals have also been identified, such as sustained smiling and direct eye contact, and these are commonly used by both sexes (Givens, 1978; Eibl-Eibesfeldt, 1989).

Although there has been work addressing proceptive behavior in humans (e.g., Givens, 1978; Perper and Weis, 1987; Moore, 1985, 1995; Simpson, Gangestad and Biek, 1993; Grammer et al., 1999, 2000), proceptivity's role in mediating perceptions of attractiveness has been neglected, possibly because this role has been taken for granted. Proceptive signals are designed to attract sexual attention from receivers by definition after all, but this effect is not obligatory; male rhesus monkeys are unresponsive to female sexual advances outside of the breeding season, for instance (Zehr et al., 1998). If proceptive signals are designed to manipulate receiver's perceptions of the signaler, it may not be in the receiver's best interests to attend to them because the goals of the signaler do not necessarily coincide with those of the audience. It is not clear how people respond to proceptive signals, nor is it clear how these responses would function to facilitate adaptive allocation of mating effort. Neither question has been satisfactorily addressed or answered.

Hill's (1988) review of how women's sexual behavior varies with menstrual phase concludes that both proceptivity and attractivity need to be further explored, but makes no causal connection between them. Schmitt and Buss's (1996) participants predicted that displaying cues of sexual availability would be an effective self-promotion tactic, but more so for women than men. Similarly, Schmitt et al. (2001) found that interviewed women who gave a response suggestive of easy sexual access were rated as more desirable short-term mates than women whose response was suggestive of relationship exclusivity. Both of these studies suggest that proceptive behavior may enhance judgments of attractiveness but neither does so directly and neither relies on actual observations of proceptive behavior.

One reason to expect proceptive signals to influence attractiveness is that they may serve as good indicators of mate value. Skilled social behavior is difficult to produce and may therefore be an honest signal of quality (Miller, 2000). For instance, humour

production is a common feature of proceptive behavior and has been found to positively influence women's judgments of men's attractiveness (Bressler et al., 2006). Interestingly, men appear to value humour appreciation - also associated with proceptivity - but not humour production in prospective mates (Bressler and Balshine, 2006). Producing proceptive behavior competently may therefore be an honest signal of quality. It may also display social confidence, which in turn may usefully predict social status, and vigour. Women may obtain additional information from proceptive signals; proceptive behavior is often described as playful and childish (Givens, 1978; Eibl-Eibesfeldt, 1989) and may signal low physical threat. At the very least it exhibits that the signaler is willing to invest effort in courtship rather than simple coercion. Campbell (1999) argued that women should weigh physical threats more heavily than men because the consequences of personal physical injury for offspring survival are greater for women. Human sexual size dimorphism also predicts that a woman in an opposite-sex dyad will usually pose less of a threat than the man. Therefore, women in particular may value proceptivity if it communicates a low risk of physical injury.

Another reason to expect that proceptivity will influence perceptions of attractiveness is its direct relevance to mating effort expenditure. For humans, as for other animals, mating effort is costly in time, energy and resources. Bi-parental care is common in humans and both sexes are therefore expected to exhibit some degree of competition and mate choice (Johnstone et al., 1996), and the costs associated with mating effort are not likely to be negligible for either sex. This suggests that individuals should be attracted to others who exhibit signals that indicate a high probable rate of return for costly mating effort (i.e. sexual readiness/availability and interest). This is somewhat similar to Schmitt and Buss's (1996) argument that men will prefer women displaying signals of sexual availability to maximize partner quantity, although the emphasis here is on saving mating effort and is not limited to a short-term mating context as per Schmitt and Buss (1996).

Proceptive behavior may be relevant to mate choice for multiple reasons that are not mutually exclusive, and they all predict a positive response (i.e. an increase in attractiveness associated with proceptivity). Differentiating the psychological mechanisms that underlie these responses is therefore problematic, but may be partially realized by manipulating the direction of proceptive or unreceptive signals. Proceptive signals do not necessarily indicate high return for mating effort for an observer unless those signals are directed at him/her and consequently may be disregarded when they are not. Conversely, if receivers respond positively to proceptivity solely because it signals high mate quality and/or low physical threat then the intended direction of proceptive signals will be irrelevant. This crucial distinction has not been investigated in prior research, although there is some evidence that gaze direction influences stimulation of neural reward centers in some neuropsychological studies (e.g., Kampe et al., 2001).

In summary, I predicted that acting proceptively would enhance a person's attractiveness to opposite-sex individuals relative to acting unreceptively, but only if the proceptive signals are directed towards the observers. If he/she directs his/her signals towards other individuals the effect will be attenuated, or reversed. If proceptivity does not interact with signal direction this would suggest that receivers do not attend to proceptive signals in part to aid efficient use of costly mating effort.

Materials and Methods

To test my hypotheses about how proceptivity and direction of proceptive signals affect people's perceptions of opposite-sex individuals I prepared video clips of actors behaving proceptively and unreceptively, manipulated the clips for apparent direction and presented them to participants who rated the actors for attractiveness.

Ninety-four men, aged 18-27 years (Mean age \pm *SD* = 19.6 \pm 1.6), and 89 women, aged 17-23 years (Mean age \pm *SD* = 18.5 \pm 1.2), enrolled in a first-year psychology course at McMaster University participated in the experiment, for which they received course credit.

The stimuli were composed of videotaped mock interviews of four female actors aged 20 to 22, and four male actors aged 20 to 23. Actors were recruited from the School of the Arts at McMaster University and were paid \$20 CAD. Recruitment was specifically targeted at students with acting experience in the hope that they would better able to convincingly mimic a proceptive and unreceptive state. Each interview consisted of a different set of five innocuous questions posed by an opposite-sex interviewer (played by a male and female confederate). Each actor performed two versions of the same interview: one in which he/she answered while in a proceptive state and one in which he/she answered while in an unreceptive state. The content of his/her answers remained constant between the two conditions. Each actor was briefed about the purposes of the experiment and about typical proceptive and unreceptive behaviors but, in an attempt to elicit naturalistic displays, his/her primary instruction was to act as though he/she were trying to encourage further interaction with the interviewer (for proceptive behavior) or as though he/she were trying to discourage it (for unreceptive behavior).

Each interview was captured and edited to create two directional conditions: one in which the actor appeared to be speaking to the interviewer, and one in which he/she appears to be directing his/her answers towards the participant. The video for the participant-directed condition was captured by a camera located roughly two metres behind the interviewer and directed over his/her shoulder towards the actor's face. Instead of making eye contact with the interviewer, the actor looked into the camera behind the interviewer. The video for the interviewer-directed condition was captured from a camera located roughly two metres perpendicular to the line between the interviewer and the actor. This camera angle depicted the actor and interviewer facing each other. Although the actor was not making eye contact with the interviewer this was not apparent from the point of view of the perpendicular camera, so this angle depicted the actor directing his/her answers to the interviewer. In the interviewer-directed condition, the entire interview was displayed as a continuous clip. In the participant-directed condition, the interview was divided into five separate clips with the interviewer's voice edited out. During the experiment, participants were given a list of questions they could choose from, identical to those the interviewer had asked. When a participant clicked on a question, the clip featuring the appropriate answer was played. This "interactive" element was included to enhance the illusion that the actor was directing his/her responses (and his/her behavior) towards the participant.

Stills depicting each actor with neutral expression were rated for attractiveness by 21 male and 32 female raters in an online task located at a website dedicated to face research (www.faceresearch.org). The raters were aged 14-59 years (Mean age \pm *SD* = 29.7

± 8.9).

To verify that the instructions to the actors were effective and that the contrast between proceptive and unreceptive performances was roughly similar for both sexes of actor, the proceptive and unreceptive interviews for each actor were rated on a scale ranging from 3 to -3, with “proceptive” and “unreceptive” anchoring the positive and negative ends respectively. The raters were 10 men and 17 women aged 16-43 years (Mean age ± *SD* = 19.9 ± 5.3) participating in exchange for course credit in a first-year psychology course at McMaster University. They were provided with operational definitions of proceptivity and unreceptivity before the rating task and were required to pass a quiz testing their functional understanding of these definitions. The average difference between the ratings for proceptive and unreceptive videos for the female actors ranged from 3 to 4.2. For the male actors the average difference ranged from 2.9 to 4.2.

Sixteen different stimulus sets were created (two signal direction conditions x two proceptive state conditions x four actors) for each sex of actor. Participants saw opposite-sex actors only and each participant saw each actor once and each combination of conditions once (four out of 16 possible stimulus sets). The stimulus sets were presented sequentially, in random order, and each possible combination of sets (24 in total) was presented roughly equally often.

Before the experiment began, each participant was assured of his anonymity, seated at a computer and given headphones to wear for the duration of the task. The computers displayed instructions and then proceeded to display the stimulus sets. Each set was preceded by an introductory slide displaying a still frame of the featured actor with neutral facial expression and an alias label. For the participant-directed sets, participants could play any clip as often as they liked and were given the option to proceed after three different clips had been played. Participants were asked to rate the attractiveness of the actor who had appeared in the preceding video(s) on a scale of 1-10 before the next stimulus set was presented. After all sets were presented, participants completed a questionnaire that included demographic items (such as age and sexual preference).

Results

Figures 1 and 2 show the mean attractiveness ratings for each actor in each combination of conditions seen by male and female participants, respectively.

Figure 1. Mean attractiveness ratings ($\pm S.E.M.$) for each female actor in each combination of proceptive state and signal direction in experiment 2.

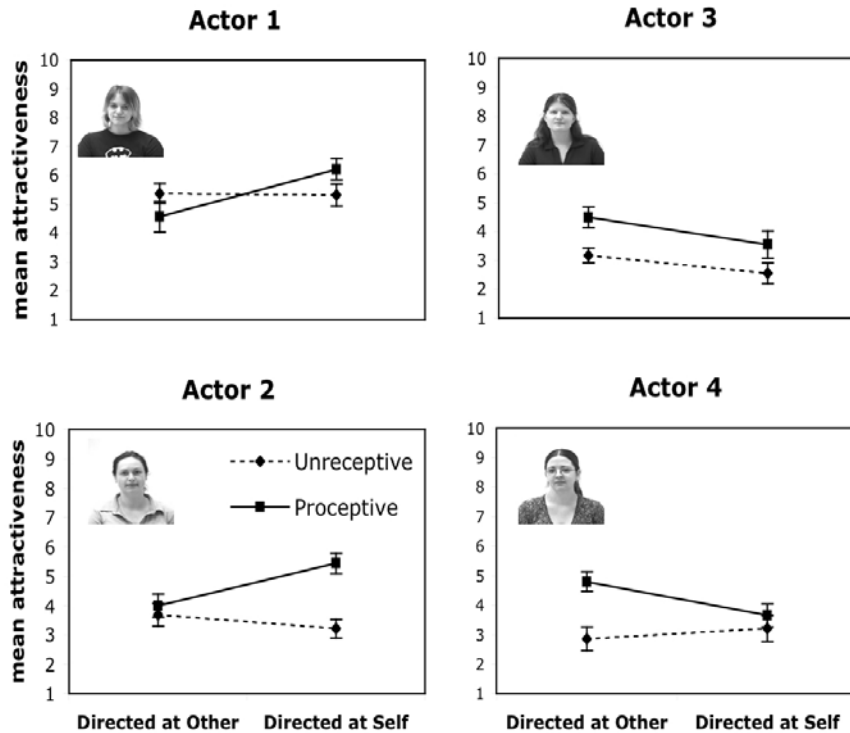
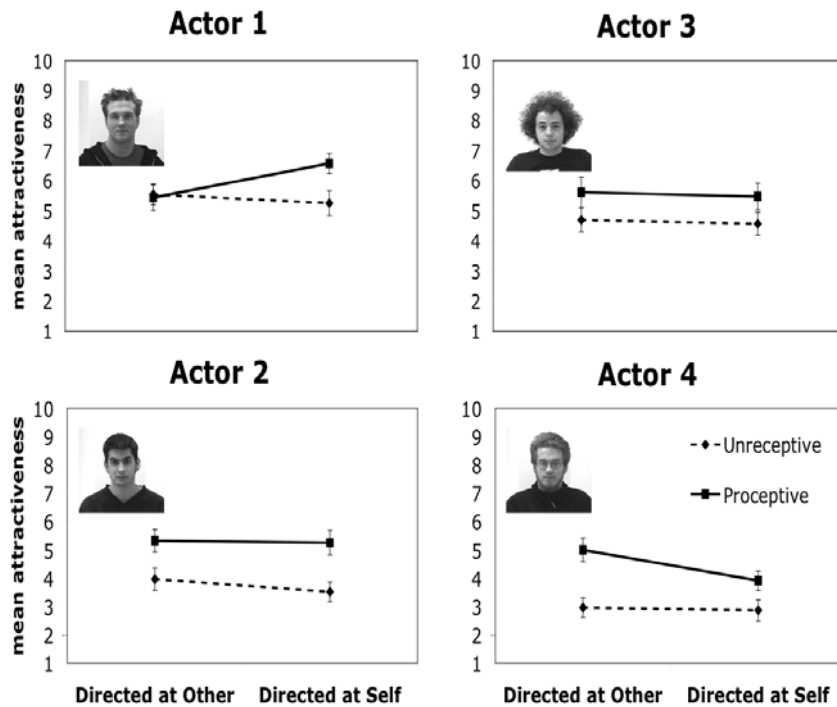


Figure 2. Mean attractiveness ratings ($\pm S.E.M.$) for each male actor in each combination of proceptive state and signal direction in experiment 2.



Analyzing these results is not a straightforward task because a simple two-way repeated measures ANOVA would conflate the effects of individual actors, and if these effects differ they may dilute or cancel each other out. Therefore, the results were analysed using a linear mixed model design in SPSS 11 for Mac OSX. Actor identity was entered as the repeated variable, participant identity was entered as the subject variable, and proceptive state (proceptive/unreceptive) and signal direction (toward interviewer/toward participant) were entered as factors nested within actor identity. This nesting allows for effects to be considered within the context of each target. Sex of actor was not included as a variable because it was necessarily conflated with actor identity and was therefore redundant. Actor attractiveness as rated by laboratory participants from the videotaped interviews was the dependent variable.

Overall, there were significant effects of proceptive state ($F_{8,85.497} = 9.35, p < 0.001$) and of signal direction ($F_{8,85.497} = 3.03, p = 0.005$) both nested within actor identity. Proceptive stimuli were generally judged to be more attractive than unreceptive stimuli. As seen in Figure 1, a clear effect of direction was apparent only for female Actor 3, who was less attractive in the participant-directed condition. There was also a significant interaction between these two factors ($F_{8,85.497} = 2.56, p = 0.015$) nested within actor identity. Surprisingly, the nature of this interaction appeared to vary considerably between actors. For instance, female Actor 2 was most attractive when proceptive in the participant-directed condition and least attractive when unreceptive in the participant-directed condition; differences between proceptive states were attenuated within the interviewer-directed condition, conforming well to my stated prediction. However, female Actor 4 showed entirely the opposite pattern.

Although a direct comparison between the sexes cannot be built into the overall model, it is possible to analyze each sex separately. Within male participants (judging female actors) there were significant effects of proceptive state ($F_{4,86} = 8.97, p < 0.001$) and of signal direction ($F_{4,86} = 4.94, p = 0.001$) both nested within actor identity. There was also a significant interaction between these two factors ($F_{4,86} = 3.71, p = 0.008$) nested within actor identity. Within female participants (judging male actors) there was a significant effect of proceptive state ($F_{4,85} = 9.74, p < 0.001$) but not of signal direction ($F_{4,85} = 1.12, p = 0.35$), both nested within actor identity, and there was no significant interaction between these two factors ($F_{4,85} = 1.41, p = 0.24$) nested within actor identity.

Considerable variation in the effect of signal direction was observed between actors, particularly within the proceptive condition. A visual inspection of Figs. 1 and 2 suggests that this variation may covary with physical/structural attractiveness as gauged by the average attractiveness ratings of each actor's neutral photograph as judged by online raters (listed in Table 1).

Table 1. The means and standard deviations (Mean \pm SD) of attractiveness ratings for each actor as judged by online raters from neutral photos by actor.

		attractiveness from photos
Female Actors	Actor 1	4.2 \pm 1.2
	Actor 2	3.3 \pm 1.3
	Actor 3	2.5 \pm 1.0
	Actor 4	2.1 \pm 1.0
Male Actors	Actor 1	3.9 \pm 1.3
	Actor 2	3.3 \pm 1.1
	Actor 3	2.7 \pm 1.3
	Actor 4	2.6 \pm 1.2

Of particular note is the difference between female Actors 1 and 2 on the one hand, who were both judged to be most attractive while directing proceptive signals toward the participant, and female Actors 3 and 4 on the other, who were both judged to be most attractive while directing proceptive signals toward the interviewer. A similar pattern can be seen among the male actors. A difference score measuring the extent of this effect was calculated by subtracting each actor's average attractiveness scores in proceptive participant-directed videos from their scores in proceptive interviewer-directed videos. There was a significant correlation between this difference score and the average attractiveness score of each actor as rated from still photos (Spearman's $\rho = 0.922$, $p = 0.001$, $n = 8$).

Discussion

Both men and women perceived opposite-sex actors to be more attractive when the actors were observed behaving proceptively as opposed to unreceptively, consistent with the notion that members of both sexes make use of proceptive signals to facilitate adaptive allocations of mating effort. Furthermore, a significant interaction between proceptive state and signal direction was found, supporting the hypothesis that part of the reason receivers value proceptive signals is to gather information about probable return on mating effort.

There was a significant main effect of signal direction in both the overall ANOVA and the one including only male participants, a result that was not predicted and is somewhat difficult to interpret. A main effect of direction could reflect a tendency for participants to judge an actor as more or less attractive based purely on whether he/she were directing his/her attention toward the participant or the interviewer. However, it might alternately reflect a difference in apparent physical attractiveness of an actor in the portrait view depicted in the participant-directed condition compared to in the longer side view depicted in the interviewer-directed condition. In either case, such a bias should not interfere with the proceptive state/signal direction interaction which is of main interest in this study. Furthermore, Figure 1 suggests that a clear effect of direction was only apparent for female Actor 3.

Attracting interest

Although it was not specifically predicted, the individual actors may have had an effect on how observers reacted to the signals that were displayed, either because of variation in the quality of the signals displayed or because of variation in other characteristics inherent to different actors. Certainly this is suggested from a glance at the figures, where it is evident that the pattern of interaction between proceptive state and signal direction varied considerably between actors. For some actors the interaction appears to be very strong, but it appears to be completely absent for others. For those actors for which the interaction is absent however, the positive effect of proceptivity is still very evident. This suggests that proceptive signals do have value to observers independent of signal direction, such as indicating mate quality and/or status. It also cannot be ruled out that a target's proceptive behavior towards another person may be interpreted as predictive of their behavior towards oneself, at least in some cases. The model that represents the best fit for these results is that attending to proceptivity may function to facilitate adaptive mating effort both by way of signaling mate quality and by way of indicating probable return on mating effort, although the latter function may not apply to all signalers/receivers.

The extent to which interaction patterns varied between actors was surprising, and a rigorous examination of this variation is not possible here. However, two factors immediately present themselves as candidates of interest for further study. The first of these is sex. A significant interaction between proceptive state and signal direction was found only among the male participants judging female actors when the sexes were analysed separately. Of course, with only four actors representing each sex this may be mere coincidence. However, there is some reason to expect that male observers should attend to signal direction more closely than female observers should. Women's lower potential reproductive rate and higher minimum parental investment results in greater costs of discrimination for men and greater costs of indiscriminate mating for women (Clutton-Brock and Parker, 1992; Johnstone et al., 1996; Trivers, 1972). The consequences are deftly illustrated in a study by Clark and Hatfield (1989): men and women responded yes with the same probability (~50%) to a stranger's request for a date, but in response to a stranger's request for sexual intercourse, 72% of men responded yes, whereas all women said no. It would seem that finding a mate, if only for the purposes of gametic transfer, is easier for women than men. Although mating effort may not be cheap for either sex, it may be particularly costly for men and should be more limiting to male reproductive success. If mating effort costs are lower for women it follows that women have less to gain from attending to signal direction simply because they have less pressure to maintain a high rate of return for mating effort.

The second factor that might explain patterns of interaction between proceptive state and signal direction is the physical/structural attractiveness of the actors. The mediating effect of signal direction was more apparent within the proceptive stimuli, and a difference score measuring the extent of this effect for each actor within the proceptive state did significantly correlate with the actor's attractiveness scores based on a still photo. Actors whose static images were scored highly were judged to be most attractive directing proceptive signals toward the participant, while actors whose static images received lower scores were judged to be most attractive while directing proceptive signals toward the interviewer. It is interesting to speculate about why such a relationship might exist. One possibility is that observers may jump on the chance to further an interaction with an attractive signaler while the opportunity exists but will reserve their enthusiasm for an

unattractive one until their window for opportunity with him/her appears to be closing (i.e. when he/she appears to entertain other options). The point at which a given observer switches from one tactic to another presumably depends on his/her own attractiveness. Of course, it is possible that physical attractiveness is simply a corollary of variation in interaction patterns between actors rather than a direct driving force behind it. Perhaps more attractive people produce more convincing or more impressive proceptive signals than unattractive people, perhaps because of increased confidence or because they are better able to afford the costs of signal production.

Even if not primarily mediated by physical attractiveness, the variation in interaction pattern between actors does demonstrate that proceptive displays will have implications that differ by individual. Some people will appear most attractive to a target observer when directing proceptive signals toward that target, and others will be most attractive when directing proceptive signals toward someone other than the target. A person must therefore be able to monitor which class they belong to, according to the perceptions of the target, in order to manipulate their own attractiveness favorably. The most basic implication is that different individuals will have a different range of suitable behavioral options, but this implication introduces yet another dimension of complexity to the emerging pattern of human mating.

In conclusion, proceptive signals did have a positive effect on judgments of opposite-sex signalers' attractiveness for both male and female observers and as predicted this effect was mediated by signal direction in an overall analysis, supporting the idea that proceptive behavior is valued, at least in part, for information it provides about probable rate of return on mating effort. However, the interactions between proceptive state and signal direction appeared to vary substantially between actors, and positive effects of proceptivity were evident even when signal direction did not appear to play a mediating role, suggesting that proceptive signals hold information value even when direction cues are ignored, possibly by indicating mate quality. Intriguingly, interaction patterns appeared to vary with actor attractiveness as rated by still images, and possibly by actor sex, although the evidence is far from conclusive and further research is needed.

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References

- Beach, F. A. (1976). Sexual attractivity, proceptivity, and receptivity in female mammals. *Hormones and Behavior*, 7, 105–138.
- Bressler, E. R., and Balshine, S. (2006). The influence of humor on desirability. *Evolution*

and *Human Behavior*, 27, 29-39.

- Bressler, E. R., Martin, R. A., and Balshine, S. (2006). Production and appreciation of humor as sexually selected traits. *Evolution and Human Behavior*, 27, 121-130.
- Brown, W. M., Cronk, L., Grochow, K., Jacobson, A., Liu, K., Popovi, Z., and Trivers, R. (2005). Dance reveals symmetry especially in young men. *Nature*, 438, 1148-1150.
- Campbell, A. (1999). Staying alive: Evolution, culture, and women's intrasexual aggression. *Behavioral and Brain Sciences*, 22, 203-252.
- Chambers, K. C., and Phoenix, C. H. (1987). Differences among ovariectomized female rhesus macaques in the display of sexual behavior without and with estradiol treatment. *Behavioral Neuroscience*, 101, 303-308.
- Clark, R. D., and Hatfield, E. (1989). Gender differences in receptivity to sexual offers. *Journal of Psychology and Human Sexuality*, 2, 39-55.
- Clutton-Brock, T. H., and Parker G. A. (1992). Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, 67, 437-456.
- DeBruine, L. M. (2004). Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces. *Proceedings of the Royal Society of London, Series B*, 271, 2085-2090.
- Eibl-Eibesfeldt, I. (1989). *Human ethology*. New York: Aldine de Gruyter.
- Fedigan, L. M. (1992). *Primate paradigms* (2nd ed.). Chicago: University of Chicago Press.
- Fink, B., and Penton-Voak, I. S. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science*, 11, 154-158.
- Gangestad, S. W., and Scheyd, G. J. (2005). The evolution of human physical attractiveness. *Annual Review of Anthropology*, 34, 523-548.
- Grammer K., Honda R., Schmitt A., and Jütte A. (1999). Fuzziness of nonverbal courtship communication. Unblurred by motion energy detection. *Journal of Personality and Social Psychology*, 77, 487-508.
- Grammer K., Kruck K., Juette A., and Fink B. (2000). Non-verbal behavior as courtship signals: The role of control and choice in selecting partners. *Evolution and Human Behavior*, 21, 371-390.
- Givens, D. B. (1978). The nonverbal basis of attraction: Flirtation, courtship, and seduction. *Psychiatry*, 41, 346-359.
- Hausfater, G., and Takacs, D. (1987). Structure and function of hindquarter presentations in yellow baboons (*Papio cynocephalus*). *Ethology*, 74, 297-319.
- Hill, E. M. (1988). The menstrual cycle and components of human female sexual behavior. *Journal of Social and Biological Structures*, 11, 443-455.
- Johnsgard, P. A. (1994). *Arena Birds: Sexual selection and behavior*. Washington, D. C.: Smithsonian Institution Press.
- Johnstone, R. A., Reynolds, J. D., and Deutsch, J. C. (1996). Mutual mate choice and sex differences in choosiness. *Evolution*, 50, 1382-1391.
- Jones, B. C., Little, A. C., Burt, D. M., and Perrett, D. I. (2004). When facial attractiveness is only skin deep. *Perception*, 33, 569-576.
- Jouventin, B., and Lequette, B. (1990). The dance of the Wandering Albatross *Diomedea exulans*. *Emu*, 90, 123-131.
- Kampe, K. K. W., Frith, C. D., Dolan, R. J., and Frith, U. (2001). Reward value of attractiveness and gaze. *Nature*, 413, 589.

- Madlafousek, J., and Hlinak, Z. (1977). Sexual behavior of the female laboratory rat: inventory, patterning, and measurement. *Behaviour*, 63, 129–174.
- Miller, G. F. (2000). *The mating mind*. London: Heinemann.
- Moore, M. M. (1985). Nonverbal courtship patterns in women: Context and consequences. *Ethology and Sociobiology*, 6, 237-247.
- Moore, M. M. (1995). Courtship signaling and adolescents: 'Girls just wanna have fun'? *Journal of Sex Research*, 32, 319-328.
- Perper, T., and Weis, D. (1987). Proceptive and rejective strategies of U.S. and Canadian college women. *The Journal of Sex Research*, 23, 455-480.
- Rubenstein, A. J. (2005). Variation in perceived attractiveness. *Psychological Science*, 16, 759–762.
- Schmitt, D. P., and Buss, D. M. (1996). Strategic self-promotion and competitor derogation: Sex and context effects on the perceived effectiveness of mate attraction tactics. *Journal of Personality and Social Psychology*, 70, 1185-1204.
- Schmitt, D. P., Couden, A., and Baker, M. (2001). Sex, temporal context, and romantic desire: An experimental evaluation of Sexual Strategies Theory. *Personality and Social Psychology Bulletin*, 27, 833-847.
- Simpson, J. A., Gangestad, S. W., and Biek, M. (1993). Personality and nonverbal social behavior: An ethological perspective of relationship initiation. *Journal of Experimental Social Psychology*, 29, 434-461.
- Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology*, 65, 293-307.
- Thompson-Handler, N., Malenky, R., and Badrian, N. (1984). Sexual behavior of *Pan paniscus* under natural conditions in the Lomako Forest, Equateur, Zaire. In R. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 347-368). New York: Plenum Press.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136-179). Chicago: Aldine Publishing Company.
- Zehr, J. L., Maestriperi, D., and Wallen, K. (1998). Estradiol increases female sexual initiation independent of male responsiveness in rhesus monkeys. *Hormones and Behavior*, 33, 95-103.