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Preparation for fatherhood: A role for olfactory communication during human pregnancy?

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Abstract:

There is evidence across a range of bi-parental species that physiological changes may occur in partnered males prior to the birth of an infant. It has been hypothesised that these hormonal changes might facilitate care-giving behaviours, which could augment infant survival. The mechanism that induces these changes has not been identified, but evidence from several species suggests that odour may play a role. The current study investigated this in humans by recording testosterone and psychological measures related to infant interest and care in men (n=91) both before and after exposure to odours from either pregnant women or non-pregnant control women. We found no evidence for effect of odour cues of pregnancy on psychological measures including self-reported sociosexual orientation and social dominance scores, ratings of adult faces, or testosterone levels. However, we found that brief exposure to post-partum odours significantly increased the reward value of infant faces. Our study is the first to show that the odour of peri-partum women may lead to upregulation of men's interest in infants.

Key words: Olfactory communication, Pregnancy, Testosterone, Bi-parental care

Introduction

In species with bi-parental offspring care, it may be adaptive to signal the presence of a pregnancy to the paired male. Communication of pregnancy status could potentially induce physiological and behavioural changes in the male partner that have subsequent influence on paternal motivation and offspring care. Indeed, there is some evidence that olfactory cues may act in this way among some non-human species.

For example, in cotton-top tamarins (*Saguinus oedipus* – a monogamous species showing bi-parental offspring care), changes in urinary glucocorticoids occur in pregnant females, that have been implicated in the upregulation of cortisol and corticosterone in male partners within 1-2 weeks (Ziegler, 2004). Males also show a peak in prolactin during their partners' mid-pregnancy (Ziegler and Snowdon, 2000). In gerbils (*Meriones unguiculatus* – also monogamous, with paternal care), males that were housed with their pregnant mates exhibited elevated plasma prolactin levels compared to unmated males (Brown et al., 1995). In monogamous and bi-parental mandarin voles (*Microtus mandarinus*), male faecal testosterone levels were reduced after the birth of a litter (Smorkatcheva et al., 2009).

However, not all studies investigating bi-parental species have found evidence of pre-birth hormonal changes. Jones and Wynne-Edwards (2001) found no effect of female contact during pregnancy on expression of male paternal and midwifery behaviours in Djungarian hamsters (*Phodopus campbelli*), which also show bi-parental care. Gubernick and Nelson (1989) found that male California mice (*Peromyscus californicus*) housed with their pregnant mates showed a rise in prolactin after the birth of their pups, but not prior to this. Gerbil males showed no decreases in testosterone

following birth and no change in paternal behaviour (Juana et al., 2010). Finally, studies have found that Siamang gibbons (*Symphalangus syndactylus*) display direct paternal care to offspring (unlike all other gibbons), but the hormonal changes which may underpin these behaviours appear to be specific to the post-partum period and dependent on father-infant proximity, rather than experience during pregnancy (Rafacz, Margulis, & Santymire, 2012).

Although the evidence across species is mixed, it should be noted that many of the studies described above are correlational. However, in an experimental study, Simoncelli and colleagues (2010) report that they were able to manipulate paternal behaviour in monogamous and bi-parental prairie voles (*Microtus ochrogaster*) by altering the level of contact with the female partner during gestation. After mating, male voles either remained in full contact with the female, were given only distal cues of the female (housed in the same room but a separate cage), or were prevented from receiving any cues from the female by housing them separately. A further group of males were also left unmated and allowed distal cues of females. At mid-gestation, all males were exposed to infants. Although most showed paternal behaviour, mated males that received either tactile or distal cues of their pregnant partner approached the infants faster, and were more likely to care for them, than unmated males that had received distal female cues or mated males prevented from any contact. Moreover, males with experience of tactile cues showed the highest level of infant contact, and had the lowest levels of observed non-social behaviour, suggesting that close physical contact with a pregnant female in some way altered paternal behaviour.

These studies in non-human species raise the question of whether there is potential for female influence on male paternal motivation and behaviour in humans,

which have altricial offspring and an extended period of infant dependency. Like marmosets, tamarins, gerbils and some voles, humans are generally monogamous, form relatively stable pair-bonds, and tend to show cooperative care of offspring, making them potential candidates for the use of chemical signalling between mates during pregnancy. In support of this, many studies have found associations between male hormone levels and their parental status. These studies investigate a range of hormones (for an overview see Wynne-Edwards, 2001, Berg & Wynne-Edwards, 2001, & Wynne-Edwards & Reburn, 200), however, the principal hormone investigated in this regard is testosterone (Wynne-Edwards, 2001), which is central to the 'challenge hypothesis' first proposed by Wingfield and colleagues (1990), which states that testosterone facilitates reproductive effort at the expense of parenting effort. Consequently, in monogamous species showing bi-parental care, it is predicted that testosterone levels may be down-regulated in order to initiate effective infant care behaviours in males. Gray and colleagues (2006) found, in their sample of 126 Chinese men, that fathers had significantly lower testosterone levels than married and unmarried non-fathers. While it could be argued that this effect arises because men with lower testosterone levels are more likely to become fathers, Gettler and colleagues (2011) have found evidence to suggest that this is not the case. In a longitudinal study of 624 Philippine men, they found that those who were not fathers at baseline and had higher levels of testosterone were more likely to have become partnered fathers at follow-up, four and a half years later, compared with those who had lower levels of testosterone at baseline. Additionally, these men showed larger declines in testosterone levels over this time frame than their single, non-father counterparts. In further support of this, Edelstein and colleagues (2015) reported longitudinal declines in men's testosterone levels during

their partners pregnancy. Furthermore, Storey et al. (2000) found that co-habiting men and women expecting a child together showed higher plasma prolactin and estradiol levels in late gestation compared to early gestation, and that these levels were strongly correlated within relationships.

The research to date appears to suggest that it is at least plausible that human males may undergo hormonal changes prior to parturition. The remaining question then is what are the mechanisms for these endocrinological changes? A number of the studies in non-human animals discussed above implicate olfactory cues, and there is a growing body of literature uncovering the vast array of information which is detectable from human body odour (for an overview see Havlíček et al., 2017). More specifically, research has shown that exposure to female body odours can affect hormones such as testosterone in men (e.g. Miller & Maner, 2010). Furthermore, Vaglio et al. (2009) found that pregnant women developed distinctive patterns of five volatile chemical compounds in sweat samples taken from the para-axillary and areolar regions. These chemicals were not found in non-pregnant, non-lactating women and there was a change in the patterns of their concentrations from early to late gestation. This suggests that odor changes could provide information on pregnancy status, and could underpin pregnancy related endocrinological changes in men.

The literature reviewed above suggests that in species where bi-parental care is important, there are potential hormonal changes which may influence care-giving behaviour in males. More specifically, consistent with indications in non-human species with bi-parental care, the literature suggests that testosterone levels in expectant human fathers decreases prior to parturition, and that this may facilitate care-giving behaviours. Furthermore, evidence suggests that human axillary odours contain cues

indicating pregnancy, and that these represent one potential mechanism for inducing endocrinological changes in men. However, this has not yet been experimentally tested in humans. The current study aimed to investigate this by exposing male participants to odour from pregnant women. We used a repeated measures design whereby we obtained measures of salivary testosterone and of mating effort and interest in offspring from men both before and after odour exposure. Male participants were grouped into one of five odour conditions. Three of these groups were exposed to odour from women in early pregnancy, late pregnancy, or at 6-10 months post-partum (odours were from the same women at each time point). The remaining two groups were controls, who received either a 'blank odour' or the odour from non-pregnant women. We tested the predictions that men who were exposed to pregnant female odour would reduce interest in mating effort, demonstrate increased paternal motivation, and reduced salivary testosterone levels compared to controls.

Methods

This study received ethical approval from the University of Stirling Ethics review board.

Odour donors

Five pregnant women, aged 27-33 years (mean = 29.8, SD = 2.59, all caucasian), were recruited via social media and word of mouth to provide axillary odour samples. Each woman provided informed consent and odour samples from three time points: early gestation (20-23 weeks, mean = 21.4, SD = 1.14), late gestation (31-39 weeks, mean = 33.83, SD = 3.49) and post-pregnancy (25-43 weeks post-partum, mean = 30.6, SD = 7.67, 3 of the donors were breastfeeding at this follow up period). These time

points reflect those investigated by Vaglio and colleagues (2009). At each time point, each donor provided two pairs of axillary samples using cotton pads sewn into t-shirts. Each pair of samples (i.e. from both left and right axillae) was collected over a 24hr period, on two consecutive days of wear (one donor provided only one sample pair, per time point). This duration of odour collection has previously been found to produce better quality samples than shorter time frames (see Havlíček et al. 2011). Methods for odour collection followed that of Allen et al. (2015), with the only amendment to this protocol being that the cotton pads were sewn into the armpits of cotton t-shirts (washed with a fragrance-free detergent) instead of being taped to the underarms, in order to make the pregnant donors as comfortable as possible during odour collection.

Similarly, following the same methodology for odour collection, five non-pregnant, Caucasian women, aged 24-29 (mean = 26.4, SD = 1.95), provided two pairs of axillary odour samples over two consecutive days (again, one donor only provided one pair of samples). These women were all using hormonal contraception, to avoid any possible effect of menstrual cycle fluctuations on their odour (e.g. Kuukasjärvi et al., 2004). All ten of the female donors were non-smokers.

To minimise the influence of individual donor differences on the male participants, we then created composite odours from pads worn in each of the conditions: early pregnancy, late pregnancy, post-pregnancy, and control (non-pregnant) women. Studies have shown that using composites does not positively or negatively affect the perceptual qualities of odour samples (Fialová et al., 2018). A further control condition was included, using blank (i.e. unworn) pads. For each condition, two identical composites were created. This was done by cutting in half each cotton pad and placing the two halves in separate glass jars with screw top lids. This

produced two jars for each odour condition, each containing one half of every sample (both left and right axilla for all donors) that had been provided for that condition, ensuring that each jar contained the same number of identical samples. These were stored in the freezer until testing, as is standard procedure (see Allen et al., 2015; Lenochova et al., 2008).

Participants

A convenience sample of ninety-one men aged 18-44 (mean = 22.63, SD= .519) were recruited via word of mouth and social media to participate in a lab-based study. Eighty of these men reported being heterosexual, with 6 being homosexual and 5 bisexual; 47 (51.6%) were in a romantic relationship at the time of the study. There was an approximately even split between single and partnered males in each of the odour conditions (Table 1), with no significant between-condition differences (chi square = 3.22, d.f. = 4, p = .522). Among those men who were in a relationship, there was no difference in relationship duration across conditions ($F_{4,41}$ = 1.66, p = .178).

Table 1 Number and relationship status of participants in each odour condition. The final column shows mean relationship duration (in months, ± SEM) of those participants who had a partner.

Condition	Number of participants	Partnered participants	Single participants	Relationship duration
Blank pads	18	8	10	10.6 ± 2.99
Control female	18	9	9	45.1 ± 21.49
Early pregnancy	18	11	7	25.3 ± 6.07
Late pregnancy	18	7	11	12.4 ± 6.65
Post-pregnancy	19	12	7	48.7 ± 16.55

Measures

Participants completed an online questionnaire, developed, using Qualtrics software. The survey was comprised of three scales and basic demographic questions. Participants completed the Relationships Assessment Scale (RAS, Hendrick, 1988), a 7-item scale used to measure general relationship satisfaction (e.g. 'How well does your partner meet your needs?'). This is usually completed using a 1-5 rating scale, with one equalling low agreement with the statement and 5 equalling complete agreement, but for the purposes of this study the scale was changed to 0-100 in order to allow for greater variance in responses. Participants only completed this scale if they indicated that they were currently in a romantic relationship. Additionally, participants completed the Revised Sociosexual Orientation Index (SOI-R), a 9-item measure comprised of three sub-scales relating to behaviour, attitudes and desire (Penke & Asendorpf, 2008). The three behavioural items utilise a 9-point scale indicating varying numbers of sexual partners (in the past 12 months, on only one occasion, without having interest in a long-term relationship), which can then be coded and aggregated to form the behavioural facet. The attitude sub-scale adopts a 1-9 scale with participants selecting whether they strongly disagree (1) or strongly agree (9) with a statement (relating to attitudes about having sex in uncommitted relationships), and the final desire sub-scale asks how often participants have specific desires, answering on a 1 (never) to 9 (at least once a day) scale (related to desire and fantasies about having uncommitted sex). The attitudes and desires scale were changed from 1-9 to 0-100, to align with the RAS scale, to again allow for greater variance in responses. Finally, the participants completed an 11-item Dominance scale taken from the International Personality Item Pool (Goldberg et al.,

2006). Participants responded with their level of agreement to each presented statement, again using a 0-100 point scale.

In addition, participants completed a 'pay-per-view' key-press task measuring the incentive salience of face stimuli (Hahn, Xiao, Sprengelmeyer, & Perrett, 2013). At a computer, participants were presented with a face, with a default viewing time of 4 seconds, and they were able to increase this viewing time by alternately pressing the 'N' and 'M' keys on the keyboard, or to decrease the viewing time by alternately pressing the 'Z' and 'X' keys. A timer bar was presented on the screen next to the image indicating the time remaining before the image was changed, and as participants were pressing the keys they could see how their effort was changing the viewing time. Each alternate key-press pair was coded as one key-press unit. Key-press scores for each face were then calculated by subtracting the total number of key presses that decreased viewing duration from the total number of key presses that increased viewing duration. Faces with greater key press scores are then those that the participant was willing to expend more effort to view. This paradigm quantifies the incentive salience of an image via the amount of effort (key-presses) that is exerted to keep or remove the image (Aharon et al., 2001; Hahn et al., 2013). All participants completed a brief training task designed to familiarize them with the key-press procedure prior to beginning the experiment. Faces were not presented in this training task.

Twenty adult male faces, twenty adult female faces (varying in attractiveness) and twenty baby faces (varying in cuteness) were presented across two blocks in a counterbalanced order, with an equal number of faces from each group (male, female, baby) appearing in each block (images taken from Hahn et al., 2013). Participants were informed that the task length was predetermined; however, this was in fact determined

by their key-press behaviour. This was done in order to dissuade participants from pressing only the decrease viewing time keys in order to finish the task more quickly, and is common practice in studies employing the key-press task (Aharon et al., 2001; Hahn et al., 2013).

After completing this task, participants were also asked to rate male and female faces which had been previously presented for attractiveness (1 = not at all attractive, 7 = very attractive) and baby faces for cuteness (1 = not at all cute, 7 = very cute). An average rating score was subsequently calculated for each participant for each of the three face types (baby, female, male), both before and after odour exposure.

Participants also provided two saliva samples, one prior to and one following odour exposure, which were used to measure salivary testosterone levels. Whole saliva was collected by unstimulated passive drool. Testosterone was assessed using Salimetrics salivary testosterone ELISA kits (Salimetrics assay #1-2402) according to the manufacturer's instructions. The kits report a sensitivity of 1 pg/ml with a range of 6.1 – 600 pg/ml. All samples were assessed in duplicate and the average CV was 6.8%. In line with the assay instructions, participants were instructed to come to the session having not eaten or had anything to drink (other than water) within 1 hour of their participation. Samples were stored within a freezer at -20 Celsius within 2 hours of collection. Any samples which were obviously contaminated (with blood) were discarded (N=4), and participants were only included in the analysis if they had a saliva sample for both pre- and post-odour exposure (N=2), leaving 88 samples in total.

Procedure

Participants attended a lab session that lasted 45-60 minutes. They provided informed consent, knowing that they would be exposed to human odours (but not knowing that these were specifically from pregnant women). They were taken to a cubicle where they provided a saliva sample. Following this the experimenter left the room and the participants completed the online questionnaire providing basic demographic information (age, sexual orientation, relationship and cohabitation status and length), completed the RAS, the SOI-R and a brief dominance questionnaire. They then completed the computer key-press and face rating tasks (time 1 – pre odour exposure).

Next, they were presented with the composite odour in a jar by the experimenter. Participants were allocated to a condition based on the time that they signed up for the study on an alternate sign up basis. Participants were alone in the cubicle during odour exposure and were given onscreen instructions to guide them through the procedure. They were instructed to remove the lid and smell the sample for 20 seconds (with a 40 second break afterwards). They did this ten times (lasting ten minutes in total), with onscreen instructions and a timer to notify them when to start and stop smelling. After this, the onscreen instructions asked them to sit quietly for 5 minutes (this was timed for them) before instructing them to alert the experimenter. We reasoned that the 10 minutes of odour exposure might be sufficient in light of previous research showing that similarly short periods of odour exposure can lead to endocrinological changes (Miller & Maner, 2010; Perrot-Sinal et al., 1999).

After odour exposure, participants provided a second saliva sample and repeated the online questionnaire (this time, excluding the demographic questions and

288 the first three SOI-R questions related to behaviour, as it was not expected that this
289 information would change with odour exposure) and the computer based key-press and
290 rating tasks (time 2 – post odour exposure). They were then debriefed.

291 It was noted that some participants had not completed all ratings of faces. Four
292 participants missed one or two face ratings at time 1, one participant missed them all
293 and a number of key-press trials, and three participants missed one face rating at time
294 2. As ratings of faces were averaged for each participant it was decided that all of these
295 participants would be retained for analysis except for the one participant who missed
296 all of the face ratings and a substantial number of key-press task stimuli. All 91
297 participants completed all questions and so were included in the following analyses
298 investigating the questionnaire responses.

299 For all measures we calculated a difference score between the pre- and post-
300 odour exposure time points, and these scores were used in the following analyses. Pre-
301 exposure scores were subtracted from post-exposure scores; hence, an increase in a
302 measure would result in a positive value and a decrease would result in a smaller a
303 negative value.
304

305 ## Results

306 ***Face Ratings***

307 Three separate one-way ANOVAs were conducted for the ratings of female faces, male
308 faces and baby faces. In each, odour condition was included as a fixed factor (blank,

control female, early pregnancy, late pregnancy, post-pregnancy). We found no main effect of odour condition on change in ratings given to any face type (Table 2).

Table 2. Parameter estimates for one-way ANOVAs investigating effects of exposure to different odours on change (pre-, post-odour exposure) in ratings of different face types.

Dependent variable	Fixed factor	*df*	*F*	*p*
Ratings of baby faces	Odour condition	4,85	.466	.760
Ratings of female faces	Odour condition	4,85	.292	.883
Ratings of male faces	Odour condition	4,85	.669	.616

Key-press task

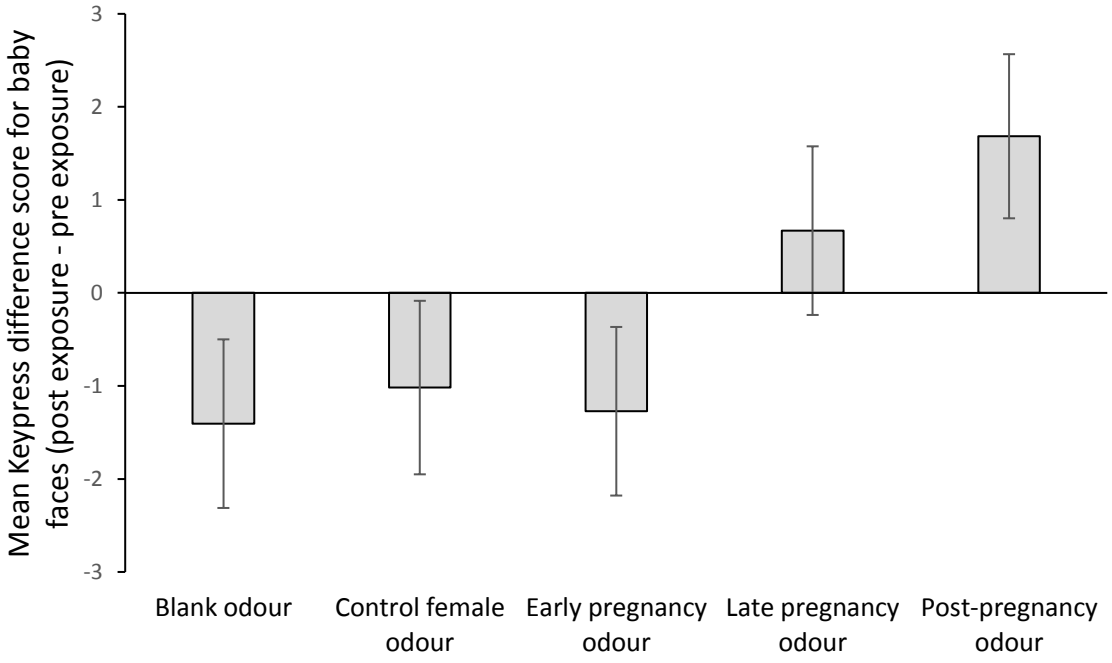
For each face that each participant viewed, the number of negative key-presses was subtracted from the number of positive key-presses, we then calculated an exposure difference score by subtracting the pre-exposure key-press score from the post exposure key-press score. These values were then averaged across face types in order to create a key-press score for each participant for each of the three face types. As with the face ratings, three one-way ANOVAs were conducted, each including odour condition as a fixed factor. As seen in Table 3, there were no main effects of odour condition on change in key-press responses to faces of men or women, but there was a marginally significant effect (p = 0.060) for key-press responses to baby faces.

We used non-orthogonal planned contrasts (Field, 2005) to investigate potential between-group differences while minimising the risk of inflating Type 1 error. We compared pre- versus post-exposure difference scores for each odour type against the difference score in the blank odour condition. We found no significant differences in key-press scores between men exposed to the blank odour and the control female

odour (contrast estimate ± s.e. = .388 ± 1.30, p = .766), early pregnancy odour (.133 ± 1.28, p = .917), or late pregnancy odour (2.08 ± 1.28, p = .109), but that post-pregnancy odour exposure resulted in a significantly higher key-press scores (3.090 ± 1.27, p = .017) for baby faces. While these results are exploratory and should be treated with caution this pattern (shown in Figure 1) provides evidence that participants engaged in the key-press task in order to increase viewing time of baby faces after exposure to odour of post-partum women compared to the blank (no odour) condition, and there is some evidence for an increasing trend for viewing time of baby faces across those men exposed to odours from early pregnancy through to late pregnancy and post pregnancy odours (see Figure 1).

Table 3 Parameter estimates for three separate one way ANOVA's investigating whether there was an effect of odour exposure on key-press responses to faces. These models employed difference scores in key-press responses given pre and post odour exposure.

Dependent variable	Fixed factor	*df*	*F*	*p*
Key-press scores for baby faces	Odour condition	4,85	2.353	.060
Key-press scores for female faces	Odour condition	4,85	.292	.883
Key-press scores for male faces	Odour condition	4,85	1.296	.278



344

345 *Figure 1 Mean Key-press difference scores given to baby faces. Higher scores indicate an increase in effort to view*
346 *faces of babies after exposure to odours. Error bars represent ±1 SEM.*

Questionnaire data

For each of our questionnaire measures, we ran independent one way ANOVAs to assess change in scores before and after odour exposure, with odour condition as a fixed effect. As can be seen from Table 4, we found no significant effect of odour condition on any of the measures.

Table 4 Parameter estimates for four separate one way ANOVA's investigating whether there was an effect of odour exposure on questionnaire responses. These models employed difference scores in questionnaire responses given pre and post odour exposure.

Dependent variable	Fixed factor	*df*	*F*	*p*
Dominance score	Odour condition	4,86	.960	.434
SOI Attitudes score	Odour condition	4,86	1.482	.215
SOI Desires score	Odour condition	4,86	1.055	.384
RAS scores	Odour condition	4,42	.507	.731

Testosterone

Of the usable data (n=88) recorded testosterone levels ranged from 67.9 pg/ml to 629.7 pg/ml. Other studies have reported salivary testosterone values with similar ranges (e.g. Penton-Voak & Chen, 2004). As with the other measures, we calculated a difference score for each participant, subtracting their post exposure testosterone value from their pre exposure value. However, in contrast to analyses reported above, we also included participants' relationship status as a fixed factor in this model, because of numerous findings showing associations between relationship status and testosterone levels (see Introduction). Indeed, in our sample, testosterone levels differed significantly between partnered and single men

(pre-odour exposure: $t(86) = 2.08$, $p = .040$; post-odour exposure: $t(86) = 2.64$, $p = .010$), with lower mean (± s.e.) levels in partnered men (pre-exposure: 191.8 ± 11.6 versus 230.2 ± 14.4; post-exposure: 185.9 ± 9.8 versus 222.8 ± 9.9 pg/ml). However, we detected no significant difference between odour exposure conditions on change in testosterone level ($F(4,78) = 1.96$, $p = .108$). There was also no difference in testosterone change depending on relationship status ($F(1,78) = 0.01$, $p = .933$), nor a significant condition x relationship status interaction ($F(4,78) = 0.69$, $p = .601$).

Discussion

Based on previous findings, we predicted that exposure to pregnant female odour would affect male participants' physiology and psychology in such a way that might prepare them for providing parental investment. This prediction was based on evidence that men's testosterone levels seem to vary in relation to their female partners' pregnancy status. The mechanism which controls this is unknown, but the discovery of specific volatile compounds in the body odour of pregnant women but not non-pregnant women (Vaglio, Minicozzi, Bonometti, Mello, & Chiarelli, 2009) may present a mechanism for inducing these physiological hormonal changes, which in turn could result in psychological and behavioural changes that would be beneficial to infant survival.

Three psychological measures were employed in the current design. It was predicted that dominance would decrease after exposure to pregnant female odour, but not after exposure to non-pregnant female odour, as dominance is likely related to mating effort and to testosterone levels (Mazur & Booth, 1998; Mehta & Josephs, 2010; Qvarnström & Forsgren, 1998; Swaddle & Reierson, 2002). However, we found no effect of odour condition

389 on self-reported dominance levels. Additionally, the study employed two sections of the SOI-
390 R, which are related to interest in mating (Penke & Asendorpf, 2008). We again predicted that
391 SOI-R scores in sexual attitudes or desires would decrease after exposure to pregnant odours,
392 but found no significant changes in these measures across odour conditions. Finally,
393 participants who reported being in a romantic relationship at the time of the study also
394 completed the RAS, a measure of relationship quality and we found no difference in these
395 scores in relation to our odour exposure. One explanation for these findings may be that the
396 psychological measures we used were not sufficiently sensitive to adequately measure the
397 changes we would expect to see. Our measures of dominance and SOI specifically focus on
398 mate choice related processes, something which we would expect to decrease in importance
399 in response to a decrease in testosterone. However, perhaps a psychological measure related
400 to infant interest, or care-giving more generally, would have been more revealing in this
401 study. Indeed, as we note below, we failed to see a change in testosterone, and it may be the
402 case that other hormones which may be involved, such as oxytocin, could alter attitudes and
403 behaviours in a different way from what we predicted here.

404 We further asked our participants to rate faces, with the prediction that ratings of
405 cuteness of baby faces would increase after exposure to pregnant female odours, but not
406 after exposure to blank, or control female odours. We failed to find any evidence of this in
407 our data set. It was also predicted that exposure to pregnant female odours would increase
408 the incentive salience of infant stimuli, as measured using a 'pay-per-view' key-press task
409 (Hahn et al., 2013). In support of our hypothesis we found preliminary evidence that exposure
410 to post-pregnancy body odours did significantly increase effort expended to view infant faces.
411 We also noted an increasing trend in infant interest, measured via key-presses, across
412 pregnancy (Figure 1). This suggests that changes in infant interest may begin during pregnancy

and peak post-pregnancy, the point at which these changes would be most beneficial for offspring.

Finally, we measured salivary testosterone levels pre and post odour exposure, predicting that exposure to pregnancy odours should lower testosterone, in line with predictions based on the challenge hypothesis, and that it may be these hormonal changes which would underpin behavioural changes (like those seen on the key-press task). We failed to find any effect of odour exposure on salivary testosterone levels. It seems contradictory that we would find changes in infant interest but fail to find evidence of endocrinological changes which likely underpin this. One explanation for this may be that we have focussed on the wrong candidate hormone. While testosterone has been viewed as important for modulating aggression, and potentially care-giving behaviours, other hormones such as estrogen, prolactin, vasopressin and oxytocin have also been posited as playing a role (Hashemian et al., 2016). It may be that these hormones, or a combination of hormonal changes, are underpinning behavioural and psychological changes required for optimal care-giving, and future work should investigate this more thoroughly. A second possibility is that potential change in testosterone levels as a result of odour exposure may have been confounded by the battery of face tasks we used to assess behavioural interest. In other words, we asked our participants to view the faces of other men and women, either of which may have had antagonistic effects on the degree and direction of testosterone change to those from the odours or the baby faces.

As our study is the first to experimentally investigate whether pregnant odours induce physiological and psychological changes in men, further investigations should incorporate methodological refinements to confirm our conclusions. For example, the current study used a relatively short-term odour exposure (20 sec per minute, for 10 minutes).It might be argued

that this was excessive and could have led to olfactory adaptation which might obscure effects. While adaptation may be an important issue in perceptual studies, we were focused primarily on hormonal changes and possible behavioural consequences, which would unlikely be affected by short-term adaptation. In contrast, we were rather more concerned with ensuring we provided a sufficient olfactory exposure to elicit such changes. The decision about exposure schedule was made based on findings that even a brief exposure to certain social odours can affect hormone levels, particularly testosterone (Miller & Maner, 2010; Perrot-Sinal et al., 1999), which we had hypothesised to be important in underlying changes related to infant interest and reduced mating effort (Wingfield et al., 1990; Wynne-Edwards, 2001). However, it may be that longer-term odour exposure and/or sustained changes in testosterone levels are required to initiate changes in infant interest. Furthermore, longer odour exposure would present a more ecologically valid experimental design. Pregnancy lasts for approximately 40 weeks, which, if expectant parents are living together, provides a much longer odour exposure time compared with our experimental study. Future research may also expand upon the odours investigated, for example amniotic fluid and infant body odour have also been suggested to play an important role in instigating infant care (Schaal & Marlier, 1998). It is also important to note that olfaction represents only one aspect of sensory perception, and cues are likely present in other modalities – such as the visual experience of a pregnant partner. After experimenting with a variety of cues in isolation, future research may benefit from combining various cues in order to better understand their relative impact.

Furthermore, future research would potentially benefit from including a measure of current and past infant involvement, as well as attitudes towards becoming a father, which were absent from this study. As we recruited from a mostly student population and most of our male participants were relatively young (mean age of 22.63), it is likely that very few were

parents themselves. Nonetheless, it would be important to measure this in the future, along with more general exposure to infant stimuli such as having a number of young siblings or working in a childcare setting. Some studies have indeed found that changes in male (tamarin) hormone levels during partner pregnancy vary with parental status (Ziegler and Snowdon, 2000). Research also suggests that parental experience of females may impact upon this chemical communication; for example, some hormonal changes in male tamarins were delayed when they were paired with primiparous pregnant female tamarins (Almond et al., 2008), although these authors note that such effects could potentially result from the presence or absence of infants in the environment. Nevertheless, this suggests that future work should take into account mothers' past experience with infants as well as men's experiences.

Finally, although our predictions were not fully supported, our findings can be seen as providing the first evidence that brief exposure to post-pregnancy females' body odour is sufficient to induce psychological and behavioural changes related to infant care, although it was insufficient to alter testosterone levels, at least in the current design. The current study benefitted from using composite odours over single samples, and from collecting odour samples from the same women at various pregnancy time points. Future work should aim to maintain these advantageous design features whilst investigating odour exposure over a longer time frame, and obtaining a variety of hormonal measures, in order to establish the mechanism underpinning these changes.

Conflict of interest statement

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Ethical approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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