

Testing the Affiliation Hypothesis of Homoerotic Motivation in Humans: The Effects of Progesterone and Priming

Diana S. Fleischman · Daniel M. T. Fessler ·
Argine Evelyn Cholakians

Received: 24 July 2012 / Revised: 2 April 2014 / Accepted: 20 August 2014 / Published online: 25 November 2014
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Abstract The frequency of homoerotic behavior among individuals who do not identify as having an exclusively homosexual sexual orientation suggests that such behavior potentially has adaptive value. Here, we define homoerotic behavior as intimate erotic contact between members of the same sex and affiliation as the motivation to make and maintain social bonds. Among both male and female nonhuman primates, affiliation is one of the main drivers of homoerotic behavior. Correspondingly, in humans, both across cultures and across historical periods, homoerotic behavior appears to play a role in promoting social bonds. However, to date, the affiliation explanation of human homoerotic behavior has not been adequately tested experimentally. We developed a measure of homoerotic motivation with a sample of 244 men and women. Next, we found that, in women ($n = 92$), homoerotic motivation was positively associated with progesterone, a hormone that has been shown to promote affiliative bonding. Lastly, we explored the effects of affiliative contexts on homoerotic motivation in men ($n = 59$), finding that men in an affiliative priming condition were more likely to endorse engaging in homoerotic behavior compared to those primed with neutral or sexual concepts, and this effect was more pronounced in men with high progesterone. These findings constitute the first experimental

support for the affiliation account of the evolution of homoerotic motivation in humans.

Keywords Homosexual behavior · Homoerotic behavior · Affiliation · Progesterone · Priming

Introduction

Many individuals appear capable of sexual arousal toward members of the same sex under the right circumstances (e.g., during adolescence; in initiation rites, see Muscarella, 2006), and the ethnographic record indicates that same-sex sexual behavior is found in a majority of societies, spanning a wide range of social complexity, and at times occurring at fairly high frequencies (Kirkpatrick, 2000; Ross & Wells, 2000; see also Rind & Yuill, 2012). In laboratory studies, self-identified heterosexual women, on average, have been shown to have a generalized genital response to both sexes, while heterosexual men have been shown to have a modest genital response to male sexual stimuli (e.g., Chivers, Rieger, Latty, & Bailey, 2004; Chivers, Seto, Lalumiere, Laan, & Grimbos, 2010; Rieger, Chivers, & Bailey, 2005). This has led a number of investigators to propose that same-sex sexual behavior may have some direct adaptive value (Kirkpatrick, 2000; Muscarella, Cevallos, Siler-Knogl, & Peterson, 2005).

Before examining the adaptationist thesis, because investigations of same-sex sexual behavior often use inconsistent terminology (Muscarella, 1999), we must first define the question at issue. Sexual orientation is commonly understood as patterned sexual desire that may lead to sexual behavior with members of one or the other sex. However, consonant with the functional explanations to be discussed below, much, if not most, same-sex sexual behavior occurs in those who do not identify as exclusively homosexual in orientation (Diamond & Wallen, 2011; Kinsey, Pomeroy, & Martin, 1948; Kirkpatrick, 2000). Our the-

D. S. Fleischman (✉)
Department of Psychology, King Henry Building, University of
Portsmouth, King Henry I St., Portsmouth, Hampshire PO1 2DY, UK
e-mail: DianaFleischman@gmail.com

D. M. T. Fessler
Center for Behavior, Evolution, & Culture and Department of
Anthropology, University of California, Los Angeles, Los Angeles,
CA, USA

A. E. Cholakians
Department of Anthropology, California State University Fullerton,
Fullerton, CA, USA

oretical focus here is on a broad category of behavior, that which is erotic and occurs with members of the same sex, and its hormonal and motivational underpinnings (which include, but are not limited to, sexual desire); we consider sexual orientation or identity only secondarily, as this is not isomorphic with behavior. Muscarella (2000) defined homoerotic behavior as “same-sex sexual behavior involving genital contact” (p. 52); however, as not all actions having an erotic component involve genital contact, we adopt a broader definition, construing as homoerotic behavior all intimate contact, be it intentionally or unintentionally erotic, involving members of the same sex, regardless of whether it involves genital contact.

Motivation to affiliate, broadly construed, has been implicated in homoerotic behavior in both male and female nonhuman primates (Vasey, 1995; Wallen & Parsons, 1997). Same-sex sexual contact has been found in 67 % of cultures in the Human Relations Area Files (Kirkpatrick, 2000), and the practice of such behavior by individuals who also engage in opposite-sex sexual contact has been prominent in many culture regions for centuries (Ross & Wells, 2000). Working in parallel, drawing on cross-species comparisons and extensive ethnographic and historical materials, Kirkpatrick (2000) and Muscarella (2000) presented overlapping evolutionary models arguing that human same-sex sexual behavior serves the adaptive function of promoting alliance formation and maintenance (Muscarella et al., 2005; see also Rind & Yuill, 2012).

Reflecting its central role in biological fitness, a strong neurological reward system undergirds sexual behavior; hence, it stands to reason that bonds, including between those of the same sex (homosocial), can be strengthened via sexual behavior. The affiliation hypothesis thus proposes that natural selection co-opted this reward system as a means of promoting same-sex social bonds. In small-scale societies that resemble those characteristic of ancestral human populations, social bonding and alliance formation play a number of critical roles, including advantage in violent inter-coalition conflict (Bowles, 2009; Van Vugt, 2009), buffering against food shortfalls (see Hill & Hurtado, 2009), alloparenting (Hrdy, 2009), and insuring against illness and injury (Sugiyama, 2004). Moreover, while some aspects of these patterns are uniquely human, the fundamental link between social connectedness and fitness has a very deep phylogeny, as there is evidence that, among both male and female nonhuman primates, social bonds translate into enhanced survival and reproductive success (Kuhle & Ratdke, 2013; Silk, Alberts, & Altmann, 2003; Silk et al., 2010). Consistent with the above patterns, in the clinical context, social connectedness has been shown to importantly influence both overall human health and prognosis after physical trauma (see Reblin & Uchino, 2008; Seeman, 1996). Likewise, in keeping with the adaptive value of strong social bonds, major physiological systems regulate both aversion towards cues of rejection and motivation towards affiliating with others. Aversion to cues of rejection has been linked to the pain system, fundamental to self-preservation (DeWall et al., 2010;

Eisenberger, Jarcho, Lieberman, & Naliboff, 2006; Eisenberger & Lieberman, 2004; MacDonald & Leary, 2005). Conversely, affiliating with others and engaging in cooperative exchange activates neural reward centers in the brain (Bora, Yucel, & Allen, 2009).

Although over a decade has passed since publication of the principal papers laying out the affiliation explanation, empirical investigations addressing it remain scarce. Recently, an interview study found that 89 % of young British men surveyed reported having kissed another man on the lips, with the majority stating that this activity was homosocial (i.e., affiliative). Only one study has attempted to experimentally test the affiliation hypothesis. Muscarella et al. (2005) found that U.S. undergraduates who read vignettes about heterosexuals engaging in homosexual behavior with a positive outcome viewed the protagonist as having higher status and more reproductive opportunities than those in the neutral or negative outcome conditions. However, this study examined only third-party perceptions of the consequences of same-sex sexual contact, but did not test the core prediction stemming from the affiliation hypothesis, namely that affiliative and homoerotic motivations should be functionally linked. Here, we aim to do exactly that. We adopt a multi-pronged strategy, examining hormonal correlates of affiliation in both sexes, and exploring the effects of priming affiliation in men.

Progesterone

Progesterone, produced mainly in the ovaries of women and the adrenal glands of men, is one of the principal hormones underlying parental behavior (Mehta & Josephs, 2010; Wirth, Meier, Fredrickson, & Schultheiss, 2007). Progesterone has been implicated in the psychology of affiliation and in response to rejection. In a repeated-measures study of women, Miller (2011) found that attention to social stimuli increased during the high-progesterone phase of the menstrual cycle and was correlated with salivary progesterone. Brown et al. (2009) found that women engaging in a task promoting social closeness showed increases in progesterone, and the extent of this increase predicted altruistic motivation in participants towards their task partner 1 week later. In both men and women, following the experience of experimental social rejection, progesterone increased when participants were told that they would have an opportunity to affiliate with others (Maner, Miller, Schmidt, & Eckel, 2010).

However, not all studies linking progesterone and affiliation have found consistent results. Heterogeneous findings have resulted from studies in which affiliation was measured through a picture story exercise (Schultheiss, Dargel, & Rohde, 2003; Schultheiss, Wirth, & Stanton, 2004; Wirth & Schultheiss, 2006) and evoked through film clips (Schultheiss et al., 2004; Wirth & Schultheiss, 2006), especially in male participants. This may partly reflect the use of mating opportunities as an affiliative prime, a manipulation

that constitutes a confound (see below). Although results are not entirely uniform across methods, there are grounds for concluding that progesterone is positively associated with affiliation in humans. As our goal here was to explore the hypothesis that homoerotic behavior serves an affiliative function, we therefore investigated whether progesterone can also predict the motivation to engage in such behavior.

Importantly, whereas progesterone has been positively associated with affiliative motivation in humans, it has not been positively associated with sexual motivation; indeed, there are suggestions of a negative association. Some research has shown a decrease in sexual function in women on hormonal contraceptives containing synthetic progestins (Adams, Gold, & Burt, 1978; Wallwiener et al., 2010; but see also Alexander, Sherwin, Bancroft, & Davidson, 1990; Guida et al., 2005). Likewise, although the degree to which circulating progesterone affects sexual motivation in men has not been adequately explored, synthetic progesterone injections have been used to reduce the testosterone and sex drive of male sexual offenders (Andersen & Tufik, 2006). Hints of a negative association between progesterone and sexual motivation thus suggest that evidence of a positive association between progesterone and homoerotic motivation is not explicable as a by-product of an increase in sexual motivation that would enhance attraction to both same and opposite sex others.

If homoerotic motives function to enhance affiliation, then, given the association between progesterone and affiliation, we can expect that progesterone should be positively correlated with homoerotic motives. In women, position in the menstrual cycle is a principal determinant of progesterone level; hence, we can expect female homoerotic motivation to exhibit corresponding cyclic variation. Importantly, however, a second factor may independently influence changes in homoerotic motivation. A fundamental characteristic of the menstrual cycle is the concentration of fertility (i.e., the probability of conception following coitus) during the periovulatory period (Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001). Given that all behaviors necessarily entail opportunity costs, we can therefore expect that, if they are governed by adaptations, motivations to engage in behaviors that are not tied directly to conception will exhibit a periovulatory reduction. For example, in many mammals, including humans, caloric intake is reduced around ovulation, thereby reducing foraging time in a manner that frees up time for mate-seeking and mating (Fessler, 2003). By the same token, independent of conscious intentions as regards reproduction, we might expect women to prioritize opposite-sex sexual contact over same-sex sexual contact during the fertile window.

Consonant with this thesis, in a repeated-measures study over one menstrual cycle, Diamond and Wallen (2011) found that, in a subset of non-lesbian women who felt that there was a role for choice in their sexual desires, homosexual fantasies and desires decreased around ovulation. Progesterone peaks during the

luteal phase, approximately 1 week after ovulation (Hatcher & Namnour, 2004), when probability of conception has declined dramatically (Wilcox et al., 2001). Hence, it is important to determine whether a mid-luteal rise in homoerotic motivation reflects (1) the enhancing effects of progesterone as a means of achieving affiliation or (2) declines in the costs of behaviors that compete with mating for time and energy. More generally, the same reasoning regarding opportunity costs suggests that, in both women and men, cues indicating the presence of favorable mating opportunities may modulate homoerotic motivation, as evolved mechanisms can be expected to prioritize the direct fitness benefits of potentially conceptive behavior with the opposite sex over the indirect fitness benefits of affiliative bonding; conversely, cues of the importance of affiliation in the current context should have the opposite effect. Accordingly, experimentally manipulating the presence of such cues should, respectively, decrease or increase homoerotic motivation.

To summarize the above, we predicted that, if, in both sexes, affiliation is an important ultimate function of homoerotic motivation, then (1) progesterone, a hormone associated with affiliative motivation, will be positively correlated with homoerotic motivation; (2) priming affiliative motivation will increase self-reported homoerotic motivation; (3) in women, homoerotic motivation will decrease as a function of the probability of conception; and (4) priming opposite-sex sexual opportunities will decrease homoerotic motivation.

Testing the above predictions requires a measure of homoerotic motivation. Existing instruments designed to measure sexual orientation (e.g., the Kinsey Scale) (Kinsey et al., 1948) are unsuitable, as they examine past behavior, not current motivation. Although Diamond and Wallen (2011) developed an instrument (modeled after Spector, Carey, & Steinberg, 1996) intended to examine female homoerotic motivation, responses were dependent on participants' social circumstances on the day of participation. In Study 1, we develop a new measure of motivation to engage in homoerotic behavior. In Study 2, we administer this measure to women in conjunction with progesterone assays and assessments of menstrual cycle position. In Study 3, we measured progesterone in men, then primed participants using word puzzles addressing affiliation, opposite-sex sexual opportunities, or neutral concepts, and then measured homoerotic motivation.

Study 1

Method

In order to develop a new measure of homoerotic motivation we collected responses to an online questionnaire and factor analyzed those questions addressing the phenomenon in question.

Participants

Participants were recruited via advertisements posted in the Volunteers section of craigslist.org and homoads.org, the latter venue being employed in order to increase representation of individuals who identified as other than exclusively heterosexual. Advertisements invited volunteers to participate in an online study described as a short survey for men and women 18 years of age about attitudes towards same-gender behaviors. A total of 1,028 individuals participated. After excluding 67 participants who did not complete the entire questionnaire, and one participant under age 18, we were left with 960 participants (69% women), age 18–79 years ($M = 32.71$, $SD = 12.81$). Initially, we did not ask participants to report their sexual orientation, but we later added the Kinsey scale (Kinsey et al., 1948), which was administered to 244 participants. This sample of 244 was 38.5% exclusively heterosexual, 16.8% heterosexual with incidental homosexual contact, 6.6% heterosexual with more than incidental homosexual contact, 9.4% bisexual, 6.6% homosexual with more than incidental heterosexual contact, 10.7% homosexual with incidental heterosexual contact and 11.5% exclusively homosexual.

Measures

The questionnaire consisted of 16 statements, 5 of which directly addressed homoerotic motivation. Four of these statements employed the present tense and addressed ongoing experience (e.g., “The idea of kissing a [wo]man seems sexually arousing to me”). One statement employed the past tense (“I have fantasized recently about having sexual contact with a [wo]man”). We included this recent experience item on the basis of the logic that, whatever the actual frequency with which such fantasizing occurred, participants would be more likely to recall and acknowledge having had such fantasies if their current state of mind included positive homoerotic motivation. For each statement, participants indicated their level of agreement using a 5-point Likert scale (1, strongly disagree, to 5, strongly agree).

Results

Factor analysis of the homoerotic motivation questions revealed that all five questions loaded onto a single factor; alphas were acceptable for all participants ($\alpha = 0.87$), for males alone ($\alpha = 0.90$), and for females alone ($\alpha = 0.85$) (see Appendix in Table 1 for questionnaire items and individual item loadings). Furthermore, the homoerotic motivation measure correlated significantly with the Kinsey score for all participants, $r(242) = .74$, $p < .001$, for males alone, $r(69) = .89$, $p < .001$, and for females alone, $r(171) = .70$, $p < .001$. Satisfied that our instrument successfully addressed the topic at issue, we then proceeded to employ it in testing predictions derived from the affiliation hypothesis.

Study 2: Progesterone’s Association with Homoerotic Motivation in Women

Participants

A total of 194 female participants, age 17–22 years ($M = 18.57$, $SD = 0.83$) were recruited from the Department of Psychology subject pool at a large university in the southwestern U.S. Of the 90 women who reported being sexually active, two women reported only engaging in homosexual sex, 88 reported only engaging in heterosexual sex, and none reported sexual activity with both men and women. Of the 194 participants, 67 reported using hormonal birth control. Among the 127 women not taking hormonal birth control, we excluded those for whom we did not obtain a valid progesterone value, those without a valid cycle day (no cycle day reported or a cycle day over 30), and those who did not complete the requisite questions, leaving 92 naturally-cycling women. Women taking hormonal contraceptives have lower levels of endogenous natural progesterone (Fleischman, Navarrete, & Fessler, 2010; Frye, 2006). While it is possible that the relevant variable for these women is the sum of endogenous progesterone and exogenous synthetic progestins, the hormone assay that we employed only measures the former. As a consequence, among our participants taking hormonal contraceptives, the majority exhibited progesterone values below the minimum sensitivity (54%) of our assay. We included all 67 participants taking hormonal contraceptives who completed the entire questionnaire and did not use assay failure as an exclusion criterion. The mean ages of the naturally-cycling and hormonal-contraceptive-using subsamples did not differ significantly from that of the total sample.

Measures

Progesterone was assayed using enzyme-linked immunosorbent assay (Salimetrics, State College, PA). The sensitivity of the assay, defined as the lower limit of detection that can be distinguished from the zero standard, was 5 pg/mL. Mean inter- and intra-assay coefficients of variation for the participants retained for analysis were 14 and 3.6%, respectively.

Estimation of Conception Risk

Using published data (Wilcox et al., 2001), we calculated conception risk via either backward counting from an actual date of next menstruation or forward counting from a previous date of menstruation. Backward counting is more reliable for predicting date of ovulation (Haselton & Gangestad, 2006); hence, we used it for all participants who returned a postcard with their date of subsequent menses (44 out of 92 participants). For those participants lacking actual date of next menstruation, we used forward counting (Gangestad & Thornhill, 1998). Conception risk values ranged from 0 to .08 ($M = 0.03$; $Mdn = 0.02$). For more

explanation of this method and its validation see Navarrete, Fessler, Fleischman, and Geyer (2009).

Procedure

Upon arrival, participants salivated into vials, which were then sealed and frozen at -20°C until analysis. Participants completed several computerized instruments in a single sitting, and were randomly assigned to one of four orders of presentation. In addition to retrospective information on the participant's menstrual cycle, participants were given a stamped postcard and asked to return it upon onset of next menstrual bleeding.

We predicted that salivary progesterone would be positively correlated with homoerotic motivation in naturally-cycling women. One previous study found that women taking hormonal contraceptives showed higher affiliative motivation than women who were naturally cycling (Schultheiss et al., 2003); however, another study found that women on hormonal contraceptives did not attend more to social stimuli like naturally cycling women in the high progesterone phase of the menstrual cycle (Miller, 2011). Accordingly, we had no predictions concerning homoerotic motivation among participants using hormonal contraceptives.

Results

Correlations with Progesterone and Conception Risk

Log transformed salivary progesterone and homoerotic motivation were significantly correlated, $r(90) = .27$, $p < .01$ (see Fig. 1). Although the highest progesterone levels occur in the luteal phase, progesterone levels first begin to rise periovulatorily, i.e., during the period of maximal conception risk. In order to fully disentangle the effects of progesterone on homoerotic motivation from any effects of conception risk on homoerotic motivation, we did a partial correlation on progesterone levels and homoerotic motivation controlling for conception risk; the correlation remained significant, $r(90) = .27$, $p < .01$ see Fig. 1.

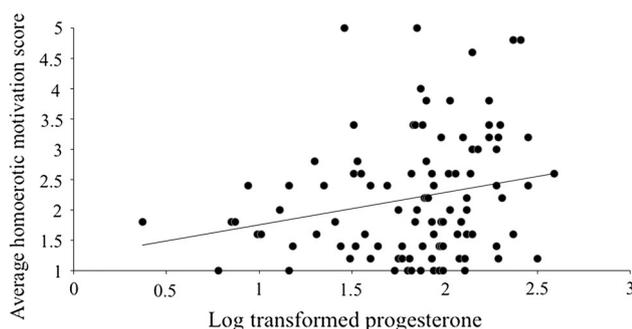


Fig. 1 Scatterplot of the relationship between log transformed progesterone and homoerotic motivation in women ($n = 92$)

Comparison of Women Taking and Not Taking Hormonal Contraceptive

Scores of homoerotic motivation did not differ significantly between women on hormonal contraceptives ($M = 2.39$, $SD = .99$), and naturally cycling women ($M = 2.23$, $SD = .98$), $t(157) = 1.01$, $p = .31$. Lastly, there was a non-significant correlation in the predicted direction between conception risk and homoerotic motivation, $r(90) = -.14$, $p = .18$ (see Fig. 2).

Discussion

Consonant with the thesis that homoerotic behavior serves an evolved affiliative function, Study 2 showed a small positive correlation in women between homoerotic motivation and progesterone, a hormone thought to be associated with affiliation. Because nonreproductive sexual behavior entails opportunity costs that detract from reproduction, if homoerotic behavior is governed by evolved adaptations, it follows that homoerotic motivation should decline as a function of conception risk. Nevertheless, Study 2 revealed only a nonsignificant trend in this direction. However, in comparing these two results, it is important to keep in mind that the first independent variable was measured directly, with far greater precision than the second independent variable, as progesterone was assayed in a sample of 104 participants, while conception risk was calculated on the basis of estimated position in the menstrual cycle in a sample of 92 participants, within which it was possible to use the more accurate backward-counting method in 49 % of cases. Lastly, individuals vary markedly from one another in progesterone levels (Jasienska & Jasienski, 2008), and this may have been a source of substantial noise in Study 2. If progesterone is a key part of the proximate mechanism that adjusts homoerotic motivation so as to minimize the trade-off between alliance formation and contraceptive behavior, then, given our between-subjects design, inter-individual variation in progesterone levels may have precluded detection of the effects of conception risk in Study 2.

With the above caveat in mind, the results of Study 2 provided preliminary evidence in support of the hypothesis that human homoerotic behavior serves the ultimate function of strengthening social bonds. Both theoretical considerations and cross-species comparisons indicate that the hypothesized function should not be limited to females. To further explore the affiliation hypothesis, we investigated homoerotic motivation in men

Study 3: Priming Affiliation and Measuring Progesterone in Men

If human homoerotic behavior serves an affiliative function, then priming the concept of affiliation and contexts in which such affiliation is valuable should increase homoerotic motivation. Likewise, if homoerotic motivation is adaptively altered in light

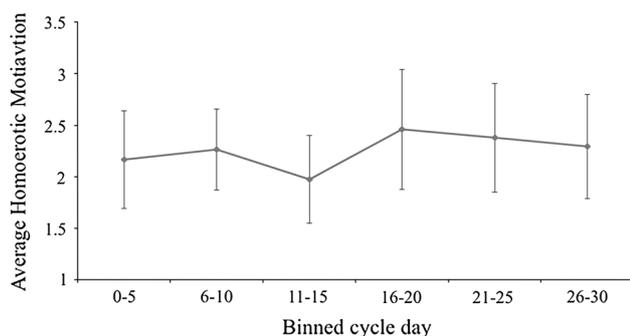


Fig. 2 Average homoerotic motivation by cycle day for 92 naturally-cycling women. Days 11–15 of the menstrual cycle are those on which ovulation is most likely to occur

of the cost/benefit ratio of homoerotic behavior, then, due to the opportunity costs of non-reproductive behavior, in the absence of cues of the value of affiliation, cues of opportunities for opposite-sex sexual contact should decrease homoerotic motivation. Such priming effects can be expected to be particularly marked in men, as our species' history of intergroup conflict appears to have exercised strong selective pressure on human males to mark group boundaries and affiliate with in-group members (Van Vugt & Park, 2010), while vastly lower obligate parental investment means that men should be particularly responsive to short-term mating cues signaling the presence of opportunities (Symons, 1979).

Conceptual priming thus offers a promising avenue for investigating the affiliation hypothesis in men. Moreover, because men produce progesterone (albeit at substantially lower levels than do women), combining conceptual priming with measurements of progesterone allows for an independent test of the patterns found in Study 2, as we can expect an interaction between priming and progesterone. We therefore predicted that (1) priming affiliation will increase homoerotic motivation in men, while priming opposite-sex sexual contexts will have the opposite effect, and (2) the effects of priming will be further mediated by progesterone level.

Participants

A total of 61 male participants, age 18–27 years ($M = 19.56$, $SD = 1.92$) were recruited from the Department of Psychology subject pool at a large university in the southwestern U.S. One participant was excluded because he did not complete all of the requisite items, leaving 60 participants.

Method

Progesterone Measure

Saliva was collected as in Study 2 before any of the questionnaires or instruments were completed. Progesterone was assayed

as in Study 2. Mean inter- and intra-assay coefficients of variation for the participants retained for analysis were 9.4 and 6.1 %, respectively. Valid progesterone values were obtained for 59 participants.

Priming

Participants were randomly assigned to one of three priming conditions: affiliative, opposite-sex sexual opportunity, or neutral. There were 21 participants in the Sexual condition, 21 participants in the affiliative condition and 17 participants in the neutral condition (after exclusion of the participant for whom we did not get a valid progesterone value). Before the measure of homoerotic motivation, participants were given a priming exercise in the form of word fragment completion puzzles composed of 40 words in two sets of 20: affiliative (e.g., Fri__ds, Friends), opposite-sex sexual opportunity (e.g., Bre__s, Breasts), and neutral (e.g., Sq_ar_, Square). Within each condition, participants were randomly assigned two of three possible lists of 20 items. In the affiliative and opposite-sex sexual priming conditions, 5 neutral words were also included in each list to conceal the priming objective. To further avoid demand characteristics many word fragments were selected such that more than one word could be constructed using the fragment (e.g., Lo__r, Lover; Tr__p, Troop). To gauge the degree of priming achieved, completed fragments were inspected to determine the percentage of responses that fit the intended prime. In both the affiliative and opposite-sex sexual conditions, there was a significant increase in percentage correct from puzzle 1 ($M: 64\%$) to puzzle 2, ($M: 70\%$), $paired\ t(41) = -2.36$, $p = .02$, suggesting that the relevant concepts were increasingly activated as the priming process continued.

Sexual Orientation

After the priming tasks and the homoerotic motivation inventory, participants completed the (1948) Kinsey scale. Of the 60 participants, 56 indicated that they were exclusively heterosexual and 4 indicated that they were heterosexual with incidental homosexual contact (Kinsey 2). Scores on the Kinsey scale were randomly associated with priming condition, $F(2, 57) = 1.15$.

Results

Effect of Priming

An ANOVA was used to compare homoerotic motivation across the three priming conditions, revealing a significant difference between conditions, $F(2, 58) = 3.62$, $p = .03$. This analysis remains significant with the inclusion of the one participant lacking a valid progesterone value and with the exclusion of 4 participants who report as Kinsey 2 s. Post hoc t -tests reveal a significant difference between homoerotic motivation in the

affiliative ($M = 1.79$, $SD = .61$) versus opposite-sex sexual condition ($M = 1.37$, $SD = .41$) $t(40) = 2.61$, $p_{\text{one-tailed}} = <.01$, and a significant difference between the affiliative ($M = 1.79$, $SD = .61$) and neutral conditions ($M = 1.47$, $SD = .54$) $t(37) = 1.64$, $p_{\text{one-tailed}} = .03$. Although those in the neutral priming condition showed higher scores on the homoerotic motivation scale than those in the opposite-sex sexual condition this was not significant.

Interaction of Priming and Progesterone

A MANOVA model using condition as a fixed factor and log transformed progesterone as a covariate predicting homoerotic motivation was significant overall $F(5, 53) = 2.94$, $p < .02$ revealing a significant interaction of priming condition and log transformed progesterone $F(2, 53) = 3.22$, $p < .048$, with main effects of condition $F(2, 53) = 2.12$, and log transformed progesterone $F(1, 53) < 1$. As illustrated in Fig. 3, performing a mean split on the basis of progesterone level revealed that men with high progesterone who were assigned to the affiliative condition reported more homoerotic motivation than both men with low progesterone in the affiliative condition and men in other conditions regardless of progesterone level.

Discussion

Results from Study 3 largely supported the affiliation hypothesis, as priming the concept of affiliation appeared to positively shift men's attitudes towards homoerotic behavior. Congruent with the results of Study 2, such priming interacted with progesterone levels, as those men who had the highest progesterone at baseline evinced the largest effect of affiliative priming. Lastly, as in Study 2, there is evidence for the opportunity cost thesis, as homoerotic motivation is lower in men primed with sexual as opposed to affiliative concepts.

General Discussion

The results presented here provide the first experimental evidence for the hypothesis that human homoerotic behavior serves the ultimate function of enhancing affiliation. In women, we found a significant correlation between homoerotic motivation and progesterone, a hormone thought to be linked to affiliation. In men, we found that priming with cues of affiliation increased homoerotic motivation relative to men primed with other concepts, and that this effect was particularly marked in men with high baseline progesterone. Men primed with words about opposite-sex sexual contact showed the lowest scores on homoerotic motivation and there was negative albeit non-significant correlation between conception risk and homoerotic motivation in women. Both of these hint at adaptive design in light of opportunity costs

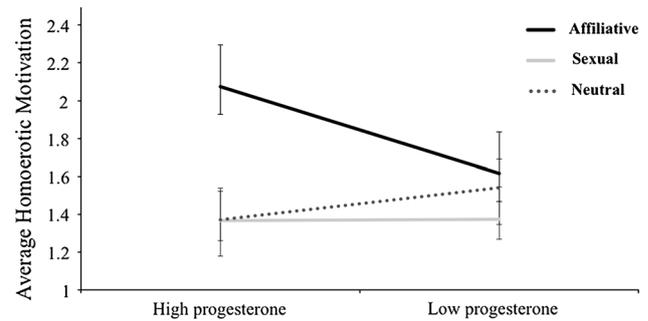


Fig. 3 The interaction of progesterone (mean split) and experimental condition on homoerotic motivation in men ($n = 59$)

such that homoerotic motivation may be downregulated in the face of the possible direct benefits of reproductive sex.

While promising, our findings should nonetheless be considered preliminary, as our investigations were subject to a number of limitations. First, while our theory predicted links between homoerotic motivation and hormonal and situational factors associated with affiliation, our between-subjects design necessarily limited our ability to specify the precise nature of these linkages. It could be, for example, that those who are chronically high in progesterone experience more homoerotic motivation overall, or that those who happened to have a higher progesterone level (perhaps because of situational factors) at the time of participation reported more homoerotic motivation. Our methods thus did not allow us to differentiate trait-level from state-level facets of progesterone profile and possible corresponding patterns of homoerotic motivation.

As we will discuss below, the affiliation hypothesis aims to explain the evolutionary persistence of both a flexible capacity for sexual attraction to both sexes and, in a subset of individuals, exclusive attraction to members of the same sex. However, there is a substantial empirical gap between our measure of homoerotic motivation and sexual orientation per se, including, among others, the possible lack of generalizability stemming from our reliance in both studies on samples composed almost exclusively of young U.S. undergraduate students, the vast majority of whom were heterosexual.

Our hormonal measures were also subject to some limitations. First, we relied on salivary assays of progesterone, a less direct measure than serum assays. Second, our measure of conception risk in women was subject to uncertainty as regards menstrual cycle position, as we were able to employ the more reliable backward-counting method in less than half of the sample. Future investigations should therefore employ ovulation tests or estradiol assays in order to measure conception risk.

Homoerotic motivation as we measured it is, of course, subject to the limitations of self-report. Although we do not have evidence that our measure of homoerotic motivation actually predicts the extent to which individuals engage in same-sex sexual behavior, nonetheless, with the caveat that cultural norms

undoubtedly shape the extent to which motivation translates into action, this is plausible given that those who are bisexual or homosexual (as indicated by the Kinsey scale) display greater homoerotic motivation on our scale. Homoerotic motivation is a necessary but not sufficient precursor to engaging in homoerotic behavior; however, it may well be the case that this motivation is not always experienced consciously (e.g., Adams, Wright, & Lohr, 1996).

Our studies examined only one potential neurochemical promoter of affiliation, progesterone. Testosterone has been shown to promote prosocial behavior in some contexts (e.g., van Honk, Montoya, Bos, van Vugt, & Terburg, 2012). More broadly, oxytocin has been implicated as an affiliative hormone in many studies (for reviews, see Bartz, Zaki, Bolger, & Ochsner, 2011; Campbell, 2008). However, concerns about such findings have recently been raised in light of problems potentially plaguing the measurement of oxytocin in humans. This is particularly important given that salivary measures of oxytocin may be especially questionable (McCullough, Churchland, & Mendez, 2013), as the invasive and intimate nature of blood draws is such that care would need to be taken not to create contexts of affiliation that could, in turn, interact with the phenomenon of interest here. In the event that such issues can be resolved, it will be important to explore whether, as the affiliation hypothesis predicts, oxytocin too undergirds homoerotic motivation.

Our findings constitute preliminary evidence that homoerotic motivation serves the adaptive function of promoting alliance formation and maintenance. Our studies primarily explored such motivation in individuals who are not exclusively homosexual, yet our findings potentially shed light on the latter as well. Exclusively homosexual orientation has posed an evolutionary puzzle, as the percentage of those with this orientation remains fairly stable despite its self-evident reproductive costs.

There is evidence for increased fertility in the maternal kin of exclusively homosexual men, suggesting a history of sexually antagonistic selection (Ciani, Cermelli, & Zanzotto, 2008; Iemmola & Camperio, 2009; VanderLaan, Forrester, Petterson, & Vasey, 2012). However, at most, this can explain only some of the variance, and only in one sex; indeed, numerous investigations have failed to find evidence of a direct adaptive benefit of exclusive homosexuality (for a review, see Rahman & Wilson, 2003). Importantly, the genetics underlying exclusive homosexuality have been elusive and not easily replicated (Gavrilets & Rice, 2006), suggesting that many loci may be involved, each of which makes only a small contribution to sexual orientation.

If homoerotic motivation is governed by many genes, then, in combination with gene–environment interactions, we would expect a continuous distribution of sexual attraction (see Poiani

& Dixon, 2010), with those in the middle of the spectrum generally having the highest fitness under ancestral conditions and constituting the bulk of the distribution. Indeed, the affiliation hypothesis predicts that, in societies where homoerotic behavior is not highly proscribed, exclusively heterosexual individuals can be expected to possess fewer and/or shallower fitness-enhancing alliances. Although the observable distribution of female sexual orientation is, in part, consistent with this model, the bimodal distribution of male sexual orientation in Western samples seems to defy it (Diamond, 1993). However, the heightened social stigma attending male homoerotic (or even affectionate homosocial) behavior in these populations may well explain the sex difference in these distributions, i.e., the sex difference observed in the degree of continuity of the distributions of sexual orientation likely stems from the greater proscriptions applied by Western cultures to male homoerotic behavior relative to female homoerotic behavior. Importantly, recent research reveals not only greater continuity in the distributions of sexual orientation in each sex than previously recognized, but also cohort effects explicable in terms of changing cultural norms that shape both action and identity (Savin-Williams & Vrangalova, 2013); relatedly, there is considerable evidence that both the targets of attraction and self-construed identity often vary across time, particularly in women (Diamond, 2012, Kuhle & Radtke, 2013). Future research will thus clearly need to address the multiple biological, social, and contextual factors shaping human homoerotic motivation.

Although much of the literature on the evolution of homosexuality portrays sexually antagonistic selection, overdominance, and homozygosity at multiple loci as mutually exclusive accounts, such exclusivity is not intrinsic to the theories themselves. Accordingly, in light of our findings, and in light of the apparent frequency of the capacity for same-sex arousal in humans, we believe that it would be a mistake for exciting developments in one area to squelch investigations in the other. Indeed, as evolutionary studies of sexuality come of age, the time has arrived for a fuller exploration of the thesis that, consonant with patterns evident in nonhuman primates, the capacity for homoerotic behavior serves an adaptive affiliative function in humans.

Acknowledgments The authors would like to thank Lianna Burton, Thomas Butler, Brian Fredrickson, Jennifer Gabrysh, Danielle Kaplan, Aspen Lewis, and Vera Wegricht for collecting data. This research was supported by a UCLA Council on Research grant to the second author.

Appendix

See Table 1.

Table 1 Factor analysis loadings for each question

	All participants <i>n</i> = 960	Male participants <i>n</i> = 298	Female participants <i>n</i> = 662
The idea of kissing a (wo)man seems sexually arousing to me.	0.90	0.90	0.89
(Wo)men's bodies are erotic.	0.80	0.90	0.70
If a (wo)man made a pass at me I would feel disgusted. (reverse scored)	0.75	0.74	0.74
I have fantasized recently about having sexual contact with a (wo)man.	0.84	0.88	0.84
I could not imagine the touch of a (wo)man being sexually arousing.	0.81	0.82	0.80
Alphas for total scale	0.87	0.90	0.85

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