Luteal phase immunosuppression and meat eating

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ABSTRACT

Immunosuppression during pregnancy makes the mother vulnerable to pathogens. Because meat is the principal source of ingestible pathogens, pregnancy raises the costs of meat eating. Natural selection has crafted a mechanism involving changes in nausea susceptibility and olfactory perception that reduces meat consumption during pregnancy. Evidence is presented showing that the luteal phase is marked by both immunosuppression and changes in nausea susceptibility and olfaction; meat consumption may be reduced during this period, suggesting a mechanism similar to pregnancy sickness. Constraints on compensatory increases in meat consumption outside of the luteal phase explain why women eat less meat than men. Meat is the principal target of acquired aversions. Women possess more aversions than men, suggesting that prophylactic mechanisms sometimes result in longstanding dietary changes. Reproductive immunosuppression explains many aspects of dietary behavior and sheds light on factors that may have contributed to gender-based divisions of labor during hominid evolution.

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SUMMARY (FOR TRANSLATION INTO ITALIAN)

Immunosuppression makes women vulnerable to pathogens during pregnancy. Pregnancy sickness alters behavior so as to reduce the risk of infection, principally by reducing meat intake through changes in olfaction, nausea susceptibility, and dietary preferences. The luteal phase of the menstrual cycle is a period of preparation for pregnancy. Periodicity in physiological measures, autoimmune disorders, chronic infections, and sleep disturbances indicate that immunosuppression also occurs during the luteal phase. This phase is marked by changes in nausea susceptibility and olfaction, paralleling changes during the first trimester of pregnancy. Evidence of reduced meat consumption during the luteal phase is reviewed. Because compensatory increases in meat consumption during other phases are necessarily incomplete, women are predicted to eat less meat than men. Data supporting this prediction are reviewed. Imperfect prophylactic mechanisms may result in long-standing aversions. Consistent with greater episodic vulnerability to pathogens, women report more acquired food aversions. Sex differences in aversions are matched by differences in olfaction and nausea susceptibility. Meat is the principal target of aversions, a pattern for which parallels exist in other animals. Vegetarianism, which is more common among women, is explicable as a product of meat aversion. Reproductive immunosuppression may have contributed to hominid behavioral dimorphism, setting the stage for a gender-based division of labor.

IMMUNOSUPPRESSION DURING THE LUTEAL PHASE

Background

Recently, Flaxman and Sherman [2000] and I [in press] presented evidence that

a) immunosuppression makes women vulnerable to pathogens during pregnancy;

b) the nausea, vomiting, and changes in dietary preferences characteristic of pregnancy function to reduce the risk of pathogen ingestion;

c) meat is both a principal avenue of disease transmission and a principal target of gestational food aversions.

Here I argue that parallels between the luteal phase of the menstrual cycle and the first trimester indicate that similar mechanisms operate outside of pregnancy as well.

For most of its' 14 days, the luteal phase is a preparatory period, as the body readys itself for implantation of a blastocyst in the endometrium. Because the blastocyst is 50% unrelated to the mother it constitutes a trigger for maternal immune responses. Both the initiation and the maintenance of pregnancy are therefore only possible through a reduction in maternal immune reactivity. Progesterone, which peaks in the middle of the first trimester, elicits the production of progesterone-induced blocking factor (PIBF) which shifts the maternal immunological balance toward anti-inflammatory signals. The result is down-regulation of maternal cell-mediated immunity, a process that allows for gestation but makes the mother vulnerable to pathogens. In the normal menstrual cycle progesterone levels begin to rise shortly before ovulation, peaking midway through the luteal phase. This suggests that, as part of the preparations for pregnancy, the luteal phase should be characterized by down-regulation of cell-mediated immunity.

Direct measures

PIBF occurs in twice as many luteal phase samples as midcycle samples, with even higher disparities in ovulatory cycles (Check *et al.* [1996]). Levels of the pro-inflammatory cytokines IL-6 (Angstwurm *et al.* [1997]) and TNF-alpha (Schwarz *et al.* [2000]) are lowest during the luteal phase, and there is a luteal drop in IL-1 (Cannon *et al.* [1998]). NK cell activity is decreased perimenstrually compared with midcycle (Agarwal *et al.* [1997], but see Gonik *et al.* [1985]). Compared with midcycle measurements, cells from the perimenstrual period produce less pro-inflammatory IFN-gamma and more anti-inflammatory IL-10 (Agarwal and Marshall [1999]). Direct immunological measures thus suggest a luteal reduction in aggressive immune response (but see also Northern *et al.* [1994]).

Autoimmune disorders

In autoimmune disorders elements in the immune system mistake part of the body for an alien or diseased entity. Fluctuations in the severity of autoimmune disorders thus shed light on immune activity during the menstrual cycle. Lupus erythematosus is associated with excess anti-inflammatory activity. In accord with the gestational shift to anti-inflammatory predominance, most lupus sufferers experience exacerbation during pregnancy (Wilder [1998]); the same also occurs during the luteal phase (Yell and Burge [1993]), suggesting a similar shift in cytokine balance. In contrast, rheumatoid arthritis is characterized by excess pro-inflammatory activity; most sufferers experience remission during pregnancy (Wilder [1998]) and a reduction in symptoms during the luteal phase (Latman [1983]).

Asthma and other allergic reactions may result from excessive anti-inflammatory activity (Bellanti [1998]). A significant proportion of women who suffer from asthma report a worsening of symptoms during the late luteal phase. Some authors explain this periodicity in psychosomatic terms, as media reports have linked asthma and premenstrual syndrome (PMS). However, South Asian subjects, unaware of purported connections with the menstrual cycle, exhibit both a) similar periodicity, and b) a positive correlation with severity of PMS (Chandler *et al.* [1997]). Atopic dermatitis flares up premenstrually in approximately 1/3 of women sufferers, and is similarly positively correlated with PMS (Kemmett and Tidman [1991]).

Chronic infections, trauma, and animal models

Fluctuations in chronic infections provide further evidence of periodic immunological changes. Vaginal Candida albicans infections often recur both during pregnancy and in the latter part of the luteal phase. C. albicans proliferates most in luteal phase serum (Kalo-Klein and Witkin [1989]), while the presence of luteal phase levels of progesterone reduces by half the proliferation of lymphocytes in response to C. albicans (Kalo-Klein and Witkin [1991]). Anti-inflammatory cytokines appear to inhibit the defense against C. albicans (Vazquez-Torres *et al.* [1999]). Pro-inflammatory cytokines play a role in the control of herpes simplex (Kobayashi *et al.* [1999]), symptoms of which often flare up premenstrually (Fisher [1982]). Surgical patients exhibit a significant depression in recovery perimenstrually compared with periovulatorily, but no discrete difference between follicular and luteal phases, suggesting that luteal immunosuppression is concentrated in the latter part of the phase (Lazzaretti *et al.* [1995]). Gruber *et al.* [1988] found decreased mouse splenocyte NK cell activity during metestrus and diestrus, but others (Page and Ben-Eliyahu [1997]) found the opposite pattern when examining rat pulmonary natural killer cell activity.

Fatigue and sleep

Pro-inflammatory cytokines are central to sleep regulation (Opp and Imeri [1999]). Fatigue is a hallmark of the first trimester (Behrenz and Monga [1999]), and fatigue and daytime sleepiness are also common during the luteal phase. Fatigue is positively correlated with severity of a) gestational nausea (Reeves *et al.* [1991]), (Suzuki *et al.* [1994]), and b) PMS (Manber and Bootzin [1997]). The first trimester is marked by insomnia and poor sleep quality and duration (Suzuki *et al.* [1994]), and lack of restful sleep is strongly correlated with daytime fatigue (Reeves *et al.* [1991]). The same features mark sleep during the luteal phase (Manber and Bootzin [1997]), and luteal fatigue/sleepiness may be a product of the quality of sleep during this period (Shibui *et al.* [1999]). A shift to anti-inflammatory predominance may disrupt normal sleep patterns, accounting for parallels between first trimester and luteal phase sleep.

Considerable evidence thus supports a luteal shift to anti-inflammatory predominance analogous to that which occurs in pregnancy, suggesting a corresponding down-regulation of cell-mediated immunity that results in increased vulnerability to pathogens.

IMMUNOSUPPRESSION AND VULNERABILITY TO MEAT-BORNE PATHOGENS

Immunosuppressed women's exposure to pathogens can be reduced through dietary changes. Of foods, meat is the most likely to carry pathogens, both because animals harbor pathogens as parasites or endosymbionts, and because pathogens proliferate on animal tissue after death. Meat is thus the most avoidable source of dietary danger to immunosuppressed women.

Reproductive-age females should be more susceptible to meat-borne pathogens than males. Toxoplasma gondii poses a severe threat to immunosuppressed pregnant women. Female mice are more susceptible to severe T. gondii infection than males (Walker *et al.* [1997]). As mice are particularly vulnerable to T. gondii, this model may exaggerate an effect that is more subtle in humans, but equivalent clinical surveys of human disease have not been conducted. Epidemiological studies on diverse populations (Clarke *et al.* [1975], Raz *et al.* [1993]) report no sex differences in the frequency of T. gondii antibodies. However, such surveys indicate that men and women have been exposed to the pathogen to the same degree, but do not reveal the severity of the infections that led to those antibodies. Moreover, if an evolved mechanism modifies female behavior so as to avoid infection during periods of heightened vulnerability, the result may be similar epidemiological profiles for women and men. Outside of studies relating to pregnancy, I have found no investigations of human sex differences in vulnerability to foodborne pathogens, nor of changes in susceptibility across the menstrual cycle.

SUBJECTIVE CHANGES DURING THE LUTEAL PHASE

Nausea

Nausea and vomiting, mechanisms motivating rejection and avoidance of harmful substances, are hallmarks of pregnancy. Consistent with a reduction in luteal immune defenses, the luteal phase often coincides with increased susceptibility to nausea: PMS involves a variety of emotional and somatic changes including nausea, vomiting, and changes in appetite (Beers and Berkow [1999]). Timing of PMS varies across subjects, from a short window immediately preceding menstruation to nearly the entire luteal phase (Beers and Berkow [1999]). Studies of Western women report incidences up to 80% (Hylan *et al.* [1999]).

Some investigators (Johnson [1987]) claim that PMS is the product of Western culture. However, similar constellations occur in Chinese (Chang *et al.* [1995]), Turkish (Dereboy *et al.*

[1994]), Israeli (Anson [1999]), Icelandic (Sveinsdottir [1998]), Moroccan (Montero *et al.* [1999]), and Nigerian (Thomas *et al.* [1990]) women. Cultural models regarding menstrual cycling can also be circumvented by examining other types of nausea. Nausea susceptibility is a unified trait that can be accessed via multiple indices (Golding [1998]), (Doherty [1999]). Western culture contains no beliefs regarding periodicity in female motion sickness, yet world-class female sailors are most likely to become motion sick premenstrually and during menstruation (Grunfeld *et al.* [1998]).

Olfaction

Olfaction, a primary elicitor of nausea, is important in the avoidance of ingestible hazards, and pregnancy is accompanied by changes in olfactory experience (Fessler [in press]). Le Magnen [1952], Vierling and Rock [1967], and Doty *et al.* [1981] found a (secondary) peak in olfactory sensitivity midluteally, when progesterone levels are at their highest in nonconceptive cycles. However, both Hummel *et al.* [1991] and Pause *et al.* [1996] failed to replicate this result. Several factors limit the applicability of these studies in the present context. First, menstrual-related variation in ability to detect an odorant is contingent on its volatility (Mair *et al.* [1978]), yet volitility has generally not been controlled for. Second, putative human pheromones are prominent in most studies, yet pheromones principally act on the vomeronasal organ, not olfactory neurons (Monti-Bloch *et al.* [1994]); timing of changes in sensitivity ought to differ between the two systems, and this may contribute to heterogeneous results (Pause *et al.* [1996]). Lastly, ecologically relevant food odors (cf. Laska *et al.* [1996]) have generally not been used.

As is likely true of pregnancy (Fessler [in press]), it may be that perception, rather than acuity, is the motivationally relevant variable in menstrual olfactory periodicity. Hummel *et al.*

failed to find changes in hedonic value, but used stimuli that were unlikely to have had evolutionary relevance. In contrast, Pause *et al.* employed citral and found that, while detection thresholds were highest during the luteal phase, at high concentrations, subjective evaluations were similar during the ovulatory and luteal phases compared to the follicular phase. Hence, while there are hints of similarity between olfaction in the luteal phase and the first trimester, the topic begs additional study.

CONSUMPTION ACROSS THE MENSTRUAL CYCLE

Although much of the data on nausea and olfaction support the existence of a pregnancy sickness-like mechanism in the luteal phase, these data are only relevant if dietary intake varies across the menstrual cycle. For several reasons, it is difficult to use published accounts of changes in food consumption across the menstrual cycle to evaluate this hypothesis. First, most authors list consumption by macronutrient rather than food type. Although meat is a principal contributor to the protein category, dairy and vegetable sources are also included, and these foods constitute different risks for immunosuppressed women, and hence responses to them should differ markedly, just as they do during pregnancy: Gestational aversions to meat may co-occur with compensatory cravings for alternate sources of protein (Fessler [in press]), and the same may be true of the luteal phase. Second, while some investigators use chemical indices to determine menstrual phase, others rely on self-report, and there is considerable variability in the precision with which the cycle is divided into phases. Other problems include failure to differentiate between ovulatory and anovulatory cycles, failure to control for activity levels, and failure to control for calendrical effects (Li *et al.* [1999]). Lastly, modern medicine pathologizes PMS, hence such individuals are often excluded from dietary studies; however, from an adaptationist perspective PMS is one pole on a spectrum of evolved strategies that weigh pathogen avoidance against foraging efficiency, hence it is precisely PMS subjects who are expected to most clearly manifest the predicted periodicity in meat consumption.

The only publication to report consumption by food type reveals a significant drop in meat consumption during the luteal phase compared to the follicular and periovulatory periods, a change that correlates with a rise in measured progesterone levels (Alberti-Fidanza *et al.* [1998]). Reporting consumption by macronutrient type, others find a slight decrease in protein as a percentage of energy consumed during the luteal phase relative to the follicular phase, although absolute protein consumption increases (Tarasuk and Beaton [1991], Eck *et al.* [1997], Li *et al.* [1999]). Abraham *et al.* [1981] state that, while reflecting changes in other macronutrients, changes in protein consumption nevertheless show more obvious periodicity, notably including a marked late luteal drop in absolute protein consumption (no data on protein as a percentage of calories are presented). However, others find no periodicity in protein consumption (Martini *et al.* [1994], Lyons *et al.* [1989]).

SEX DIFFERENCES IN MEAT CONSUMPTION

Given the advantages of meat-eating, ideally the postulated decrease in meat consumption during the luteal phase would be counterbalanced by compensatory increases during other phases. However, several factors limit the degree to which this can occur. Fewer calories are consumed during other phases, placing upper limits on total amounts of meat ingested. First, meat is energetically costly to digest and absorb relative to other food types (Westerterp *et al.* [1999]), hence considerations regarding the allocation of immediately available energy reserves may place limits on meat consumption. Second, the demands that protein places on the liver and the kidneys constrain protein intake as a percentage of calories consumed (Speth [1991]). Consistent with other parallels between pregnancy and the luteal phase, increases in renal filtration and excretory capacity seen in pregnancy also occur luteally (Chapman *et al.* [1997]) such that, relative to the luteal phase, the rest of the menstrual cycle is characterized by reduced capacity for protein utilization. Any compensatory increases in meat consumption outside of the luteal phase must therefore be incomplete. Accordingly, as a proportion of their diet, women are predicted to consume less meat than men.

The predicted sex difference in meat consumption occurs in many Western populations (Hess *et al.* [1993], Perl *et al.* [1998], Beardsworth and Bryman [1999]), and both sensory factors and disgust play roles in this difference (Santos and Booth [1996]). The generalizability of these results is limited, since Western culture emphasizes a connection between meat and masculinity (Fiddes [1991]). Both ethnographic (Wilson [1973], Spielmann [1989]) and archaeological (Cohen and Bennett [1993]) accounts indicate that, in many traditional societies, women consume(d) less meat than men, but several factors limit the direct use of the latter data in testing the predicted evolved sex difference. First, meat is generally considered a highly desirable foodstuff (Wilson [1973], Speth [1991], Simoons [1994]). Gender differences in meat consumption may thus reflect differences in the ability to obtain desirable goods. Second, because men often exercise disproportionate influence in the creation and perpetuation of cultural institutions, widespread practices of barring meat from women on cosmological or health-related grounds may be self-serving customs promulgated by men, to women's detriment (Simoons [1994]). Next, because procurement of meat is often a male task (Kaplan *et al.* [2000]), men may have preferential access to meat simply by virtue of opportunity. These factors constrain our ability to interpret widespread sex differences in meat consumption. Nevertheless, occasional ethnographic cases support the prediction: In Tamil Hindu households, where gender inequality is significant and meat is culturally devalued, men often eat more meat than women (Ferro-Luzzi [1985]). In the West, vegetarianism is an extreme form of reduced meat consumption. Among Western vegetarians, women greatly outnumber men (Worsley and Skrzypiec [1998]), (Neumark-Sztainer *et al.* [1997]), (Beardsworth and Bryman [1999]). Accounts of the process of becoming a vegetarian suggest that the practice stems from a heightened sensitivity to contamination (Fessler and Navarrete [n.d.]).

MENSTRUAL CYCLE PERIODICITY AND ACQUIRED FOOD AVERSIONS

Although periodicity in meat consumption across the menstrual cycle is the postulated optimal arrangement, serving both nutrition and disease prophylaxis, perturbations may result in learning, causing stable changes in behavior. If, during the luteal phase, consumption occurs despite disgust and nausea (due to social pressures or other exogenous factors -- cf. de Silva and Rachman [1987]), conditioned aversions may develop, resulting in prolongation of meat avoidance outside the optimal period. A similar effect may also occur if nausea is paired with olfactory exposure.

The severity of luteal phase nausea and food selectivity differs across individuals, hence interindividual variation is to be expected in the intensity of the experiences shaping ingestion during the luteal phase. The likelihood that a longstanding aversion will develop out of cyclic experiences will therefore vary across women. However, because men lack an equivalent system, a) food aversions in general will be more common among women than among men; and b) aversions to meat, in particular, will be notably prevalent.

Sex differences in acquired food aversions

Among Philadelphians between the ages of 6 and 76, Mattes [1991] found that, after age 10, a higher proportion of females than males report having one or more acquired aversions to previously liked or tolerated foods. When age categories are combined, between the ages of 11 and 50 40% of women report one or more current aversions, almost double the 22% of men who do so; similar results are reported in other studies (Bender and Matthews [1981], de Silva and Rachman [1987], but see Garb and Stunkard [1974]). Mattes found that after age 51 approximately 15% of women report current aversions, nearly the same as the approximately 11% of men doing so, suggesting that the sex difference disappears at menopause. Likewise, multiple chemical sensitivities, a condition resembling learned food aversions (cf. Siegel [1999]), is more common among young women than young men, yet occurs with equal frequency among elderly women and men (Bell *et al.* [1993]). Concerning the content of acquired aversions, Mattes notes that a higher proportion of females targeted meats. Conversely, Western men report craving meat more often than women (Weingarten and Elston [1991]).

Because the above studies were conducted in Western cultures, it is possible that the observed sex difference in learned food aversions reflects gendered cultural schemas about the meaning of food and meat. However, among inhabitants of the Ituri forest of Zaire, some individuals report avoiding particular flesh foods as a result of revulsion; girls and women possess a large number of these avoidances, reportedly because they experience disgust more readily than men (Aunger [2000]).

Meat as a target of acquired aversions

Mattes [1991] reports that meat accounts for more than 1/3 of all acquired aversions, triple the proportion of any other category; others obtain a nearly identical distribution (Rodin and Radke-Sharpe [1991], de Silva and Rachman [1987], Logue, cited in Midkiff and Bernstein [1985]). Midkiff and Bernstein [1985] surveyed 856 male and female undergraduates who reported acquired aversions and assessed the likelihood that a given aversion would occur by measuring the prominence of the food category in the typical student diet. Animal flesh made up only 16% (by item) of the diet, yet accounted for 34% of aversions, being significantly over-represented as a target of aversions. Among clinically obese patients who undergo gastric bypass surgery, meat is the principal target of aversions developed in response to nausea and vomiting (Burge *et al.* [1995]); meat is similarly prominent in aversions resulting from cancer chemotherapy (Boakes *et al.* [1993]). The privileged position of meat and other high-protein foods as the target of learned aversions is unlikely to be an artifact of special symbolic value assigned to such foods, as rats develop conditioned aversions more readily to high-protein foods than to high-carbohydrate foods (Bernstein *et al.* [1984]).

MEDIATORS OF SEX DIFFERENCES IN AVERSIONS

Olfaction

Sham feeding experiments in rats indicate that the special salience of high-protein foods involves gustatory experience; olfaction plays a central role, as the difference in ease of negative conditioning disappears when odorants are added to carbohydrates (Brot *et al.* [1987]). Olfactory stimuli are important elicitors of learned food aversions in humans (Fernandez-Marcos *et al.* [1996]), suggesting a similar role for olfaction during the acquisition process. Consistent with a greater need to detect ingestible hazards (Profet [1992]), women exhibit superior olfactory acuity (Jones *et al.* [1995], Kobal *et al.* [1996], Ship *et al.* [1996], but see Koelega [1994]). This sex difference ocurs in disparate populations (Doty *et al.* [1985], Liu *et al.* [1995]), and may decrease at menopause (Winter [1976]). Women report more dreams containing olfactory sensations (Zadra *et al.* [1998]), respond to odors with more brain activation than do men (Yousem *et al.* [1999], but see Levy *et al.* [1997]), and show superior memory for odors, but not for sounds or visual stimuli (Klutky [1990], but see Hvastja and Zanuttini [1997]). Hence, sex differences in food aversions may stem in part from olfactory differences.

Nausea and disgust

The development of food aversions is strongly tied to nausea and vomiting. A variety of data indicate that women are more susceptible to nausea and vomiting than men. European, North American, Tibetan, and Indian women all report experiencing motion sickness more often than men (Lawther and Griffin [1988], Lentz and Collins [1977], Sharma and Aparna [1997]). Lest this sex difference be attributed to cultural models of female frailty, the same pattern is evident among (presumably highly motivated) civilian pilots (Lindseth and Lindseth [1995]) and world-class sailors (Grunfeld *et al.* [1998]). Cancer chemotherapy is more likely to produce vomiting in women than in men, with women below the age of 50 being particularly sensitive (Doherty [1999]). Women are approximately twice as likely as men to experience nausea and vomiting in response to anesthesia (Fabling *et al.* [1997]). Similar patterns obtain following lumbar puncture procedures, with the sex difference disappearing in the fifth decade of life (Vilming *et al.* [1989]). Likewise, women are more likely than men to experience nausea and vomiting under conditions of both chronic heart disease (Milner *et al.* [1999]) and acute myocardial infarction (Herlitz *et al.* [1999]).

Disgust is the emotional companion of nausea. In response to a variety of stimuli, and measured in a variety of ways, Western women and girls show lower thresholds for disgust elicitation (Stapley and Haviland [1989], Haidt *et al.* [1994], Oppliger and Zillmann [1997], Koukounas and McCabe [1997], Daar [1998]). The same holds true in Japan and the Netherlands (J. Haidt, unpublished data), and among the Sumatran Bengkulu (author's notes). Simoons [1994] cites two ethnographic cases of acculturation, the Siberian Yukaghir and the Hawaiian Japanese, in which men adopted novel flesh foods but women resisted, expressing revulsion; in the former, the odor of the meat is described as particularly repulsive.

The above findings suggest a propensity to easily develop aversions to meat; the proximate workings of the mechanism are such that women are more likely to acquire aversions than men. Female reporductive immunosuppression coincides with enhanced olfactory awareness and nausea susceptibility, increasing the likelihood of aversion acquisition.

OTHER SOURCES OF COMPARISON

Rats, being omnivorous, should be subject to some of the same selective pressures facing primate omnivores, yet, in contrast to the predictions of the immunosuppression hypothesis, male rats acquire conditioned taste aversions more easily than females (Dacanay *et al.* [1984]), and these aversions are more resistant to extinction (Brot *et al.* [1987]). Either a) the immunosuppression explanation of aversions is incorrect; or b) as yet unidentified differences between rats and humans create different selective pressures in the two species.

Parallels in luteal phase changes in behavior between humans, yellow baboons (Hausfater and Skoblick [1985]), and vervets (Rapkin *et al.* [1995]) suggest that the social concomitants of PMS are not unique to humans. Laboratory and field studies of a variety of animals reveal menstrual cycle periodicity in caloric intake and/or time spent feeding that greatly resembles the periodicity evident in humans (Czaja [1975], Rosenblatt *et al.* [1980], Bielert and Busse [1983], Lyons *et al.* [1989]). However, methodological limitations (uniform lab diet, poor data resolution, and/or lack of dietary variety in field studies) preclude firm conclusions regarding periodicity in dietary preferences and selectivity. Substantial predation has been reported for common chimpanzees, white-faced capuchins, and olive baboons; in each case, males engage in significantly more hunting than females (Rose [1997], Strum [1981]), suggesting sex differences in the utility of, and attraction to, meat.

IMMUNOSUPPRESSION AND THE EVOLUTION OF HOMINID SOCIAL STRUCTURES

Among extant foragers, men concentrate more of their economic efforts on hunting than do women; the same was probably true of ancestral humans (Kaplan *et al.* [2000]). Previous attempts to explain this difference with reference to sex differences in aggressivity or the physical handicaps imposed by pregnancy and nursing are not congruent with the ethnographic corpus (Brightman [1996]). However, while cultural factors clearly play key roles in the gendered division of labor in foraging societies (Brightman [1996]), homologous patterns among nonhuman primates suggest that cultural beliefs may constitute elaborations of precultural dispositions. The special salience of meat, the sex differences in olfaction, nausea susceptibility, and disgust sensitivity, and the timing of female changes in perception and susceptibility all suggest a design to avoid pathogen transmission. Sex differences in the attraction to meat are thus likely to be both panhuman and of great antiquity. In the course of hominid evolution, this subjective difference, and the utility functions which underlie it, would have contributed to sex-specific foraging behaviors. These behaviors may then have set the stage for the cultural construction of a gender-based division of labor.

DIRECTIONS FOR FUTURE RESEARCH

The following testable predictions stem from the hypothesis that subjective changes during the luteal phase motivate dietary shifts as part of a behavioral adaptation that compensates for reproductive immunosuppression:

• Women should be at increased risk of infection in general, and infection by food-borne pathogens in particular, during the luteal phase.

• The luteal phase should be marked by changes in olfactory experience, particularly in regard to odors of spoilage, meat, and other ecologically relevant stimuli.

• The subjective appeal of meat for non-pregnant women of reproductive age should be lowest during the luteal phase.

• Such women should display maximal disgust sensitivity, particularly regarding potentially ingestible or contaminating stimuli, during the luteal phase.

• Compared to controls, vegetarians and women with a large number of acquired food aversions should exhibit more significant symptoms of PMS and, possibly on a cyclical basis, more powerful olfactory experiences, greater nausea susceptibility, and greater disgust susceptibility.

• Changes analogous (or perhaps homologous) to the above should characterize highly omnivorous nonhuman primate females.

• Differences between rodents and primates in mechanisms of maternal gestational tolerance should be such as to create different utilities for immunosuppression and behavioral prophylaxis.

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