**Classification**
Social Sciences – Psychological and Cognitive Sciences

**Title**
Hormonal regulation of women's prosocial, but not sexual, responses to kinship cues

**Short Title**
Hormonal regulation of responses to kinship cues

**Authors**
Iris J Holzleitner[a], Amanda C Hahn[b], Claire I Fisher[a], Anthony J Lee[a], Kieran J O'Shea[a], Benedict C Jones[a] & Lisa M DeBruine[a]

**Author affiliations**
[a] Institute of Neuroscience & Psychology, University of Glasgow, 58 Hillhead Street, Glasgow, G12 8QB, Scotland, UK
[b] Department of Psychology, Humboldt State University, Behavioral and Social Science Building #410, 1 Harpst Street, Arcata, CA 95519, USA

**Corresponding author**
Iris J Holzleitner (iris.holzleitner@glasgow.ac.uk), Institute of Neuroscience & Psychology, University of Glasgow, UK

**Author contributions**
Designed research: LMD, ACH, BCJ; collected data: ACH, CIF, IJH, AJL; analysed data: IJH, LMD, BCJ; drafted manuscript: IJH, LMD, BCJ; revised manuscript: IJH, LMD, BCJ, ACH, CIF, AJL, KJO

**Keywords**
kinship, endocrinology, steroid hormones, inbreeding avoidance, fertility, kin affiliation

**Data files and analysis scripts are publicly available at osf.io/wnhma.**

## Abstract

Women's affiliative behavior towards kin and responses to facial cues of kinship (self-resemblance) both change as a function of their hormonal status. Such hormone-mediated changes might serve to (1) avoid inbreeding during peak fertility and/or (2) increase kin affiliation during pregnancy. The first hypothesis predicts that responses to kinship cues will be most negative during hormonal states characteristic of high fertility (i.e., when estradiol-to-progesterone ratio is high). The second hypothesis predicts that responses to kinship cues will be most positive during hormonal states characteristic of pregnancy (i.e., when progesterone is high). We used a longitudinal design (N = 176) to investigate possible relationships between women's responses to self-resembling faces and their measured salivary hormone levels. Women's preferences for self-resembling male faces were not related to estradiol-to-progesterone ratio. However, preferences for self-resembling female faces were positively related to progesterone (and negatively to estradiol). These findings do not support the inbreeding-avoidance hypothesis, but do support the proposal that women's hormonal status influences attitudes to kin because of benefits associated with increased kin affiliation during pregnancy.


## Significance statement

Biological theories predict that kinship cues have opposite effects on sexual and prosocial responses. Two hypotheses exist to explain how these differential responses could be modulated by hormonal status in women: (1) sexual responses decrease when fertility is high, and (2) prosocial responses increase during pregnancy. We used a longitudinal design to test these hypotheses by investigating the effects of hormonal profiles linked to fertility and pregnancy on women's responses to kinship cues. Our analyses show no evidence that responses to kinship cues track changes in women's fertility, instead suggesting that women show stronger preferences for female kin when raised progesterone prepares the body for pregnancy.

**Introduction**

Kinship is an important moderator of human social interactions and outcomes. Biological theories make different predictions regarding the effect of kinship in sexual and social contexts. On the one hand, optimal outbreeding theory (1) predicts decreased sexual behavior and attitudes towards those who exhibit cues of kinship, due to the significant costs of inbreeding (2-4). On the other hand, inclusive fitness theory (5) predicts increased pro-social behavior and attitudes towards those who exhibit cues of kinship (6-12).

However, these benefits and costs of associating with kin are not fixed. For example, the cost of mating with kin might be higher at certain times than others. Similarly, help from kin might be more valuable at certain times than others. In particular, two lines of reasoning predict that, for women, the benefits and costs of associating with kin may change as a function of hormonal status.

Because the costs of mating with kin are highest when women are fertile, women may tend to avoid male kin more during the high-fertility phase of the menstrual cycle. Consistent with this hypothesis, Lieberman, Pillsworth and Haselton (13) reported that women had less phone contact with their fathers, but not mothers, during the high-fertility phase of the menstrual cycle.

Social support during pregnancy has benefits for reproductive success, and female kin are likely to be a particularly good source of social support for women (14-17). Consequently, women may show enhanced affiliative responses to female kin when pregnant. Because raised progesterone is characteristic of pregnancy (18), they may also show enhanced affliative responses to kin when progesterone is high outside of pregnancy. Consistent with this hypothesis, DeBruine, Jones and Perrett (19) reported that women's preferences for self-resembling female, but not male, faces were correlated with estimated progesterone levels.

Thus, there are two different, though not mutually exclusive, hypotheses that predict an effect of women's hormonal status on their preference for kinship cues: increased inbreeding avoidance when fertility is high (i.e., when estradiol-to-progesterone ratio is high, 20, 21) and increased kin affiliation when raised progesterone prepares the body for pregnancy. While there is some previous evidence for both hypotheses (13, 19), these studies did not measure actual hormone levels.

In light of the above, we carried out a longitudinal study to investigate the hormonal correlates of responses to facial self-resemblance in a large sample of women. Each woman (N=176) was tested weekly over at least four weeks. In each test session, women provided saliva samples, which were

assayed for estradiol and progesterone. In each test session, women also completed tasks identical to those used to assess responses to self-resembling faces in DeBruine*, et al.* (22). These tasks assessed responses to target faces versus each of ten non-target faces. On half of the trials, the target face had been manipulated to resemble the participant. On the other half of the trials, the target face had been manipulated to resemble an age-, ethnicity- and sex-matched control participant. Both male and female versions of target faces were created. Attractiveness and trustworthiness judgments of male and female faces were made in four separate blocks of trials.

The inbreeding-avoidance hypothesis predicts that preference for self-resembling male faces will be negatively associated with estradiol-to-progesterone ratio. The kin-affiliation hypothesis predicts that preference for self-resembling female faces will be positively associated with progesterone.

**Results**

***Testing the inbreeding-avoidance hypothesis.*** We used a binomial mixed model (23, 24) to predict responses to male faces on the two-alternative forced-choice task (1=chose target face, 0=chose non-target face). Categorical predictors were self resemblance (1=target face resembled self, 0=target face resembled control) and judgment type (0.5=trustworthiness, −0.5=attractiveness). Continuous predictors were estradiol, progesterone, and estradiol-to-progesterone ratio. Each hormone was subject-mean centered and scaled so the majority of the distribution ranged from −0.5 to 0.5 for the purposes of model fitting. Random effects were specified maximally, following Barr (25) and Barr, Levy, Scheepers and Tily (26). Data file and analysis script are publicly available (27).

A significant main effect of self resemblance (beta=0.15, SE=0.03, z=5.67, p<.001) indicated that self-resembling faces were chosen more often than control-resembling faces. Crucially, this effect of self resemblance was not qualified by an interaction with estradiol-to-progesterone ratio (beta=0.22, SE=0.14, z=1.54, p=0.125). Note that this positive non-significant interaction was in the opposite direction to what would be predicted by the inbreeding-avoidance hypothesis. No other effects or interactions were significant (all p>.156), other than an interaction between self resemblance and judgment type (beta=−0.13, SE=0.06, z=−2.22, p=.027). This interaction indicated that the effect of self resemblance was stronger for attractiveness than trustworthiness judgments.

Some studies investigating fertility-linked hormonal correlates of mating psychology have used the interaction between estradiol and progesterone as

a proxy for fertility, rather than estradiol-to-progesterone ratio (21). Repeating this analysis with estradiol-to-progesterone ratio replaced by the interaction between estradiol and progesterone also showed no evidence that aversion to kinship cues in men's faces was stronger in hormonal states associated with high fertility (see supplemental materials).

***Testing the kin-affiliation hypothesis.*** We used an identical model to predict responses to female faces. This model also showed a significant main effect of self resemblance (beta=0.28, SE=0.03, z=10.43, p<.001), indicating that self-resembling faces were chosen more often than control-resembling faces. Consistent with the kin-affiliation hypothesis, this effect of self resemblance was qualified by an interaction with progesterone (beta=0.40, SE=0.18, z=2.16, p=.031); preferences for self resemblance were stronger when progesterone was higher. Unexpectedly, the effect of self resemblance was also qualified by an interaction with estradiol (beta=−0.51, SE=0.23, z=−2.20, p=.028); preferences for self resemblance were weaker when estradiol was higher (note that this effect is independent of the predicted interaction between progesterone and self resemblance). The interaction between self resemblance and judgment type was not significant (beta=−0.12, SE=0.06, z=−1.89, p=.059), although the effect of self-resemblance again tended to be stronger for attractiveness than trustworthiness judgments. No other effects or interactions were significant (all p>.148).

The predicted interaction between progesterone and self resemblance was also significant when estradiol-to-progesterone ratio was replaced in the model by the interaction between estradiol and progesterone (see supplemental materials).

***Additional Analyses.*** The supplemental materials report additional analyses testing for possible effects of cortisol and testosterone. These analyses showed no effects of these hormones on responses to self-resembling faces.

**Discussion**

Here we tested two hypotheses about the relationship between women's hormones and responses to the kinship cue of facial resemblance. Our data showed no evidence for the inbreeding avoidance hypothesis; responses to self-resemblance in male faces did not track changes in estradiol-to-progesterone ratio, which is a hormonal correlate of fertility. By contrast, our data support the kin affiliation hypothesis; responses to self-resemblance in female faces increased when raised progesterone prepares the body for pregnancy.

Our findings complement previous research showing that preferences for self-resembling female, but not male, faces were greater when estimated progesterone levels were higher (19). In contrast, our findings are not consistent with previous research showing that phone contact with male, but not female, kin was decreased when estimated fertility was higher (13). These findings could be reconciled if different kinship cues are related to behavioral outcomes in different ways.

The dominant model of the architecture of human kin recognition proposes that kinship cues are integrated into a single kinship index that regulates prosocial and sexual behaviors (10). However, previous research contradicts this model by showing that family composition was related to sexual, but not prosocial, responses to facial resemblance (22). Here, we show that within-woman changes in hormones are related to prosocial, but not sexual, responses to facial resemblance. Together, these findings suggest a necessary revision to the model of human kin recognition, where different kinship cues are able to influence sexual and prosocial behaviors in different ways.

**Methods**

***Participants.*** Participants were recruited as part of a bigger project on the influence of endogenous hormones on social perception, in which participants took part in up to three blocks of five weekly test sessions completing a number of different experimental tasks (28-30). From this bigger set of participants, data from those participants in Block 1 was analyzed who consistently reported not to have used hormonal contraceptives at the time of the study or in the 90 days prior to their participation, and who completed the reported experimental task in all weekly test sessions (n=145). Participants' data from Block 2 was included if participants had not previously completed the experimental task in Block 1 or if reported hormonal contraceptive use changed from "yes" in Block 1 to "no" in Block 2 (N=31). Each participant was paired with a control participant from the same sample who was approximately matched for age (mean absolute age difference between controls and participants = 0.80 y, SD=1.32 y) (1).

***Materials.*** Self-resembling target faces were created by applying 50% of the shape difference between each participant's face and a same-sex (i.e. female) composite face to same-sex and opposite-sex composite faces, to produce same-sex and opposite-sex self-resembling faces (22, 31). Note that this method of manipulating self-resemblance in opposite-sex faces avoids the feminization of male stimulus faces that can be observed when simply

blending self and opposite-sex faces. Non-target faces were made by using the same methods on 10 female individual faces from a different data set.

***Procedure.*** The effect of self-resemblance on face preferences was tested by following the exact procedure from DeBruine*, et al.* (22). Faces were presented in four randomly ordered blocks: male attractiveness, male trustworthiness, female attractiveness, and female trustworthiness. In each block, 20 face pairs were presented: 10 self–non-target pairs and 10 control–non-target pairs. Participants viewed pairs on a computer screen and indicated which face they found more physically attractive or more trustworthy by clicking on the face. The order of presentation of face pairs was randomized for each block, and the side of presentation of faces was randomized for each trial.

***Saliva samples.*** Participants provided a saliva sample via passive drool (32) in each test session. Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, smoking, drinking, chewing gum, or brushing their teeth in the 60 minutes prior to participation. Each woman's test sessions took place at approximately the same time of day to minimize effects of diurnal changes in hormone levels (33, 34).

Saliva samples were frozen immediately and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary 17β-Estradiol Enzyme Immunoassay Kit 1-3702 (M=2.79pg/mL, SD=1.00pg/mL, sensitivity=0.1 pg/mL, intra-assay CV=7.13%, inter-assay CV=7.45%) and Salivary Progesterone Enzyme Immunoassay Kit 1-1502 (M=154.58pg/mL, SD=103.74pg/mL, sensitivity=5 pg/mL, intra-assay CV=6.20%, inter-assay CV=7.55%). Hormone levels more than three standard deviations from the sample mean for that hormone or where Salimetrics indicated levels were outside their sensitivity range were excluded from the dataset (<.1% of hormone measures were excluded for these reasons). The descriptive statistics given above to not include these excluded values.

**Acknowledgments**
This research was supported by European Research Council grants awarded to LMD (KINSHP) and BCJ (OCMATE).

**References**


1. Bateson P (1983) Optimal outbreeding. in *Mate Choice*, ed Bateson P (Cambridge University Press, Cambridge, New York, Melbourne), pp 257-277.
2. Charlesworth D & Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Ann. Rev. Ecol. Syst.* 18:237-268.
3. Charlesworth D & Willis JH (2009) The genetics of inbreeding depression. *Nature Review Genetics* 10(11):783-796.
4. Keller LF & Waller DM (2002) Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17(5):230-241.
5. Hamilton WD (1964) The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1-16.
6. Bailenson JN, Iyengar S, Yee N, & Collins NA (2008) Facial similarity between voters and candidates causes influence. *The Public Opinion Quarterly* 72(5):935-961.
7. DeBruine LM (2002) Facial resemblance enhances trust. *Proceedings of the Royal Society B: Biological Sciences* 269:1307-1312.
8. DeBruine LM (2005) Trustworthy but not lust-worthy: context-specific effects of facial resemblance. *Proceedings of the Royal Society B: Biological Sciences* 272:919-922.
9. Krupp DB, DeBruine LM, & Barclay P (2008) A cue of kinship promotes cooperation for the public good. *Evol. Hum. Behav.* 29:49-55.
10. Lieberman D, Tooby J, & Cosmides L (2007) The architecture of human kin detection. *Nature* 445(7129):727-731.
11. Richter N, Tiddeman B, & Haun DBM (2016) Social preference in preschoolers: effects of morphological self-similarity and familiarity. *PLOS ONE* 11(1):e0145443.
12. Sznycer D, De Smet D, Billingsley J, & Lieberman D (2016) Coresidence duration and cues of maternal investment regulate sibling altruism across cultures. *Journal of Personality and Social Psychology* 111(2):159-177.
13. Lieberman D, Pillsworth EG, & Haselton MG (2011) Kin affiliation across the ovulatory cycle. *Psychological Science* 22(1):13-18.
14. Nuckolls KB, Cassel J, & Kaplan BH (1972) Psychosocial assets, life crisis and the prognosis of pregnancy. *American Journal of Epidemiology* 95(5):431-441.
15. Sear R & Mace R (2008) Who keeps children alive? A review of the effects of kin on child survival. *Evol. Hum. Behav.* 29(1):1-18.
16. Silk JB, Alberts SC, & Altmann J (2003) Social Bonds of Female Baboons Enhance Infant Survival. *Science* 302:1231-1234.
17. Silk JB*, et al.* (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences* 276:3099-3104.
18. Johnson MH (2007) *Essential Reproduction* (Blackwell Publishing) 6 Ed.
19. DeBruine LM, Jones BC, & Perrett DI (2005) Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. *Hormones and Behavior* 47:379-383.

20. Gangestad SW & Haselton MG (2015) Human estrus: implications for relationship science. *Current Opinion in Psychology* 1:45-51.
21. Puts DA*, et al.* (2013) Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. *Hormones and Behavior* 63(1):13-19.
22. DeBruine LM*, et al.* (2011) Opposite-sex siblings decrease attraction, but not prosocial attributions, to self-resembling opposite-sex faces. *Proc Natl Acad Sci USA* 108:11710-11714.
23. R Core Team (2017) R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria).
24. Bates D, Maechler M, Bolker B, & Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67(1):1-48.
25. Barr DJ (2013) Random effects structure for testing interactions in linear mixed-effects models. *Frontiers in Psychology* 4(328).
26. Barr DJ, Levy R, Scheepers C, & Tily HJ (2013) Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language* 68(3):255-278.
27. Holzleitner IJ*, et al.* (2017) Hormonal regulation of women's prosocial, but not sexual, responses to kinship cues. DOI:10.17605/OSF.IO/WNHMA.
28. Jones BC*, et al.* (2017) General sexual desire, but not desire for uncommitted sexual relationships, tracks changes in women's hormonal status. DOI:10.1101/155788.
29. Jones BC*, et al.* (2017) Hormonal correlates of pathogen disgust: Testing the Compensatory Prophylaxis Hypothesis. DOI:10.1101/156430.
30. Jones BC*, et al.* (2017) Women's Preferences For Facial Masculinity Are Not Related To Their Hormonal Status. DOI:10.1101/136549.
31. DeBruine LM, Jones BC, Little AC, & Perrett DI (2008) Social perception of facial resemblance in humans. *Archives of Sexual Behavior* 37:64-77.
32. Papacosta E & Nassis GP (2011) Saliva as a tool for monitoring steroid, peptide and immune markers in sport and exercise science. *Journal of Science and Medicine in Sport* 14(5):424-434.
33. Bao AM*, et al.* (2003) Diurnal rhythm of free estradiol during the menstrual cycle. *European Journal of Endocrinology* 148(2):227-232.
34. Veldhuis JD*, et al.* (1988) Physiological Profiles of Episodic Progesterone Release During the Midluteal Phase of the Human Menstrual Cycle: Analysis of Circadian and Ultradian Rhythms, Discrete Pulse Properties, and Correlations With Simultaneous Luteinizing Hormone Release. *The Journal of Clinical Endocrinology & Metabolism* 66(2):414-421.