Evidence of adaptation for mate choice within women's memory.

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Evidence of adaptation for mate choice within women's memory.

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Abstract

Sexually dimorphic characteristics in men may act as cues, advertising long-term health, dominance, and reproductive potential to prospective mates. Evolution has accordingly adapted human cognition so that women perceive sexually dimorphic facial features as important when judging the attractiveness and suitability of potential mates. Here we provide evidence showing, for the first time, that women's memory for details encountered in recently experienced episodes is also systematically biased by the presence of men's facial cues signaling enhanced or reduced sexual dimorphism. Importantly, the direction and strength of this bias are predicted by individual differences in women's preferences for masculine versus feminine facial features in men and are triggered specifically while viewing images of male but not female faces. No analogous effects were observed in male participants viewing images of feminized and masculinized women's faces despite the fact that male participants showed strong preferences for feminized facial features. These findings reveal a preference-dependent memory enhancement in women that would promote retention of information from encounters with preferred potential mates. We propose that women's memory for recently experienced episodes may therefore be functionally specialized for mate choice and in particular for the comparative evaluation of alternative potential mates. This also raises the possibility that similar specialization may be present in other species where it has been established that precursor, 'episodic-like' forms of memory exist.

Keywords: Mate choice; Long-term memory; Sexual dimorphism; Comparative evaluation

1. Introduction

The attractiveness of a particular man as a potential mate is unlikely to be an absolute function of his mate-quality cues (Appicella et al., 2007). Instead, decision mechanisms involved in mate choice may function more adaptively if the value of a potential mate is assessed relative to available alternative mates (Bateson and Healy, 2005). Most work on such comparative evaluation has focussed on the context specificity of mate choice, examining how asymmetrically dominated decoys alter preference judgements based upon multiple simultaneously presented traits (e.g., evaluating a potential partner relative to competitors in terms of their attractiveness and their sense of humor; see Sedikides et al., 1999). Bateson and Healy (2005) observed, however, that memories of past encounters with the opposite sex are essential for comparative evaluation when all available 'options' are not currently present. They further emphasized that such memories may be particularly crucial in circum- stances where the interpretation of mate quality is complex, either because multiple uncorrelated cues are involved or if particular cues convey conflicting information in relation to partner suitability.

In humans, masculine physical traits are positively correlated with indices of men's long-term health (e.g., Rhodes et al., 2003; Thornhill and Gangestad, 2006; see also Gangestad and Thornhill, 2003; Little et al., 2008) and dominance (Fink et al., 2007) and have been linked to increased reproductive success in a natural fertility population (Appicella et al., 2007). However, masculine traits in men are also correlated with behavioral traits that, in certain relationship contexts, may be less desirable, such as greater preference for short-term over long-term relationships (e.g., Boothroyd et al., 2008; Rhodes et al., 2005) and a higher likelihood of marital problems or divorce (Booth and Dabbs,

1993). Thus, any indirect fitness-related benefit from mating with a relatively masculine man may trade off against the direct fitness costs of their behavioral tendencies within a long-term relationship (Gangestad and Simpson, 2000). Consistent with this proposal, women's preference for masculine or feminine facial features is sensitive to various hormonal, environmental, and sociosexual factors (DeBruine et al., 2010; Little et al., 2002; Penton-Voak et al., 1999; Welling et al., 2007), suggesting the existence of adaptations that function to maximize the potential benefits of women's mate choices by balancing the possible costs. Regardless of whether relatively masculine or relatively feminine men are preferred, however, the validity of the cost—benefit analysis involved in mate choice hinges upon whether the behavior of potential mates runs true to form—i.e., lives up to one's expectations based upon their observable signs of masculinity—femininity.

While facial cues of sexual dimorphism provide women with an important dimension along which men can be comparatively evaluated, the suitability of a particular man as a potential partner may in fact depend on the degree to which their behavior conforms (or indeed does not conform) to beliefs about the character of relatively masculine vs. relatively feminine men. In line with Bateson and Healy's (2005) emphasis on the role of memory, we propose here that knowledge about particular individuals that derives from one's past experience may qualify (e.g., by enhancing or undermining) the value of preferred physical characteristics in the opposite sex. This proposal implies that it may be important for women to remember information associated with men who display desirable sexually dimorphic facial traits, so that this knowledge can enter into future mate choice decisions. Hence, the functional contribution of memory to comparative evaluation may have been shaped, at least in part, by a specific selection pressure acting upon 'episodic memory,' the cognitive system that supports our ability to recollect details from specific episodes (Tulving, 1983; for further ethological analysis of episodic memory function, see Clayton and Dickinson, 1998; Clayton et al., 2001).

If episodic memory function in women has been shaped by sexual selection pressures to contribute to mate choice, we may be able to observe an enhanced ability to encode and accurately retain episodic details that co-occur with men who display the sexually dimorphic facial characteristics indicative of a desirable mate. This hypothesis leads us to a series of predictions that we test in the experiment reported below. Firstly, women's preferences for sexually dimorphic facial features in men should predict their ability to retain detailed information from encounters with males who differ in the degree to which they display the preferred features. Specifically, women who currently prefer exaggerated masculine facial characteristics in men should show improved memory for details associated with such individuals, while women who have the opposite preference should show the reversed pattern—i.e., their memory should be particularly attuned to details that co-occur with relatively feminine-looking men. Secondly, if such effects are linked to women's mate choice, they should be triggered specifically by men who exhibit preferred sexually dimorphic facial characteristics and not by women who display sexually dimorphic facial characteristics perceived as attractive. Thirdly, if such effects result from selection pressures that arise from problems of mate choice specific to women, we should not be able to observe analogous effects of women's sexually dimorphic facial cues upon men's memory. We base this final prediction on the assumption that women's mate choice will depend upon the ability to retrieve memories from a variety of past contexts that give insight into the personality and behavior of specific male individuals, whereas men's mate choice by contrast may be relatively more dependent upon a women's purely physical characteristics (Landolt, Lalumiere & Quinsey, 1995).

To test these predictions, we examined how cues of facial sexual dimorphism affect memory for objects that co-occur with images of male and female faces. We chose a varied set of arbitrary objects as the details to be remembered (Fig. 1), on the assumption that the future utility of particular episodic details may be unpredictable in principle. Hence, it should be possible to elicit memory effects even for apparently arbitrary and quite incidental kinds of episodic detail. Our experiment employed a well-established computer-based transformation technique that enhances and reduces sexually dimorphic structural features in facial images (see 'Methods' for details). We asked young healthy adult men and women to view a series of these facial images, next to which we presented images depicting a variety of different living and nonliving things (Fig. 1). Half of the facial images were of men and half were of women. Within each face sex, half of the images were masculinized and half were feminized. After viewing this series of face—object image pairs, we tested participants' memory for the objects using a two-alternative forced-choice (2AFC) procedure. On each trial, participants were asked to discriminate the previously shown image from a similar previously unseen foil image. Finally, each participant was asked to view pairs of masculinized and feminized images of male or female faces and to rate, using a Likert scale, the image in each pair that they preferred, i.e., found most attractive. These procedures allow us to determine, first, whether women's ability to remember details that co-occur with images of masculinized and feminized

men is predicted by their preference for masculine or feminine facial characteristics in men. Second, we can determine whether such effects in women are triggered specifically by men's and not other women's faces. Third, we can determine whether or not analogous effects occur in male participants.

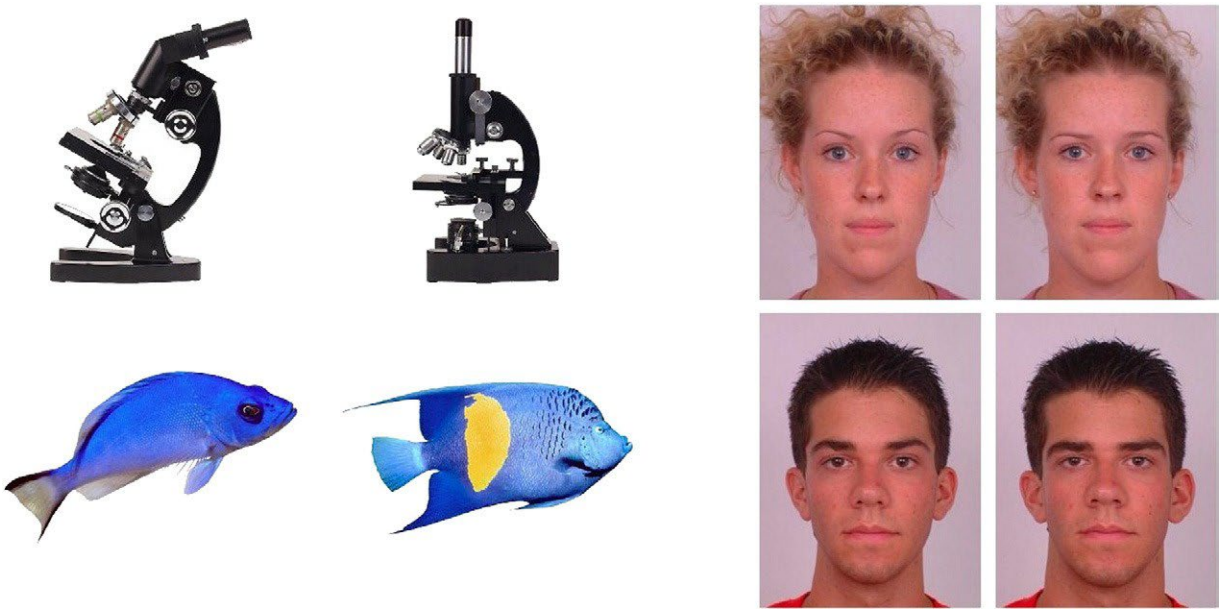

Fig. 1. Examples of object stimuli and the face stimuli they were paired with during encoding (masculinized face images on the right and feminized face images on the left).

2. Methods

2.1. Participants

In return for course credit, we recruited undergraduate psychology students (50 female, mean age=21.7 years, S.D.=6.8; 77 male, mean age=22.0, S.D.=3.8). We only recruited female participants who were not currently taking hormonal contraceptives because of prior work suggesting that hormonal contraceptive use can disrupt adaptive behavioral responses to potential mates (e.g., Feinberg et al., 2008; Roberts et al., 2008; Smith et al., 2009; Vukovic et al., 2008).

2.2. Stimuli

Thirty-two full-color, full-face digital images of young adults (16 male, 16 female) were employed. Object images were taken from a commercially available photo clip-art image database (Hemera Technologies, Inc., Quebec, Canada). Prototype-based techniques (Tiddeman et al., 2001) were used to manipulate the masculinity and femininity of the 16 male and 16 female images, producing masculinized and feminized images differing only in their two-dimensional shape and not in identity, skin color, or texture. This method is widely used in studies of masculinity preferences (e.g., DeBruine et al., 2006; Smith et al., 2009; Penton-Voak et al., 1999; Welling et al., 2007) and has been shown to produce images that differ reliably in perceived masculinity—femininity (e.g., DeBruine et al., 2006; Welling et al., 2007). From the object image database, we picked two closely matching but not identical examples of 32 different objects (64 objects in total), each superimposed on a white background.

During the learning trials, each participant was shown 32 unique face—object pairs: 16 with a male face (8 masculinized, 8 feminized) and 16 with a female face (8 masculinized, 8 feminized). During the recognition trials, object memory was tested by presenting the previously shown object alongside its previously unseen similar foil. We controlled for any effects due to differential memorability of particular objects by ensuring that each version was

paired equally often with masculinized male, feminized male, masculinized female, or feminized female images across counterbalanced conditions. Participants were randomly assigned to one of these counterbalanced conditions.

2.3. Learning/recognition procedure

Participants were run in groups of between 10 and 30 individuals, each of whom was seated in front of the 15-in. screen of a desktop PC running Microsoft Windows HP, on which the experimental program could be accessed via the Firefox web browser. Participants were told that they would view a set of 32 unique face—object pairs and that each pair would be shown twice (once with the face on the left and once with the face on the right to control for side biases) on each occasion for a presentation time of 2 s. The order of presentation of face—object pairs was fully randomized between participants. Their task was simply to pay attention to each image pair. Participants were then instructed that their memory for the objects would be tested and that, on each trial, they would see a pair of similar objects, one previously shown and one previously unseen. The side of presentation of the previously shown object was randomized by trial, and the order of trials was fully randomized between participants. Participants' task was to pick the previously shown object by clicking on it using the computer mouse. The test phase was self-paced.

2.4. Preference task

Preferences for masculine versus feminine versions of male and female faces were obtained using well-established methods (e.g., Welling et al., 2007). Participants viewed 32 trials, each containing two pictures of the same individual from the 32 individuals used in the memory task, one masculinized and one feminized. Participants chose which face in each pair was more attractive and whether it was 'slightly more attractive,' 'somewhat more attractive,' 'more attractive,' or 'much more attractive.' The order in which pairs of faces were presented and the side of the screen on which any particular image appeared were fully randomized.

3. Results

Object memory scores were calculated for each participant as the percentage of seen objects correctly identified in each of the four conditions. On average, women correctly identified objects paired with masculine men on 84.7% of trials, correctly identified objects paired with masculine women on 84.5% of trials, correctly identified objects paired with feminine men on 85.2% of trials, and correctly identified objects paired with feminine women on 86.0% of trials. The corresponding data from the male participants were 84.2%, 85.9%, 85.7%, and 86.0%. Note that analyses of these data within each participant-sex using analysis of variance revealed no significant effects of face-sex, facial sexual dimorphism, or any interactions between these two factors. In the analyses that follow, analysis of covariance (ANCOVA) was used to analyze the data for objects paired with male and female faces separately in order to fully consider the effects of the face-sex-specific covariates of preference for male masculinity and preference for female femininity.

3.1. Male faces

In female participants, for objects paired with male faces, ANCOVA [within-subjects factor: facial masculinity (masculinized, feminized); covariate: masculinity preference for male faces] revealed the predicted interaction between facial masculinity and masculinity preference ($F_{1,48}$=4.13, p=.040). The dependent variable (DV) here is the size of the difference between correct 2AFC recognition for objects paired with masculinized vs. feminized male faces. The interaction occurs because the extent to which objects paired with masculine male faces were recognized better than objects paired with feminine male faces was positively correlated with the strength of women's preference for masculine male faces (r=.29, p=.040, two-tailed, Fig. 2). No such pattern was present in the data from the male participants (all Fs<1).

3.2. Female faces

In female participants, for objects paired with female faces, ANCOVA [within-subjects factor: facial masculinity (masculinized, feminized); covariate: femininity preference for female faces] revealed no significant effects (all $F_{1,48}$b0.34 all *p*sN.56). The DV here is the size of the difference between correct 2AFC recognition for objects paired with masculinized vs. feminized female faces. The extent to which objects paired with feminine female faces were recognized better than objects paired with masculine female faces was not correlated with women's preference for feminine female faces (r=−.07, p=.61). Once again, no effects were present in the data from the male participants (all Fs<1).

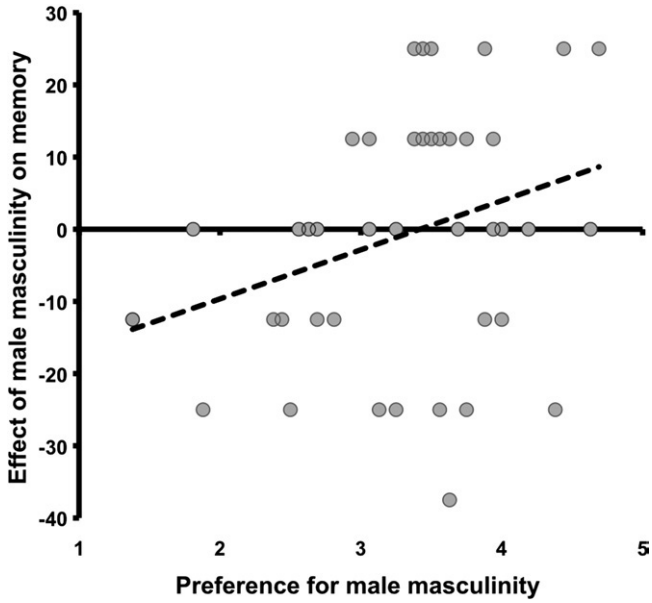

Fig. 2. The significant correlation between the strength of women's preference for masculinity in men's faces and the difference in the number of objects correctly remembered when paired with masculine vs. feminine men (a positive difference score indicates enhanced memory for objects paired with masculine faces).

3.3. Preference data

Following Welling et al. (2007), responses were coded on a 0 to 7 scale such that 0 equals feminized male or masculinized female face judged 'much more attractive' and 7 equals masculinized male or feminized female face judged 'much more attractive.' We calculated each participant's average score for male faces and, separately, the average score for female faces. These scores were used in the analyses that follow below. Scores higher than 3.5 (chance, i.e., no preference) indicate a preference for exaggerated sex-typical shapes in faces (i.e., masculine men and feminine women).

Preferences for masculinized or feminized male and female faces were analyzed using one-sample *t* tests, comparing to the chance value of 3.5. As in many previous studies using similar stimuli and methods, women expressed no overall preference for masculinized or feminized male faces (t_{49}=−1.56, p=.12, mean=3.34, S.E.M.=0.10), but did show a strong preference for feminized versions of female faces (t_{49}= 11. 34, p<.001, mean= 4. 40, S.E.M.=0.08). Men expressed robust preferences for femininity within female faces (t_{76}=2.78, p<.01, mean=4.84, S.E.M.=.01) and for masculinity within male faces (t_{76}=4.00, p<.001, mean=3.86, S.E.M.=0.09).

4. Discussion

Our findings reveal the predicted link between women's memory and mate choice relevant cues in the opposite sex (Bateson and Healy, 2005; see also Nairne and Pandeirada, 2008). Women demonstrated a preference-dependent

effect on memory for event-specific details involving men displaying different levels of facial sexual dimorphism, whereby women who demonstrated particularly strong preferences for masculine men demonstrated enhanced memory for objects encountered while viewing images of male faces with exaggerated masculine features. Women who demonstrated particularly strong preferences for feminine men demonstrated the reverse pattern, i.e., enhanced memory for objects encountered while viewing images of male faces with reduced masculine features (Fig. 2). In contrast to these findings for male facial sexual dimorphism and women's memory, no corresponding effect on women's memory was observed when sexually dimorphic characteristics were manipulated in women's faces, and no effects whatsoever were observed in our male participants. Collectively, these findings suggest that sexual selection pressures have shaped women's memory for recent experiences in ways that will promote the retention of details from interactions involving preferred mates.

Our findings therefore suggest that constraints from mate choice have shaped the function of women's memory, so that it is sensitive to the presence of desirable features in the opposite sex. To the extent that desire for such features fluctuates within an individual (e.g., across the menstrual cycle), the memory modulations we demonstrate here may themselves fluctuate in strength, and this may be a promising avenue for future research. A further issue, not addressed by our present study, concerns whether women's recognition of men per se is enhanced or impaired by their facial masculinity—femininity cues, and this perhaps deserves more attention in its own right (e.g., see O'Toole et al., 1998, for evidence of sensitivity to masculinity cues in women's recognition of men's faces). Our findings do however suggest that women's memory is content sensitive, and we wish to clearly distinguish two separable points here. First, there is prior evidence that memory in women is sensitive to the location of recently encountered foodstuffs (New et al., 2007), raising the possibility that different underlying mechanisms could be involved in women's enhanced memory for reproductively versus nutritionally valuable resources. Further work is also needed to establish whether the effect of facial sexual dimorphism in men upon women's memory depends upon the same or different mechanisms that are responsible for the prioritized retention of information encoded in relation to its general survival value (reviewed in Nairne and Pandeirada, 2008). We note, however, that the pattern of face sexual dimorphism's effect on women's memory suggests an opposite-sex-specific, perhaps hormonally influenced mechanism whose apparent bias is unlikely to suit the demands of foraging or of other general aspects of survival. Moreover, it must be emphasized that the mere presence of attractive facial characteristics is not sufficient to trigger memory enhancement in women (i.e., women showed strong preferences for feminine female faces but did not demonstrate a corresponding effect on memory for objects that co-occurred with feminine female faces), suggesting a fairly high degree of domain specificity in the observed memory bias. We therefore suggest that exploring the extent to which different types of potentially adaptive biases in memory (mate choice, foraging, general survival) reflect shared and common mechanisms is a highly promising area for future research.

There is a further distinct issue in relation to whether the current findings reflect content-specific mechanisms. Our study shows that women's memory is sensitive to the presence of facial cues indicating sexual dimorphism in men. Our study does not, however, examine whether women's memory is sensitive to particular kinds of episodic detail that are associated with men. As we state in the 'Introduction,' our approach has been guided by the assumption that the future utility of information associated with men may be hard to predict, and for this reason, it may be beneficial for memory to encode details that co-occur with preferred potential mates without regard to the particular content of those details. If only certain kinds of detail were preferentially encoded, for example, social information pertaining to the affiliations or resources of an individual, this would tend to focus the contribution of memory during mate choice onto such details. While this may be beneficial, it would occur to the relative exclusion of other kinds of information that could have future utility. In any case, if our assumption is wrong and women's memory is in fact sensitive to the kind of episodic detail that co-occurs with men who display characteristics desired in a potential mate, this would presumably have reduced our power to detect such effects in the present experiment. Hence, our current findings may actually be underestimating the effect that facial cues of sexual dimorphism in men can exert upon women's memory. This issue is quite amenable to empirical test, and it deserves further study not least because it may shed light upon the nature of the underlying mechanisms.

Our current view on the nature of the mechanisms involved is as follows: Because the memory modulation occurs for various kinds of incidental episodic detail, this suggests to us that we may be dealing with a generalized effect that is consequential upon increased arousal or attention during episodes in which a preferred male face is presented. But note that the generality of this effect refers to the capture of various co-occurring details and should not be taken

to imply a simple process such as increases in attention on trials where any preferred type of face is being viewed. In other words, it does not seem likely to us that the memory modulation is a functionless by-product of changes in attention or arousal that might occur whenever one viewed a preferred type of face; such an account would predict memory modulations when women view objects paired with preferred versus nonpreferred women's faces and when men view objects paired with preferred versus nonpreferred women's faces. Contrary to such predictions, our data show that the memory modulation is specifically triggered in women viewing opposite-sex male faces that exhibit preferred facial cues of sexual dimorphism.

Returning to the cognitively elaborate decision-making heuristic proposed by Bateson and Healy (2005), enhanced memory for past encounters with desirable males may generate particular benefits for female mate choice. Most notably, perhaps, bias deriving from memory could shift mate choice either towards or away from specific individuals depending on how retrieved information qualifies the value of preferred physical characteristics in those individuals. The functional contribution of memory therefore resides in reducing the likelihood of choosing an unsuitable partner or increasing the likelihood of choosing a suitable partner—a valuable contribution indeed, given that the costs of choosing an unsuitable partner are relatively high for women compared to men, which may go some way towards explaining why we could find no evidence of analogous effects in our male participants.

Enhanced memory for preferred mates may therefore directly facilitate women's ability to find a suitable partner with preferred physical characteristics, by allowing an extrapolation to be made from their actual past behaviors to possible future behaviors within a relationship context. It is also worth noting that biases in memory that promote comparative evaluation of potential mates need not be unique to human females. Martin-Ordas et al. (2010) have found, for example, evidence of 'episodic-like' memory (Clayton and Dickinson, 1998; Clayton et al., 2001) in other great ape species such as chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and orangutans (*Pongo pygmaeus*). Our present findings suggest that it may be worthwhile to examine whether episodic-like memory in these species also prioritizes the retention of information from encounters with preferred mates, which would suggest that they too are endowed with cognitively elaborate mechanisms supporting the evaluation of potential mates.

Finally, although we have viewed our findings from an explicitly adaptationist perspective, we do acknowledge that other nonadaptationist accounts may well be possible, and we would highlight one such account. According to the self memory system (SMS) model of Conway and colleagues (Conway, 2009), the ability to remember specific episodic details is modulated by their relevance to one's currently active goal states. This model is of particular interest to us because of prior evidence showing that preferences for masculine facial features in men are enhanced when women rate men's attractiveness in the context of a short-versus long-term relationship (Little et al., 2002). This suggests that our current findings could reflect the influence of different underlying mating goals (i.e., short term versus long term) upon women's memory function. So in terms of the SMS model, the modulatory effect of desirable facial characteristics in men upon women's memory may be due to the goal- directed nature of memory function. While Conway and colleagues claim that a memory system tuned to goal-relevant information may broadly function in an adaptive way, so far as we are aware of, their model does not incorporate domain- and sex-specific mechanisms that would account for our present findings. Hence, future work examining the influence of different mating goals upon the memory effects reported here would be of considerable interest for the refinement of the SMS model, as well as for the more explicitly adaptationist account.

References

Appicella, C. L., Feinberg, D. R., & Marlowe, F. W. (2007). Voice pitch predicts reproductive success in male hunter—gatherers. *Biology Letters*, *3*, 682—684.

Bateson, M., & Healy, S. D. (2005). Comparative evaluation and its implications for mate choice. *Trends Ecology & Evolution*, *20*(12), 659—664.

Booth, A., & Dabbs, J. (1993). Testosterone and men's marriages. *Social Forces*, *72*, 463—477.

Boothroyd, L. G., Jones, B. C., Burt, D. M., DeBruine, L. M., & Perrett, D. I. (2008). Facial correlates of sociosexuality. *Evolution & Human Behavior*, *29*, 211—218.

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, *395*, 272—274.

Clayton, N. S., Griffiths, D. P., Emery, N. J., & Dickinson, A. (2001). Elements of episodic-like memory in animals. *Proceedings of the Royal Society of London B*, *356*, 1483—1491.

Conway, M. A. (2009). Episodic memories. *Neuropsychologia*, *47*, 2305—2313.

DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L. M., & Little, A. C. (2010). The health of a nation predicts their mate preferences: cross-cultural variation in women's preferences for masculinized male faces. *Proceedings of the Royal Society of London B*, *277*, 2405—2410.

DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., Penton- Voak, I. S., Cooper, P. A., Penke, L., & Tiddeman, B. P. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society of London B*, *273*, 1355—1360.

Feinberg, D. R., DeBruine, L. M., Jones, B. C., & Little, A. C. (2008). Correlated preferences for men's facial and vocal masculinity. *Evolution and Human Behavior*, *29*, 233—241.

Fink, B., Neave, N., & Seydel, H. (2007). Male facial appearance signals physical strength to women. *American Journal of Human Biology*, *19*, 82—87.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: trade-offs and strategic pluralism. *Behavioral & Brain Science*, *32*, 573—644.

Gangestad, S. W., & Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution & Human Behavior*, *24*, 231—241.

Landolt, M. A., Lalumiere, M. L., & quinsy, V. L. (1995). Sex difference in intra-sex variations in human mating tactics: an evolutionary approach. *Ethology and Sociobiology*, *16*, 3—23.

Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society of London B*, *269*, 1095—1100.

Little, A. C., Jones, B. C., Waitt, C., Tiddeman, B. P., Feinberg, D. R., & Perrett, D. I. (2008). Symmetry is related to sexual dimorphism in faces: data across culture and species. *PLoS One*, *3*, 2106.

Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. (2010). Keeping track of time: evidence for episodic-like memory in great apes. *Animal Cognition*, *13*, 331—340.

Nairne, J. S., & Pandeirada, J. N. S. (2008). Adaptive memory: remembering with a stone-age brain. *Current Directions in Psychological Science*, *17*, 239—243.

New, J., Krasnow, M. M., Truxaw, D., & Gaulin, S. J. C. (2007). Spatial adaptations for plant foraging: women excel and calories count. *Proceedings of the Royal Society of London B*, *274*, 2679—2684.

O'Toole, A. J., Deffenbacher, K. A., Valentin, D., McKee, K., Huff, D., & Abdi, H. (1998). The perception of face gender: the role of stimulus structure in recognition and classification. *Memory and Cognition*, *26*, 146—160.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., & Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, *399*, 741—742.

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society of London B*, *270*(S1), S93—S95.

Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behaviour: does attractiveness enhance mating success? *Evolution & Human Behavior*, *26*, 186—201.

Roberts, S. C., Gosling, L. M., Carter, V., & Petrie, M. (2008). MHC-correlated odour preferences in humans and the use of oral contraceptives. *Proceedings of the Royal Society of London B*, *275*, 2715—2722.

Sedikides, C., Ariely, D., & Olsen, N. (1999). Contextual and procedural determinants of partner selection: of asymmetric dominance and prominence. *Social Cognition*, *17*(2), 118—139.

Smith, F. G., Jones, B. C., DeBruine, L. M., Welling, L. L. M., Vukovic, J., & Conway, C. (2009). Hormonal contraceptive use and perceptions of trust modulate the effect of relationship context on women's preferences for sexual dimorphism in male face shape. *Journal of Evolutionary Psychology*, *7*, 195—210.

Tiddeman, B. P., Perrett, D. I., & Burt, D. M. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics Applications*, *21*, 42—50.

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution & Human Behavior*, *27*, 131—144.

Tulving, E. (1983). *Elements of episodic memory*. Oxford: Oxford University Press.

Vukovic, J., Feinberg, D. R., Jones, B. C., DeBruine, L. M., Welling, L. L. M, Little, A. C., & Smith, F. G. (2008). Self-rated attractiveness predicts individual differences in women's preferences for masculine men's voices. *Personality and Individual Differences*, *45*, 451—456.

Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A., Law Smith, M. J., Little, A. C., Feinberg, D. R., Sharp, M., & Al-Dujaili, E. A. S. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Hormones & Behavior*, *52*, 156—161.