

The reward value of infant facial cuteness tracks within-subject changes in women's salivary testosterone

Amanda C Hahn^a, Lisa M DeBruine^a, Claire I Fisher^a & Benedict C Jones^a

a. Institute of Neuroscience & Psychology, University of Glasgow, Glasgow, G12 8QB, UK.

Corresponding author address: Amanda Hahn, Institute of Neuroscience & Psychology, University of Glasgow, Glasgow, G12 8QB, UK.

Corresponding author telephone: 0141-330-1677

Corresponding author email: Amanda.Hahn@glasgow.ac.uk

The reward value of infant facial cuteness tracks within-subject changes in women's salivary testosterone

Abstract

“Baby schema” refers to infant characteristics, such as facial cues, that positively influence cuteness perceptions and trigger caregiving and protective behaviors in adults. Current models of hormonal regulation of parenting behaviors address how hormones may modulate protective behaviors and nurturance, but not how hormones may modulate responses to infant cuteness. To explore this issue, we investigated possible relationships between the reward value of infant facial cuteness and within-woman changes in testosterone, estradiol, and progesterone levels. Multilevel modeling of these data showed that infant cuteness was more rewarding when women's salivary testosterone levels were high. Moreover, this within-woman effect of testosterone was independent of the possible effects of estradiol and progesterone and was not simply a consequence of changes in women's cuteness perceptions. These results suggest that testosterone may modulate differential responses to infant facial cuteness, potentially revealing a new route through which testosterone shapes selective allocation of parental resources.

Keywords: parenting; testosterone; reward; face perception; incentive salience

Introduction

Konrad Lorenz suggested that infant cues (“baby schema”), and infant *facial* cues in particular, function in part to motivate adult caregiving and protective behavior (Lorenz, 1943). Consistent with this proposal, exaggerating baby schema in images of infant faces increases the perceived cuteness of infants (Alley, 1981, 1983a; Glocker et al., 2008; Little, 2012). Moreover, adults typically report being more likely to care for, protect, and form close bonds with infants displaying facial cues that are perceived to be cute (Alley, 1981, 1983b; Glocker et al., 2008; Hildebrandt & Fitzgerald, 1978). Similar patterns of results have also been observed in studies of both the actual care provided for infants (Badr-Zahr & Abdallah, 2001) and the strength of mother-infant bonds (Hildebrandt & Fitzgerald, 1983; Langlois et al., 1995).

Recent studies of the reward value of infant facial cues have also underlined the importance of infant cuteness. For example, Glocker et al. (2009) reported that women showed greater activity in brain regions associated with the processing of rewards (e.g., nucleus accumbens and anterior cingulate cortex) when viewing high-cuteness versions of images of infant faces (i.e., versions in which baby schema was exaggerated) than when viewing low-cuteness versions (i.e., versions in which baby schema was reduced). Studies using behavioral measures of the reward value of faces, such as key-press tasks (Aharon et al., 2001), also suggest that viewing cute infant faces is rewarding; people are willing to expend more effort to view high-cuteness versions of infant face images than they are to view low-cuteness versions (Hahn et al., 2013). This pattern of results has also been observed using

unmanipulated infant faces (Parsons et al., 2011; Sprengelmeyer et al., 2013).

Several lines of evidence suggest that perceptions of adult faces covary with hormone levels in women. For example, preferences for masculine characteristics in men's faces tend to be stronger when women's testosterone (Bobst et al., 2014; Welling et al., 2007) and/or estradiol (Roney & Simmons, 2008; Roney et al., 2011) levels are high. While these studies focused on women's judgments of the attractiveness of men's faces, other studies have investigated the effects of changes in women's hormone levels on their perceptions of emotional expressions in adult faces (Conway et al., 2007; Derntl et al., 2008; Guapo et al., 2009). For example, women appear to be more sensitive to facial expressions associated with threat when their progesterone levels are high (Conway et al., 2007; Derntl et al., 2008).

Given the large and rapidly growing body of research demonstrating links between hormone levels and women's responses to adult faces, together with the importance of facial cues for motivating care and protection of infants (Alley, 1983b; Glocker et al., 2008) and links between sex hormones and parental behaviors (Rilling, 2013), it is perhaps surprising that relatively little work has investigated whether women's hormone levels also predict their responses to infant facial cuteness. The current study sought to address this issue, focusing on the possibility that within-subject changes in women's hormone levels may predict the reward value of infant facial cuteness.

To explore the possible links between within-subject changes in women's hormone levels and the reward value of infant facial cuteness, we assessed the reward value of infant facial cuteness to women in five weekly test sessions. Reward value was assessed via a standard key-press task similar to those used to assess the reward value of infant faces in previous research (Hahn et al., 2013; Parsons et al., 2013; Yamamoto et al., 2009). Saliva samples were also collected in each test session and analyzed for testosterone, estradiol, and progesterone levels. Multilevel modeling was then used to test whether changes in the reward value of infant facial cuteness were predicted by changes in salivary testosterone, estradiol, or progesterone levels. Following other recent research on responses to infant facial cuteness (Hahn et al., 2013; Lobmaier et al., 2010; Sprengelmeyer et al., 2009), stimuli were images of infant faces in which shape characteristics associated with perceived cuteness had been exaggerated or reduced using computer graphic methods (see Figure 1).



Figure 1. Examples of high-cuteness (left) and low-cuteness (right) versions of faces used in our study. High-cuteness and low-cuteness versions differ in 2D shape only along an empirically defined perceived cuteness dimension.

Methods

Participants

Sixty heterosexual women (mean age=21.03 years, SD=2.81 years) participated in the study. All participants were students at the University of Glasgow (Scotland, UK) and provided informed consent prior to participation. None of these women were currently pregnant, breastfeeding, or taking any form of hormonal supplement, and all indicated that they had not taken any form of hormonal supplement in the 90 days prior to participation. None of our participants had children. Data from 37 of these participants are also reported in Pisanski et al's (2014) recent study of hormone-modulated voice preferences. Data from 44 of these participants are also reported in Wang et al's (in press) recent study of hormone-modulated responses to adult facial cues. Note that, other than the hormone values, there was no overlap in the data analyzed across these three pieces of work.

Infant face stimuli

The techniques we used to manufacture high-cuteness and low-cuteness versions of infant faces have been used to manufacture stimuli in many previous studies of women's responses to infant facial cues (Hahn et al., 2013; Lobmaier et al., 2010; Sprengelmeyer et al., 2009). First, we used established computer-graphic techniques for manufacturing face prototypes (Tiddeman et al., 2001) to create high-cuteness and low-cuteness prototypes with the average shape information of images of the 20 infant faces that received the highest cuteness ratings (for the high-cuteness prototype) and 20 infant faces that received the lowest cuteness ratings (for the low-cuteness

prototype) in a previous study of cuteness ratings of 58 White infant faces (Sprenelmeyer et al., 2009). Following Hahn et al. (2013), we then created high-cuteness versions of 10 different infant face images by adding 50% of the linear differences in 2D shape between the high-cuteness and low-cuteness infant prototypes to each of the 10 infant face images. Low-cuteness versions of the 10 infant face images were also created by subtracting 50% of the linear differences in 2D shape between the high-cuteness and low-cuteness infant prototypes from each of the 10 infant face images. The computer graphic methods used to transform shape information in face images are described in Tiddeman et al. (2001). Following Hahn et al. (2013), mouth shape was held constant between the high-cuteness and low-cuteness versions of each image, controlling for the possible effects of expression on responses to infant faces (Lobmaier et al., 2010). Example images are shown in Figure 1.

Procedure

Each woman completed five weekly test sessions. During each test session, participants provided a saliva sample via passive drool (Papacosta & Nassis, 2011). Each woman's test sessions took place at the same time of day to control for possible effects of diurnal changes in hormone levels (Bao et al., 2003; Veldhuis et al., 1988). In each test session, participants completed two tasks (rating task and key-press task) in a randomized order.

Key-press task. The key-press task that we used to measure the reward value of infant facial cuteness has also been used to assess the reward value of

infant faces in several previous studies (Charles et al., 2013; Hahn et al., 2013; Parsons et al., 2011, 2013; Yamamoto et al., 2009). In this key-press task, all 20 infant face images (i.e., the high-cuteness and low-cuteness versions of the 10 infant faces) were presented in a fully randomized order. Participants controlled the viewing duration of each face image by repeatedly pressing designated keys on their keyboard after initiating each trial by pressing the space bar. Participants could either increase the length of time a given face was displayed by alternately pressing the 7 and 8 keys or decrease the length of time a given face was displayed by alternately pressing the 1 and 2 keys. Each key press increased or decreased the viewing duration by 100ms. The default viewing duration for each image (i.e., the length of time a face remained onscreen if no keys were pressed) was 4 seconds. Participants were told that the key-press task would last for a total of 1.5 minutes in order to discourage responses aimed at changing the length of engagement with the task. However, in reality, the total length of the key-press task was dependent on participants' responses. All participants key pressed at least once in all test sessions (mean number of total key presses=269.21, SD=212.67). Participants completed a block of practice trials at the start of each test session to ensure they understood the key-press task (face images were not shown in this block of practice trials).

Following previous studies of the reward value of infant facial cues (e.g., Hahn et al., 2013; Parsons et al., 2013; Yamamoto et al., 2009), key-press scores for each face were calculated by subtracting the number of key presses made to decrease viewing time from those made to increase viewing time. These

key-press scores were used to calculate each participant's *cuteness reward score* separately for each test session by subtracting the mean key-press score for the low-cuteness versions of infant faces from the mean key-press score for the high-cuteness versions ($M=2.63$, $SD=5.54$). Higher scores indicate a greater positive effect of the cuteness manipulation on the reward value of infant faces.

Rating task. The rating task that we used to assess the effect of infant facial cues on women's perceptions of infant cuteness has been used in several previous studies of women's perceptions of infant facial cues (e.g., Glocker et al., 2009; Hahn et al., 2013; Little, 2012). In this task, all 20 infant face images (i.e., the high-cuteness and low-cuteness versions of the 10 infant faces) were presented in a fully randomized order and were rated for cuteness on a 1 (not cute) to 7 (very cute) scale.

We calculated each participant's *cuteness perception score* separately for each test session by subtracting the mean rating they gave to the low-cuteness versions of infant faces from the mean rating they gave to the high-cuteness versions ($M=0.28$, $SD=0.43$). Higher scores indicate that the cuteness manipulation had a greater positive effect on women's ratings of infant faces.

Hormonal Assays

Saliva samples were frozen immediately and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis.

Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, drinking, chewing gum or brushing their teeth in the 60 minutes prior to participation. Samples were assayed by Salimetrics using the Salivary 17β -Estradiol Enzyme Immunoassay Kit 1-3702 (M=4.31 pg/mL, SD=1.40 pg/mL, intra-assay CV = 7.13%, inter-assay CV = 7.45%, sensitivity = 0.1 pg/mL), Salivary Progesterone Enzyme Immunoassay Kit 1-1502 (M=146.33 pg/mL, SD=103.20 pg/mL, intra-assay CV = 6.20%, inter-assay CV = 7.55%, sensitivity = 5 pg/mL), and Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (M=82.86 pg/mL, SD=22.53 pg/mL, intra-assay CV = 4.60%, inter-assay CV = 9.83%, sensitivity = < 1.0 pg/mL). All assays passed Salimetrics' quality control.

Analysis

We used multilevel modeling to test for within-subject effects of hormone levels on the reward value of infant facial cuteness. Analyses were conducted using R (R Core Team, 2013), *lme4* (Bates et al., 2014), and *lmerTest* (Kuznetsova et al., 2013). Responses on the key-press task were used to calculate *cuteness reward scores*, which reflected the difference in reward value between high-cuteness and low-cuteness versions of infant faces. These difference scores served as our dependent variable. Higher *cuteness reward scores* indicate a greater positive effect of the cuteness manipulation on the reward value of infant faces. Testosterone, estradiol, and progesterone (each centered on their grand means) were entered simultaneously at the test

session level to test for independent within-subject effects of these hormones. The intercept was allowed to vary by participant.

Results

Our analysis of *cuteness reward scores* showed a significant intercept ($t=6.97$, $p<.001$), confirming that high-cuteness versions of infant faces were more rewarding than low-cuteness versions. There was also a significant, positive within-subject effect of testosterone levels ($t=2.67$, $p=.009$), indicating that the positive effect of cuteness on the reward value of infant faces was greater in test sessions where salivary testosterone levels were high. The corresponding effects for estradiol ($t=0.60$, $p=.55$) and progesterone ($t=-1.36$, $p=.18$) levels were not significant. Together, these results suggest that testosterone modulates the reward value of infant facial cuteness in women. Figure 2 illustrates the within-subject effects of testosterone, estradiol, and progesterone on *cuteness reward scores*. The effect of testosterone level described above remained significant when we excluded the three women who showed the greatest change in *cuteness reward scores* across the five test sessions from the dataset ($t=2.96$, $p=.004$), confirming that these women were not driving the significant effect of testosterone in our initial analysis. Estradiol ($t=-0.75$, $p=.46$) and progesterone ($t=-1.13$, $p=.26$) did not have significant effects in this additional analysis.

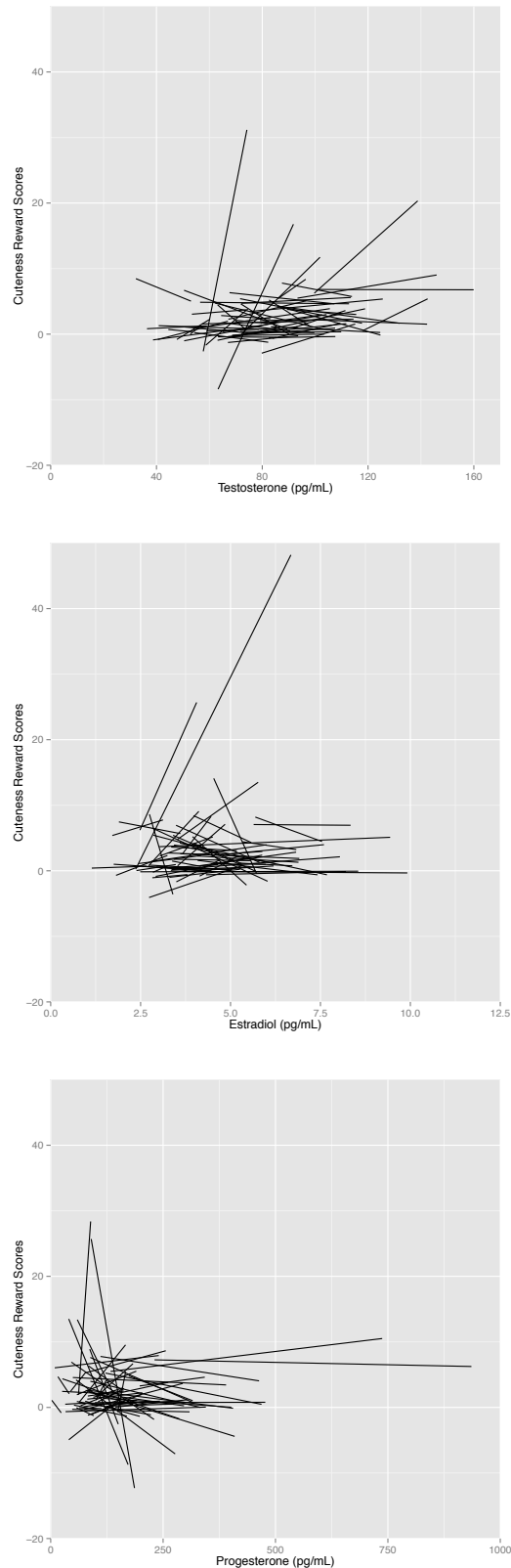


Figure 2. Changes in *cuteness reward scores* as a function of testosterone, estradiol, and progesterone levels. Only the effect of testosterone was significant. Graphs show lines of best fit for individual participants. The pattern of results did not change when the three women showing the largest change in cuteness reward scores were excluded from the dataset.

Additional analyses in which key-press scores for high- and low-cuteness versions of infant faces were analyzed separately showed that testosterone had significant positive effects on the reward value of both high-cuteness ($t=3.21$, $p=.001$) and low-cuteness versions ($t=2.61$, $p=.009$) of infant faces. Thus, the effect of testosterone on *cuteness reward scores* described in our initial analysis reflects a greater positive effect of testosterone on the reward value of high-cuteness infants than on low-cuteness infants.

So that we could investigate the possibility that changes in women's *perceptions* of infant cuteness mediate the observed testosterone-related change in *cuteness reward scores*, women also rated the cuteness of the face stimuli in each test session. These ratings were used to calculate *cuteness perception scores*, which reflected the difference in ratings between high-cuteness and low-cuteness versions of infant faces. Higher *cuteness perception scores* indicate a greater positive effect of the cuteness manipulation on cuteness ratings of infant faces.

First, we repeated our initial analysis, this time with *cuteness perception scores* as our dependent variable. In this analysis of *cuteness perception scores*, the intercept was again significant ($t=7.62$, $p<.001$), confirming that women generally rated high-cuteness versions of infant faces to be cuter than low-cuteness versions. The effects of testosterone ($t=1.01$, $p=.32$), estradiol ($t=-1.23$, $p=.22$), and progesterone ($t=0.17$, $p=.86$) levels were not significant in this analysis, however.

Next, we repeated our initial analysis of *cuteness reward scores*, this time with *cuteness perception scores* entered as an additional predictor at the test session level. As in our initial analysis of *cuteness reward scores*, this analysis showed a significant, positive within-subject effect of testosterone level ($t=2.61$, $p=.010$). This result confirmed that the effect of testosterone on *cuteness reward scores* was not simply a consequence of changes in women's perceptions of infant cuteness. The effects for estradiol ($t=0.68$, $p=.50$) and progesterone ($t=-1.27$, $p=.21$) were not significant in this analysis. This analysis also showed that women tended to have higher *cuteness reward scores* in test sessions where they had higher *cuteness perception scores* ($t=1.85$, $p=.065$), although this within-subject effect of *cuteness perception scores* was not significant.

The equations and full results for these models are given in our Supplemental Materials. Including *participant age*, *estradiol-to-progesterone ratio*, or *session number* (1, 2, 3, 4, 5) as an additional predictor in each of the models did not alter the patterns of results described for any of the models. Furthermore, there were no significant effects of *estradiol-to-progesterone ratio* in any of these analyses (all $|t|<0.06$, all $p>.95$). Our Supplemental Materials also report additional analyses showing that the relationship between our measured hormone levels and menstrual cycle phase are consistent with those reported in previous work.

Discussion

Our analyses of women's responses to high-cuteness and low-cuteness versions of infant faces demonstrated that high-cuteness versions of infant faces generally had greater reward value than low-cuteness versions. This effect of cuteness on the reward value of infant faces is consistent with the results of previous behavioral (Hahn et al., 2013) and neuroimaging (Glocker et al., 2009) studies investigating the reward value of cute infant facial characteristics.

While our results show that cuteness influences the reward value of infant faces in general, our analyses also revealed systematic variation in the extent to which infant facial cuteness was rewarding. The effect of cuteness on the reward value of infant faces (i.e., the extent to which high-cuteness versions of infant faces were more rewarding than low-cuteness versions) was greater in test sessions where women's salivary testosterone levels were high. The effect of testosterone level on the reward value of infant facial cuteness was independent of the possible effects of estradiol and progesterone.

Additionally, neither estradiol nor progesterone had significant effects on the reward value of infant facial cuteness. Note that additional analyses showed that the reward value of both high- and low-cuteness versions of infant faces was increased when testosterone level was high, indicating that, although testosterone generally increases the reward value of infant faces, this effect is greater for cuter infant faces. Together, these results suggest that women's testosterone may modulate the reward value of cute characteristics in infant faces, potentially implicating hormonal changes in variation in the reward value of infant facial cuteness.

Previous work suggests that administering testosterone to women enhances responses to infant vocalizations in the thalamocingulate circuit, a network of brain regions implicated in both reward processing and parental behavior (Bos et al., 2010). Note, however, that Bos et al. (2010) did not manipulate the perceived cuteness of the vocalizations. Our results linking endogenous testosterone in women to the reward value of infant facial cuteness complement this finding and extend it by suggesting that testosterone level may also enhance differential responses to infants (i.e., may also enhance the extent to which the reward value of infants perceived to be particularly cute is greater than that of infants perceived to be less cute). Although further research is needed to investigate whether *administering* testosterone to women increases the reward value of infant facial cuteness, our and Bos et al.'s (2010) results together suggest that testosterone may modulate women's responses to both facial and vocal cues in infants. While our results suggest that the reward value of infant facial cuteness tracks within-subject changes in women's testosterone levels, the extent to which different sources of variation in women's testosterone level (e.g., menstrual cycle phase, various situational factors) contribute to these within-subject changes are unknown. That the effects of administering testosterone to women on the reward value of infant vocalizations and the relationship between naturally occurring within-subject variation in women's testosterone levels and the reward value of infant facial cuteness are similar suggests that the effects observed in the current work are unlikely to be specific to any single source of variation in testosterone levels.

While our results complement Bos et al's (2010) findings for testosterone and infant vocalizations, they differ somewhat from the findings of two studies examining the possible effects of hormonal condition on responses to infant facial cuteness. Sprengelmeyer et al. (2009) found that women using hormonal contraceptives showed greater perceptual sensitivity to infant facial cuteness than did women with natural menstrual cycles (but see Sprengelmeyer et al., 2013 for an unsuccessful replication of this effect) and that pre-menopausal women showed greater perceptual sensitivity to infant facial cuteness than did post-menopausal women. They interpreted these differences as evidence that estradiol and/or progesterone levels influence women's perceptual judgments of infant cuteness. By contrast with the results of these between-subject comparisons, and using a within-subject design and measured hormone levels, we found no evidence that sex hormones regulate women's perceptual judgments of infant cuteness. More recently, Sprengelmeyer et al. (2013) found no differences in the reward value of infant facial cuteness (assessed using a key press paradigm similar to the paradigm we used) among test sessions scheduled during the late follicular, luteal, and menstrual phases of the menstrual cycle in a sample of 11 women. By contrast, we observed within-subject changes in the reward value of infant facial cuteness that occurred as a function of within-subject changes in measured testosterone levels. The differences between these results and those of our study could reflect our use of a larger sample of women (N=60 versus N=11), our focus on measured hormone levels (rather than cycle phase), or both of these factors.

Recent models of the role that hormones may play in parental behaviors propose that testosterone increases behaviors that function to protect offspring, but decreases nurturance behavior (reviewed in van Anders et al., 2011). Such models emphasize the role testosterone may play in generalized motivational dispositions related to parenting. By contrast with this strong emphasis on general motivational dispositions, our data highlight an additional role that testosterone may play in responses to infant cues: enhancing differential motivational responses to infant facial cues that are important for selective allocation of parental resources (i.e., cuteness). Thus, our data integrate concepts and ideas from both current neuroendocrinological models of parental behavior (van Anders et al., 2011) and models that highlight the importance of differential allocation of parental effort according to the perceived cuteness of infants (Alley, 1983b; Glocker et al., 2008). Our results suggest that the reward value of both high-cuteness and low-cuteness versions of infant faces is increased when testosterone level is high, consistent with the proposal that increases in testosterone level may increase women's motivation to engage in protective behaviors (van Anders et al., 2011). However, our results also suggest that the positive effect of testosterone on the reward value of high-cuteness versions of infant faces is particularly pronounced, suggesting that the effect of testosterone on women's motivation to engage in protective behaviors may be more pronounced for cuter infants. Given facial cuteness is correlated with physical condition in infants (Volk et al., 2005), such differential responses may function to optimize allocation of parental effort and resources.

Our results may also shed light on the neurobiological mechanisms through which testosterone influences motivational responses to infant cues. One possibility is that testosterone influences such responses via conversion to estradiol (Bos et al., 2010), as appears to be the case for male parental behaviors in some non-human animals (Trainor & Marler, 2002). That the reward value of infant facial cuteness was related to women's testosterone levels independently of the possible effects of estradiol in the current study does not support this explanation, however. Our data then offer indirect support for the alternative account of the neurobiological mechanisms through which testosterone influences responses to infant cues that was suggested by Bos et al. (2010), in which testosterone influences responses to infant cues because of its role in the synthesis of vasopressin (de Vries, 2008). The specificity of the effects of testosterone observed in the current study is also unclear. For example, administering testosterone to women increases the reward value of financial incentives (Hermans et al., 2010), suggesting that testosterone may play an important role in regulating women's reward sensitivity in multiple domains.

By contrast with our results for the reward value of infant facial cuteness, the effect of cuteness on perceptual ratings of infant faces was not related to changes in women's hormone levels. Moreover, the effect of testosterone level on the reward value of infant facial cuteness remained significant when we controlled for changes in women's cuteness ratings of the infant faces. These results demonstrate that the relationship between testosterone and the

reward value of infant facial cuteness in women was not simply due to changes in perceptions of infant faces. This pattern of results is consistent with the proposal (Parsons et al., 2011; Yamamoto et al., 2009) that infant facial cuteness can have dissociable effects on measures of wanting (i.e., reward) and liking (i.e., ratings).

In common with previous studies of the reward value of infant cues (Bos et al., 2010; Glocker et al., 2009), we tested only nulliparous, young women. Further research is needed to investigate the effects of parity on the reward value of infant cues and how these effects might interact with within-subject changes in hormone levels.

In conclusion, our analyses of women's responses to high-cuteness versus low-cuteness versions of infant faces suggest that testosterone, rather than estradiol or progesterone, may modulate the reward value of infant facial cuteness. These data extend previous research suggesting that testosterone increases protective parenting behaviors and decreases nurturance (van Anders et al., 2011), by demonstrating that testosterone might also enhance differential responses to infant facial cues that play an important role in the selective allocation of parental resources (Alley, 1983b; Glocker et al., 2009). While previous work on links between hormone levels and responses to facial cues investigated women's responses to characteristics in adult faces, our research demonstrates that changes in women's hormone levels also covary with the reward value of infant facial cuteness.

Acknowledgements

This research was funded by European Research Council Grant 282655.

References

- Aharon, I., Etcoff, N., Ariely, D., Chabris, C.F., O'Connor, E., and Breiter, H.C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32, 537–551.
- Alley, T.R. (1981). Head shape and the perception of cuteness. *Dev Psychol* 17, 650–654.
- Alley, T.R. (1983a). Age-related changes in body proportions, body size, and perceived cuteness. *Perceptual and Motor Skills*, 56, 615-622.
- Alley, T.R. (1983b). Infantile head shape as an elicitor of adult protection. *Merrill-Palmer Quarterly* 29, 411–427.
- Badr-Zahr, L.K and Abdallah, B. (2001). Physical attractiveness of premature infants affects outcome at discharge from the NICU. *Infant Behav and Dev* 24, 129–133.
- Bao, A.M., Liu, R.Y., van Someren, E.J., Hofman, M.A., Cao, Y.X., and Zhou, J.N. (2003). Diurnal rhythm of free estradiol during the menstrual cycle. *Eur J Endocrinol* 148, 227–232.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. 2014 lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6.
<http://CRAN.R-project.org/package=lme4>
- Bobst, C., Sauter, S., Foppa, A., and Lobmaier, J.S. (2014). Early follicular testosterone level predicts preference for masculinity in male faces—But not for women taking hormonal contraception. *Psychoneuroendocrinology* 41, 142-150.

- Bos, P.A., Hermans, E.J., Montoya, E.R., Ramsey, N.F., and van Honk J. (2010). Testosterone administration modulates neural responses to crying infants in young females. *Psychoneuroendocrino* 35, 114–121.
- Charles, N.E., Alexander, G.M., and Saenz, J. (2013). Motivational value and salience of images of infants. *Evol Hum Behav* 34, 373-381.
- Conway, C.A., Jones, B.C., DeBruine, L.M., Welling, L.L., Law-Smith, M.J., Perrett, D.I., Sharp, M.A., and Al-Dujalli, E.A. (2007). Salience of emotional displays of danger and contagion in faces is enhanced when progesterone levels are raised. *Horm Behav* 51, 202-206.
- de Vries, G.J. (2008). Sex differences in vasopressin and oxytocin innervation of the brain. *Prog. Brain Res* 170, 17-27.
- Derntl, B., Kryspin-Exner, I., Fernbach, E., Moser, E., and Habel, U. (2008). Emotion recognition accuracy in healthy young females is associated with cycle phase. *Horm Behav* 53, 90–5.
- Glocker, M.L., Langleben, D.D., Ruparel, K., Loughhead, J.W., Gur, R.C., and Sachser, N. (2008). Baby schema in infant faces induces cuteness perception and motivation for caretaking in adults. *Ethology* 115, 257–263.
- Glocker, M.L., Langleben, D.D., Ruparel, K., Loughhead, J.W., Valdez, J.N., Griffin, M.D., Sachser, N., and Gur, R.C. (2009). Baby schema modulates the brain reward system in nulliparous women. *P Natl Acad Sci USA* 106, 9115–9119.
- Guapo, V.G., Graeff, F.G., Zani, A.C., Labate, C.M., dos Reis, R.M., and Del-Ben, C.M. (2009). Effects of sex hormonal levels and phases of the

menstrual cycle in the processing of emotional faces.

Psychoneuroendocrino, 34, 1087–1094.

Hahn, A.C., Xiao, D., Sprengelmeyer, R., and Perrett, D.I. (2013). Gender differences in the incentive salience of adult and infant faces. *Q J Exp Psychol* 66, 200–208.

Hermans, E.J., Bos, P.A., Ossewaarde, L., Ramsey, N.F., Fernández, G., Van Honk, J., 2010. Effects of exogenous testosterone on the ventral striatal BOLD response during reward anticipation in healthy women. *Neuroimage* 52, 277-283.

Hildebrandt, K.A., and Fitzgerald, H.E. (1978). Adults' responses to infants varying in perceived cuteness. *Behav Process* 3, 159–172.

Hildebrandt, K.A., and Fitzgerald, H.E. (1983). The infant's physical attractiveness: Its effect on bonding and attachment, *Inf Mental Hlth J* 4 3-12.

Kuznetsova, A., Bruun Brockhoff, P., & Haubo Bojesen Christensen, R., 2013
lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-3.
<http://CRAN.R-project.org/package=lmerTest>

Langlois, J.H., Ritter, J.M., Casey, R.J., and Sawin, D.B. (1995). Infant face attractiveness affects maternal behaviours. *Dev Psychol* 31, 464–472.

Little, A.C. (2012). Manipulation of infant-like traits affects perceived cuteness of infant, adult and cat faces. *Ethology* 118, 775–782.

Lobmaier, J.S., Sprengelmeyer, R.H., Wiffen, B., and Perrett, D.I. (2010). Female and male responses to cuteness, age and emotion in infant faces. *Evol Hum Behav* 31, 16–21.

- Lorenz, K. (1943). Die angeborenen Formen möglicher Erfahrung. *Z Tierpsychol* 5, 235-409.
- Papacosta, E., and Nassis, G.P. (2011). Saliva as a tool for monitoring steroid, peptide and immune markers in sport and exercise science. *J Sci Med Sport* 14, 424-434.
- Parsons, C.E., Young, K.S., Bhandari, R., van Ijzendoorn, M.H., Bakermans-Kranenburg, M.J., Stein, A., and Kringelbach, M.L. (2013). The bonnie baby: experimentally manipulated temperament affects perceived cuteness and motivation to view infant faces. *Developmental Sci* 17, 1–13.
- Parsons, C.E., Young, K.S., Kumari, N., Stein, A., and Kringelbach, M.L. (2011). The motivational salience of infant faces is similar for men and women. *PLoS ONE* 6, e20632.
- R Core Team, 2013 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rilling, J.K. (2013). The neural and hormonal bases of human parental care. *Neuropsychologia*, 51, 731-747.
- Roney, J.R., and Simmons, Z.L. (2008). Women's estradiol predicts preference for facial cues of men's testosterone. *Horm Behav* 53, 14-19.
- Roney, J.R., Simmons, Z.L., and Gray, P.B. (2011). Changes in estradiol predict within-women shifts in attraction to facial cues of men's testosterone. *Psychoneuroendocrino* 36, 742-749.

- Sprengelmeyer, R.H. et al. (2009). The cutest little baby face, A hormonal link to sensitivity to cuteness in infant faces. *Psychol Sci* 20, 149–154.
- Tiddeman, B.P., Burt, D.M. and Perrett, D.I. (2001). Prototyping and transforming facial textures for perception research. *IEEE Comput Graph* 21, 42–50.
- Trainor, B.C., and Marler, C.A. (2002). Testosterone promotes paternal behaviour in a monogamous mammal via conversion to oestrogen. *Proc R Soc Lond B Biol Sci* 269, 823-829.
- van Anders, S.M., Goldey, K.L., and Kuo, P.X. (2011). The Steroid/Peptide Theory of Social Bonds: integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrino* 36, 1265-1275.
- Veldhuis, J.D., Christiansen, E., Evans, W.S., Kolp, L.A., Rogol, A.D., and Johnson, M.L. (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. *J Clin Endocrinol Metab* 66, 414-421.
- Volk, A.A., Lukjanczuk, J.M., and Quinsey, V.L. (2005). Influence of infant and child facial cues of low body weight on adults' ratings of adoption preference, cuteness, and health. *Inf Mental Hlth J* 26, 459-469.
- Welling, L.L., Jones, B.C., DeBruine, L.M., Conway, C.A., Law-Smith, M.J., Little, A.C., Feinberg, D.R., Sharp, M.A., and Al-Dujalli, E.A. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Horm Behav* 52, 156-161.

Yamamoto, R., Ariely, D., Chi, W., Langleben, D.D., and Elman, I. (2009).

Gender differences in the motivational processing of babies are determined by their facial attractiveness. *PLoS ONE* 4, e6042.