

Testosterone and dominance in men

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Abstract: In men, high levels of endogenous testosterone (T) seem to encourage behavior intended to dominate – to enhance one's status over – other people. Sometimes dominant behavior is aggressive, its apparent intent being to inflict harm on another person, but often dominance is expressed nonaggressively. Sometimes dominant behavior takes the form of antisocial behavior, including rebellion against authority and law breaking. Measurement of T at a single point in time, presumably indicative of a man's basal T level, predicts many of these dominant or antisocial behaviors. T not only affects behavior but also responds to it. The act of competing for dominant status affects male T levels in two ways. First, T rises in the face of a challenge, as if it were an anticipatory response to impending competition. Second, after the competition, T rises in winners and declines in losers. Thus, there is a reciprocity between T and dominance behavior, each affecting the other. We contrast a *reciprocal* model, in which T level is variable, acting as both a cause and effect of behavior, with a *basal* model, in which T level is assumed to be a persistent trait that influences behavior. An unusual data set on Air Force veterans, in which data were collected four times over a decade, enables us to compare the basal and reciprocal models as explanations for the relationship between T and divorce. We discuss sociological implications of these models.

Keywords: aggression; androgen, antisocial behavior, competition, dominance, testosterone

1. Dominance, aggression, and antisocial behavior

Numerous animal experiments, especially on rodents, show that raising testosterone (abbreviated T) increases aggressiveness (Monaghan & Glickman 1992; Svare 1983). In

interpreting this work, it is important to distinguish aggressive behavior from dominance behavior. An individual will be said to act *aggressively* if its apparent intent is to inflict physical injury on a member of its species. An individual will be said to act *dominantly* if its apparent intent is to achieve or maintain high status – that is, to obtain power, influence, or valued prerogatives – over a conspecific. Rodents typically dominate aggressively, but that is not true among the higher primates (Mazur 1973).

Of course, it may be difficult to appraise the intentions of an animal to distinguish dominance from aggression. But when we study humans – our focal species here – it would be naively behavioristic to deny our ability to read people's intentions, a skill that is the very basis for human sociability (see Gopnik 1993). Much interpersonal behavior is overtly or subtly concerned with managing dominance and subordination without causing physical harm. Sports, spelling bees, elections, criticism, competitions for promotion, and academic jousting all involve domination without aggression. It is harder to identify instances of aggression devoid of a dominating motive, but examples are infanticide; purely instrumental killings such as sometimes occur in the execution of felons, murder for hire, or religious sacrifice; circumcision and ritual mutilation; euthanasia, surgery, and dentistry; suicide and self-flagellation; and knowingly causing collateral casualties from military attack. We may distinguish actions, whether by ourselves or others, that are intended to dominate, or to injure, or to do both to a target person. We understand that there are different motivations for dominance and aggression, which some-



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times work concurrently. We may refer to people as dominant, submissive, aggressive, or nonaggressive, so long as we are clear whether these descriptors refer to a particular context or to a disposition toward such motivations and actions.

The distinction between aggression and dominance is particularly important for humans, because we often assert our dominance without any intent to cause physical injury. It may be the case that T is related primarily to dominance among men and not to aggression except in situations where dominance happens to be asserted aggressively. Ehrenkranz et al. (1974) showed that socially dominant but unaggressive prisoners had relatively high T, not significantly different from the T levels of aggressive prisoners (who may have been dominant, too). Nearly all primate studies that have been interpreted as linking T to aggression (Dixon 1980) may as easily be interpreted as linking T with dominance (Mazur 1976). Recent reviewers have questioned whether, among humans, T is related to aggressiveness *per se* (Albert et al. 1994; Archer 1991).

On theoretical grounds, it is clear that dominating mechanisms – whether aggressive or nonaggressive in form – would have evolutionary advantage in helping an individual acquire valued resources, especially in competition for mates. This is not simply a matter of a dominant man taking what he wants; women regard men who *look* dominant as attractive (Townsend 1993). Teenage men rated by naive judges as having “dominant looking” faces (often with prominent chins, heavy brow ridges, muscular rather than fleshy or skinny faces) report copulating earlier than their submissive-looking peers, presumably in part because they have an easier time finding willing partners (Mazur et al. 1994).

It is not obvious why there would be selective advantage in aggressiveness *per se*, apart from its dominating function. (Predation for food is a different matter, unrelated to T.) We therefore frame our inquiry around dominating (and deferential) behavior as being theoretically prior to aggressiveness, leaving as an important but subsidiary question why men sometimes dominate with intent to harm.

An important variant of dominant behavior occurs in settings like schools, prisons, the military, families, or work groups, where authority figures require behavior to conform closely to rigid standards. In these circumstances, dominant acting individuals who hold subordinate roles are relatively likely to break restrictive norms and codes of conduct. Such actions, opposed or hostile to social institutions and laws, are conventionally defined by sociologists as *antisocial behavior*, and are labeled by those in authority as rebellious or even criminal. We believe antisocial actions are often attempts to dominate figures in authority (teachers, policemen) or, more abstractly, to prevail over a constraining environment. Therefore our inquiry focuses on the relationship of T not only to dominant and aggressive actions, but also to antisocial behavior.

2. A primer on testosterone

T is the primary *androgen*, a class of steroid hormones that develop and maintain masculine features. Although T is made in the adrenal cortex and ovary of females, it is produced in far greater amounts by the Leydig cells of the

testis. T in men is secreted into the bloodstream in spurts, so measured levels can change considerably within a few minutes. The hormone has a circadian rhythm in both sexes, highest and most variable in the morning, lower and more stable during the afternoon (Dabbs 1990).

Synthetic modifications of T are pharmacologically more useful than T itself because they are absorbed more easily when taken as pills or, in the case of esters such as T propionate, have longer lasting effects when injected. Beside its *androgenic* (masculinizing) effects, T also has *anabolic* (protein tissue building) qualities that have therapeutic value (Bhasin et al. 1996). The anabolic steroids used by athletes to build muscle mass, reduce fat, and improve performance are synthetic derivatives of T, designed to maximize protein synthesis and minimize masculinizing effects; however, virilization by anabolic steroids is never wholly eliminated (Kochakian 1993).

Many effects that we explain today by T deficiency were obtained since ancient times by castration of men and animals, which was practiced not only to prevent fertility but also to prevent the development of secondary sexual characteristics, produce docility, reduce sex drive, and – in butchered animals – to produce fatter, more tender meat. (Among men, testosterone is inversely correlated with body fat [Mazur 1995].) Castrating a male chick, for example, makes its adult flesh more edible, and the capon fails to develop the rooster's head furnishings (red comb and wattles – markers of reproductive competence), does not crow or court hens, and does not fight other cocks. In Asia, eunuchs were presumed to be safe harem guards because of their lack of both interest and ability to copulate. Male sopranos and contraltos, emasculated to maintain their prepubescent voice range, were prominent in the opera and church music of seventeenth- and eighteenth-century Europe.

Our modern understanding began in the 1930s with the isolation and identification of T. Reminiscent of the Curies' heroic extraction of minute amounts of radium from a ton of pitchblende, Koch and his coworkers mashed tons of bull testicles to fractionate ounces of material sufficiently pure to make the combs of capons grow bright red (de Kruijff 1945). (Butenandt distilled 25,000 liters of policemen's urine to obtain 15 mg of another androgen, androsterone; Kochakian 1993.) Identification and synthesis followed quickly, enabling experimenters to replace or enhance T in animal subjects and human patients. An example is the classic study of hen peck-orders by Allee et al. (1939) who injected T propionate into low-ranking hens. These injected females became aggressive, and each rose in her status hierarchy, some to the top position. Furthermore, their comb size increased (a male characteristic), egg laying was suppressed, some began crowing (rare in hens), and a few began courting other hens.

Until the availability of radioimmunoassay in the 1960s, the measurement of endogenous T was elusive because it is produced by the body in tiny amounts (Nieschlag & Wickings 1981). A normal man has about $\frac{1}{100,000}$ gram of hormone per liter of blood (i.e., 10 nanograms/milliliter); women have roughly $\frac{1}{7}$ as much. Soon it was practical to measure *free* T (i.e., T not bound to protein, which is assumed to be the physiologically active portion [Rada et al. 1976a]) in saliva with a concentration of about $\frac{1}{100}$ that of total T in blood (Dabbs 1991; Dabbs et al. 1995; Landman

et al. 1976; Riad-Fahmy et al. 1982; Wang et al. 1981). Collection of saliva rather than blood has made studies on humans more practical. These remarkable improvements in method, plus the recent availability of studies including thousands of men, have expanded our knowledge greatly.

3. Testosterone works differently perinatally, at puberty, and in adulthood

It is now clear that T affects human males importantly but differently at three stages of life: perinatally (in utero and shortly after birth), during puberty, and in adulthood. This target article focuses on the adult stage, but a brief review of earlier effects is worthwhile.

The mammalian fetus of both XX and XY individuals begins with undifferentiated sexual parts. A gene on the Y chromosome has been identified that causes the asexual gonads to develop as testes; lacking this gene the gonads become ovaries. The sex chromosomes have little more to do with sex differentiation, which hereafter is driven by hormones produced in the now sex-specific gonads. The testes produce T during gestation, and production peaks again a month or two after birth, then declines by 6 months of age to the low range seen in later childhood (Winter et al. 1976). T and other testicular secretions cause the external genitalia to form into penis and scrotum rather than clitoris and labia, and internal ducts take the male form. The central nervous system is masculinized in rats and probably in humans, too. The general rule, somewhat simplified, is that early exposure to greater amounts of T will produce more male characteristics (masculinization) and fewer female characteristics (defeminization), whereas less exposure to T will produce the reverse. Perinatal manipulation of animal subjects, and developmental abnormalities among humans, show convincingly that even genetic females will show male forms if dosed early enough with T, and genetic males will show female forms if deprived of the hormone (Breedlove 1992; Naftolin 1981; Wilson et al. 1981).

Perinatal T exposure affects behavior in a number of animal species (Breedlove 1992). For example, young male rhesus monkeys normally engage in more threats and rough-and-tumble play than do females, but when T is administered to pregnant monkeys, their pseudohermaphroditic female offspring exhibit male-type play behavior. Furthermore, by limiting T administration to the later part of gestation, female offspring are produced who exhibit male-type play but retain female appearing genitals, showing that behavioral masculinization is independent of genital masculinization (Goy et al. 1988). Studies of human children exposed perinatally to abnormally high or low levels of T are hampered by methodological problems and are not fully consistent but may be construed to support the primate results (Collaer & Hines 1995; Ehrhardt & Meyer-Bahlburg 1981).

Many perinatal hormone effects are regarded as *organizing* the architecture of the body and brain and the distribution of hormone receptors into a relatively male-like configuration. When male T increases later in life, it *activates* these preexisting structures. Thus, behaviors derive from the interaction of long-term organizational and shorter-term activational effects.

The testes greatly increase production of T at puberty, elevating prepubescent serum levels from under 100 ng/dl to adult levels 10 or more times higher. This promotes growth of the penis, larynx (and deeper voice), muscles, beard and body hair, sex interest, and perhaps combativeness. Boys who are hypogonadal or castrated before puberty do not experience these changes, but they can be induced by T replacement therapy.

The best known research on T and aggression among adolescent boys is that of Olweus and his colleagues in Sweden (Mattsson et al. 1980; Olweus et al. 1980; 1988). Because reviewers sometimes interpret these results more strongly than do the original investigators, it is worth examining them closely. A group of 40 delinquent boys, ages 14 to 19 years (mean = 16 years), living in an institution for serious recidivist youth offenders, was compared with a group of 58 nondelinquent high school students, ages 15 to 17 years (mean = 16 years). The result: T of the delinquents was slightly but not significantly higher than that of the nondelinquents.

Attempts to relate T to aggressiveness *within* the delinquent sample produced marginal results. Boys who committed the most violent crimes had slightly but not significantly higher T than boys who committed only property crimes. Ratings of the boys' aggressiveness by institution staff were not related to T, nor were evaluations of aggressiveness by a psychiatrist. The boys completed several paper-and-pencil inventories of personality. Four scales measured forms of aggressiveness, and a fifth measured dominance/assertiveness. Only one of these five scales correlated significantly with T. By comparing the eight delinquents with highest T and the eight with lowest T, one additional scale reached significance with a t-test. For the delinquent sample overall, the investigators concluded that relationships between T and their behavioral and personality variables are small in degree (Mattsson et al. 1980).

Comparable attempts were made to relate T to aggressiveness within the nondelinquent sample of high school boys. Student peers rated the boys on three forms of aggressive behavior, none of which significantly related to T (by two-tail tests, although one scale did reach $p = 0.05$ with a one-tail test). The boys completed paper-and-pencil inventories, mostly the same ones given to the delinquents. Four scales measured forms of aggressiveness, and a fifth measured antisocial behavior. Only two of these scales correlated significantly with T. The investigators, summarizing their results for the nondelinquent boys, note that inventory items that most clearly correlate with T are those involving an aggressive *response to provocation* ("When a teacher criticizes me, I tend to answer back and protest") as opposed to expressions of unprovoked aggression ("I fight with other boys at school" [Olweus et al. 1980; 1988]). This interpretation associates T with responses to challenge rather than with aggressiveness *per se*, but as we have seen, the empirical results are ambiguous. Acknowledging this uncertainty, the Swedish investigators suggest that the causal effects of T be evaluated further using a longitudinal design.

Udry and his colleagues have used just such a longitudinal method. In preliminary work, Udry examined the correlation of T with behavior in a cross-sectional study of boys 12- to 13-years old, the approximate age of puberty. He

reported a correlation between T and sexual activity (sexual ideation, petting, and first coitus), and between T and norm-violating problem behavior (aggression, dominance, antisocial acts), even when the level of pubertal development (pubic hair, genital growth) is controlled (Udry et al. 1985; Udry 1988; 1990). However, when Udry and his colleagues attempted to extend these results with a 3-year panel study, following similar boys until ages 15 or 16 years, they found no correlation between T, measured in the later years of the study, and behavior during those same years. Nor were changes in T related to behavior. They conclude that there was no direct hormone effect on the boys' behavior. Instead, they argue, T acts indirectly through pubertal development, which is a social stimulus explaining sexual and antisocial behavior among young adolescent boys (Drigotas & Udry 1993; Halpern et al. 1993).

Other researchers also report little or no relationship between level of serum T and problem behavior among young boys. A pair of studies of 86 normal boys, ages 9 to 14 years, showed no correlation between T and aggression as measured from videotapes and mothers' reports (Inoff-Germain et al. 1988; Susman et al. 1987). In a study of 18 highly aggressive prepubertal boys, ages 4 to 10, T levels were no higher than those of nonaggressive controls (Constantino et al. 1993).

Based on the work at hand, especially the methodologically strong studies by Udry's group, we believe that around puberty, the effect of T on behavior works primarily through long-term reorganization of the body, including increased size, muscle mass, and the appearance of secondary sexual characteristics. (This physical transition from boy to young man probably builds on structures laid down perinatally.) Maturation produces profound social effects on the adolescent. His peers, parents, and other authorities all treat him differently because he has "suddenly" grown up. Thus, T affects adolescent behavior mostly through indirect social responses elicited by maturation, rather than through direct activation of target receptors by T in the bloodstream. This is a provisional conclusion because much remains to be learned, but studies to date give little consistent indication that circulating T level *per se* affects behavior as much as the overall masculinization of the body during the teen years.

By the late teens, with puberty over, the physical shape and organization of the body and neurohormonal system are established (until the degradations of old age), so our concern during adulthood is solely with the behavioral effects of T circulating in the blood, available to receptors in the brain and other organs (McEwen 1981; Strumf & Sar 1978). T levels peak in the late teens and early 20s, and then usually decline slowly throughout adult life in men (Dabbs 1990; Davidson et al. 1983; Simon et al. 1992; but see Tsitouras et al. 1982 for a contrary result). There are similar age trends for male libido, aggressiveness, and antisocial deviance, all being highest among teenagers and men in their early 20s, then diminishing (Davidson et al. 1983; Segall 1979; Wilson & Herrnstein 1985). However, the causal connection between hormones and behavior remains open to question.

Most evidence indicates that men require a minimum level of circulating T for normal sexual activity (e.g., Bagatell et al. 1994; Davidson et al. 1979). The literature does contain reports of castrated men who continue sexual relations in varying degrees – sometimes approaching nor-

mal – without T replacement (Carter 1992). Questions may be raised about the authenticity of some of these reports, but some appear reliable. Castrates are not totally devoid of T; they produce a small amount in the adrenal cortex (Nieschlag & Wickings 1981). The common occurrence of penile erection in prepubertal boys shows that vaginal penetration could be obtained with little circulating T. However, most researchers agree that a full repertoire of male sexual behaviors, including libidinous feelings and ejaculation, is unlikely without a T level near normal.

Does high circulating T make a man more sexual than average in his behavior? Reviewing the limited literature, Kemper (1990) argues, partly on theoretical grounds, that a normal man's temporal fluctuations in T substantially affect his sexuality, with heightened T especially causing an increase in libidinous feelings and tendency to masturbate. We are dubious and tentatively accept at face value the usual finding that level of circulating T explains little – at most modest – variation in sexual behavior, as long as hormones are within the normal range (Brown et al. 1978; Davidson et al. 1983; Sadowsky et al. 1993; Tsitouras et al. 1982; Yesavage et al. 1985). Also, we know that causation can work in the opposite direction, as when men's T rises after viewing erotic material (Hellhammer et al. 1985) or after coitus (Kraemer et al. 1976). The administration of exogenous T to 31 normal men in stable heterosexual relationships, nearly doubling circulating T for up to 8 weeks, had no more effect than a placebo on overt sexual behavior, but it did increase some sexual attitudes (Anderson et al. 1992). The usual decline of T with age explains little of the decline in sexual activity with age (Davidson et al. 1983; Tsitouras et al. 1982). Overall, fluctuations in T (within the normal range) have little effect on men's sexual behavior as long as a minimum amount of hormone is present. May the same be said for T's effect on dominance and aggression?

4. Dominance and aggression in adulthood

By the end of puberty, usually about age 16 years, the physical form of a boy has changed into that of a man, so T can no longer influence behavior through major reorganization of the body. However, the level of T circulating in the bloodstream may affect dominating or aggressive behavior by activating receptors in organs or the nervous system.

Because of the practical and ethical difficulties in observing or even allowing high aggression in human subjects, researchers are often tempted to measure aggression, or aggressive or hostile *feelings*, by administering paper-and-pencil tests. A few positive correlations have been reported between T and such measures (Ehrenkranz et al. 1974; Harris et al. 1996; Olweus et al. 1980; 1988; Persky et al. 1971), but more typical are *failures* to find this relationship (Anderson et al. 1992; Bagatell et al. 1994; Brown & Davis 1975; Dabbs et al. 1991; Doering et al. 1975; Huesmann et al. 1984; Kreuz & Rose 1972; Meyer-Bahlburg et al. 1973; Monti et al. 1977; Rada et al. 1976b). It seems clear that T is not related in any consistent way to aggression as measured on common personality scales. Furthermore, performance on these paper-and-pencil tests is not always correlated with actual aggressive acts and there is little evidence of their relevance to violent or dominant behavior (Brain

1994; Buss et al. 1968; Kreuz & Rose 1972). We agree with Archer (1991) that studies based on self-assessment of aggressive traits or predispositions have limited relevance.

Focusing on more concrete indicators of behavior, and on males who have passed through puberty, there are several reports associating relatively high T with dominant, aggressive, or antisocial actors, including several studies of men in jail. Kreuz and Rose (1972), studying 21 prisoners aged 18 to 35 years, found no significant T difference between those who fought a lot while in prison and those who did not fight; however, prisoners with a prior record of violent and aggressive crimes had significantly higher T than those without such a history. Ehrenkranz et al. (1974) studied 36 prisoners aged 18 to 45 years who were sorted into three groups: those with chronic aggressive behavior, those socially dominant without physical aggressiveness, and those who were neither aggressive nor dominant. T levels were not significantly different between the aggressive and dominant groups, but both had significantly higher T than the group that was neither aggressive nor dominant. Rada et al. (1976b) report that rapists who were most violent in the act have higher T than less violent rapists or normal men. There were only five rapists in their "most violent" group, however, and they could not clearly replicate their finding in a subsequent study (Rada et al. 1983). Dabbs et al. (1987), studying 89 adult male inmates, found T related to the violence of their crimes and peer ratings of toughness. In another group of 113 male inmates, aged 17 to 18 years, Dabbs et al. (1991) found that those high in T committed more violent crimes, were judged more harshly by the parole board, and violated prison rules more often than those low in T. In yet another group of 490 prison inmates, their mean age 20 years, T was related to the violence of the crime, and with violating rules in prison, especially rules involving overt confrontation, leading the investigators to characterize high-T individuals as "dominant and confrontational" (Dabbs et al. 1995). On the other hand, Bain et al. (1987) found no significant difference in T between men charged with murder or assault and those charged with property crimes.

Studies done outside prison walls show mostly corroborative results if we again focus on behavioral indicators rather than paper-and-pencil personality tests, and on males who have completed puberty. Scaramella and Brown (1978), studying 14 male college hockey players aged 18 to 23, found a significant correlation between T and coach's ratings of players' aggressiveness in response to threat. Jeffcoate et al. (1986), studying 4 male physicians aged 28 to 38 who were confined on a boat for a 2-week holiday cruise, report T to be correlated with the physicians' assertive and dominant behavior, as ranked by 3 women also on the boat. Lindman et al. (1987), studying 25 men aged 22 to 27, found significantly higher T among those judged by their peers to be most aggressive while drunk. Banks and Dabbs (1996) found higher mean T among 16 young men they classified as "delinquent," based on flamboyant dress, drug use, and violence, than among 15 college men. Using an unusually large sample of 4,462 male army veterans in their 30s and 40s, several investigators (Booth & Dabbs 1993; Booth & Osgood 1993; Dabbs & Morris 1990; Mazur 1995) show T to be significantly related to self-reports of diverse antisocial behaviors, including childhood truancy, trouble as an adult on the job and with the law, marital disruption, drug and alcohol abuse, violent behavior, and military

AWOL – mostly indicators of rebelliousness and assertive norm breaking.

Overall, there is considerable evidence from a variety of settings that in men, circulating T is correlated with dominant or aggressive behavior, and antisocial norm breaking. Of course, correlation does not imply causation, and the question remains: Is high T a *cause* of dominant and antisocial behavior? This question could be answered with a double-blind experiment comparing the behavior of normal men whose T levels had been altered to that of a control group. Recent interest in T as a male contraceptive has led to studies of this kind, primarily to assess the effect of altered T on sexual behavior (Anderson et al. 1992; Bagatell et al. 1994). Subjects in both studies were given paper-and-pencil measures of aggression, which showed no change in the hypothesized direction, but we have already seen that these tests are inadequate. The incorporation of established laboratory methods for measuring dominant behavior would improve such experiments as tests of the dominance hypothesis (e.g., Gladue et al. 1989; Kalma 1991; Mazur & Cataldo 1989; Weisfeld & Beresford 1982).

Kouri et al. (1995) have moved in this direction, but with only six subjects. These normal young men were given increasingly high doses of T cypionate (150 mg/week for 2 weeks, 300 mg/week for 2 weeks, and 600 mg/week for 2 weeks) or a placebo using a double-blind, randomized, cross-over design. Each subject was tested for "aggressive" behavior by being placed in a lab setting and paired with another (fictitious) subject. The experimenter explained that each member of this pair could, by pushing an appropriate button, reduce the cash that would be paid to his opposite number. The subject was then made to believe that his fictitious opposite was indeed taking this punitive action against him. In this provocative situation, subjects made significantly more punitive button pushes while receiving T than the placebo. (Nonpunitive button pushes did not differ between T and placebo conditions.)

Further attempts have been made to evaluate the causal effect of T by looking at the treatment of prisoners or patients with castration or chemical androgen suppressors to control aggression (Brain 1984; 1994; Heim & Hirsch 1979). It is difficult to assess claims of reduced violence and recidivism because reports are often anecdotal, based on few cases, and when castration is involved there is no way to separate the effect of T reduction from the symbolic effect of mutilation. Some reports are so zealous in their advocacy of treatment that they lack credibility (Mazur 1983). Rates of violence and recidivism after treatment are not always compared with rates for similar men who were not treated. As a result, the record of these treatments tells us little more than is known from the long history of castration.

Attempts have also been made to evaluate the behavioral effect of T by analogy with the behavioral effects of anabolic steroids (Bahrke 1993). Illegal use of these drugs by young men (and some women) to improve their athletic performance, aggressiveness, or physical appearance is now widespread. Many different steroids are used, often "stacked" in diverse combinations and regimens. There have been numerous claims of violent outbursts or "roid rages," and of psychotic symptoms, as a result of doses that far exceed therapeutic levels (Pope & Katz 1990; Taylor 1991). These, too, are difficult to evaluate because of their anecdotal nature and our ignorance of the prevalence of morbid symptoms among athletes in the absence of steroid use.

Methodological improvements were made in Pope and Katz's (1994) comparison of 88 athletes who were using steroids with 68 nonuser athletes. Nearly $\frac{1}{4}$ of the users reported major mood syndromes (mania, hypomania, or major depression), a significantly higher rate than reported by these same men in the absence of steroid exposure, and significantly higher than the rate for nonuser athletes. Su et al. (1993) produced diverse mood changes – positive and negative – in 20 normal men, compared to a placebo condition, by administering an anabolic steroid (methyl T) at therapeutic doses (far below illicit dosage). The latter studies strengthen the claim that anabolic steroids can affect mood in a morbid way, but the association of such mood changes with aggressive, dominant, or antisocial behavior remains anecdotal. Also, recall that anabolic steroids are deliberately designed to minimize androgenic consequences, so their behavioral effects should differ from those of endogenous T. Furthermore, steroid abusers take amounts that far exceed normal physiological levels, which makes the relevance of their results to the normal situation dubious. Overall, available data on illicit experiences with anabolic steroids tell us little about the effect of T on dominance.

It seems likely that in the near future, properly controlled experiments will convincingly test whether or not T is a cause of dominant behavior in men. At present, however, this remains an unconfirmed hypothesis.

5. Reciprocal causation

If there is a link between T and dominance, primate studies suggest a reciprocity of effects. Not only does T affect dominance, but changes in dominance behavior or in social status cause changes in T level (Rose et al. 1975). We have stronger evidence on this *reverse* effect in humans because studies of it require no drug administration and can therefore be done by researchers other than physicians; also, T levels can be obtained from subjects' saliva, which is easily collected. By now there have been several reports of T changes in young men during athletic events, which are convenient research settings because they are stylized dominance contests involving face-to-face competition with a clear winner and loser.

Male T varies in predictable ways both before and after competitive matches. First, athletes' T rises shortly before their matches, as if in anticipation of the competition (Booth et al. 1989; Campbell et al. 1988). This precompetition boost may make the individual more willing to take risks (Daltzman & Zuckerman 1980) and improve coordination, cognitive performance, and concentration (Herrmann et al. 1976; Kemper 1990; Klaiber et al. 1971).

Second, for one or two hours after the match, T levels of winners are high relative to those of losers (Booth et al. 1989; Campbell et al. 1988; Elias 1981; Mazur & Lamb 1980; also see Johnsen & Zuk 1995, for the same effect in male red jungle fowl). This rise in T following a win is associated with the subject's elated mood. If the mood elevation is lessened because the subject has won by luck rather than through his own efforts, or because he does not regard the win as important, then the rise in T is lessened or does not occur at all (Mazur & Lamb 1980; McCaul et al. 1992). When Salvadore et al. (1987) did not obtain the win-loss effect on T among amateur judo competitors, they

explained that their subjects did not take the matches seriously.

The above results were obtained in physically taxing sports. However, as theorists we are more interested in the less vigorous competition of everyday social interaction and symbolic changes in social status (Kemper 1990; Mazur 1985). Additional studies show the same pattern of male T responses during nonphysical contests or ritual status manipulations. First, T rises shortly before chess matches (Mazur et al. 1992) or laboratory contests of reaction time (Gladue et al. 1989; Fig. 1), and in subjects confronted with a symbolic challenge from an insult (Nisbett & Cohen 1996). Second, T levels of winners are high relative to those of losers following chess matches (Mazur et al. 1992) and contests of reaction time, especially if subjects' moods are appropriately positive or negative (Gladue et al. 1989; McCaul et al. 1992). Similar effects occur among sports fans who are not themselves participants in the physical competition. Following the 1994 World Cup soccer tournament in which Brazil beat Italy, T increased significantly in Brazilian fans who had watched the match on television, and decreased in Italian fans (Fielden et al. 1994).

The hormone-depressing effect of status loss is shown in a study by Kreuz et al. (1972), who found that the T of officer candidates was abnormally low during the early, most degrading weeks of Officer Candidate School, but their T returned to normal during the relaxed weeks just prior to graduation. Similarly, T among prisoners dropped after admission to an incarceration program modeled after military boot camp (Thompson et al. 1990). Mazur and Lamb (1980) found that T of medical students rose after their graduation ceremony, when their mood was elated. During the first days of freedom for 52 Americans who had been held captive in Iran for 15 months, a period of elation over their improvement in status, the former hostages' T was highly elevated (Rahe et al. 1990). Thus, the T pattern appears in nonphysical as well as physical competition, and in response to symbolic challenges and status changes among men.

The function of the elevated T following a win and the drop in T following a loss is not known. One possibility is that winners are soon likely to face other challengers; the high T may prepare them for this eventuality. The drop in T among losers may encourage withdrawal from other challenges, thus preventing further injury.

6. T in women

Despite considerable speculation that T is associated with aggression or status in women (Kemper 1990), the empirical literature is scant and disparate. Purifoy and Koopmans (1979) report that T in 55 women increased with the status of their occupations. Ehlers et al. (1980), studying women who were patients in a neurological clinic, found significantly higher T among relatively aggressive patients compared to less aggressive ones, but these groups also differed in diagnosis, making the comparison suspect. Dabbs et al. (in press) saw no difference in T between 84 women in prison and 15 college women, but women convicted of unprovoked violence had higher T than other prisoners. Dabbs and Hargrove (1996) found no significant relationship between T and the extent of criminal violence among 87 female inmates, but T was significantly related to "aggressive dominant behavior" while the women were in

prison. Banks and Dabbs (1996) found higher mean T in 13 delinquent young women than in 21 female college students. Gladue (1991) found T to be negatively related to self-reported aggression in 32 women. Cashdan (1995) found status (as judged by peer assessments) among 32 college women to be negatively correlated with T, although the women's self-assessment of their own status was positively correlated with the hormone. Also among these college women, T was negatively correlated with frequency of smiling, the absence of which is sometimes regarded as an indicator of dominance. The lack of consistency among these correlational findings is a caution to await further research.

The issue of sex differences has been addressed by asking how men and women respond to an identical competitive situation. T was assayed from saliva given by young men and women before, during, and after competing with a same-sex partner in a video game (Mazur et al. 1997). The hormonal response to the competition was different in each sex. Males showed the usual pre-contest rise in T but females did not. Males did *not* show the usual result that T of winners is higher than that of losers, apparently because the video game produced no mood difference between male winners and losers. A mood difference was produced between female winners and losers, but even with this precondition met, female T showed no specific response to the competitor. Booth and Dabbs (1995) report a consistent finding from their study of six female basketball players, whose T was generally not responsive to the anticipation or outcome of their games. These results suggest that the effect of competition on T is specific to men.

7. Dominance contests

Does T play a role in daily challenges to status, either from strangers or from people well known to us? Like all primates, humans in face-to-face groups form themselves into fairly consistent dominance/status hierarchies so that higher-ranked members have more power, influence, and valued prerogatives than lower-ranked ones (Mazur 1973). Ranks are allocated either *cooperatively*, by consensus of those involved, or *competitively*, when there is disagreement over who should outrank whom.

To appreciate a person's decision to compete or cooperate, visualize two individuals, Ego and Alter, meeting for the first time. If their interaction is very brief or casual, the notion of ranking may never arise. In more extended or serious meetings, however, each will size up the other and gain some sense of their relative standings. If Ego thinks that Alter's status does or should exceed his own, he may defer to Alter without any dispute. In human terms, Ego may believe that Alter belongs in the higher rank, that Alter deserves it, that Alter could easily take it if Ego resisted, or that Alter would be more competent in the duties of high rank. In any case, ranks are allocated quickly and cooperatively. If Ego and Alter do not agree on their relative standings, then they may either break off the interaction or vie for the contested rank.

Ego's decision to compete or to comply will also depend on his motivation to dominate, which we believe is related to his T level (among other factors). A man who has experienced a recent rise in T, perhaps from a victory or a symbolic elevation in status, will be unusually assertive and may challenge someone of relatively high status. If both

Ego and Alter decide to compete, their relative ranks are then determined by the outcome of one or more short dominance contests between them.

Nonhuman primates are commonly observed to establish and maintain their status hierarchies through a series of short face-to-face competitions between members of the group. Some competitions involve fierce combat; others are mild, as when one animal is obviously the more powerful and assertive or the other appears fearful. In such cases, a simple stare by the powerful animal, followed by the fearful animal's eye aversion or by its yielding something of value (perhaps food or a sitting place), may suffice. Sometimes a single contest is all that is needed to allocate ranks or to verify a preexisting rank relationship, but often the outcome is settled only after a series of contests.

According to our model of dominance contests (Brinkerhoff & Booth 1981; Mazur 1985; 1994), a psychophysiological mechanism operating across this range of competition is the manipulation of stress levels. An exchange of threats or attacks is seen as an attempt by each animal to "outstress" or intimidate the other by inducing fear, anxiety, or other discomfort. Stress is experienced as both a feeling of discomfort and a syndrome of neurological responses (Axelrod & Reisine 1984). The animal that outstresses his adversary is the winner.

The model becomes clearer if we consider a concrete example (Mazur et al. 1980). Consider two strangers, Ego and Alter, whose eyes meet, by chance, across a room. Let us say that one of the strangers, Ego, decides to hold the stare. The chance eye contact now becomes a dominance encounter. Ego's stare makes Alter uncomfortable. Alter may then avert his eyes, thus relieving his discomfort while, in effect, surrendering, or he may stare back, making Ego uncomfortable in return. In the latter case, the staredown would continue, with each individual attempting to outstress the other until finally one person succumbed to the discomfort (and the challenger) by averting his eyes. The matter thus settled, the yielder usually avoids further eye contact, though the winner may occasionally look at the loser as if to verify his victory.

In this example, Ego's stare is assumed to elicit feelings of stress in Alter. Alter's eye aversion is assumed to relieve his own felt stress. Staring – the stress-inducing behavior – is a dominant sign associated with high status. Eye aversion is a deferential sign associated with low status. In other words, a dominant act (staring) elicits stress in the recipient; a submissive act (eye aversion) relieves stress in the actor. It is a central assumption of this model that most dominant and deferential acts work this way, inducing or relieving stress, respectively. These acts are the means whereby the adversaries wage their stress contest, each aiming "darts" at the other. Finally, when the stress is too great for one, he switches from dominant to deferential actions, thereby relieving his stress and simultaneously signaling his acceptance of the lower rank.

Within hours of this outcome, we assume Ego (the loser) experiences a drop in T, reducing his assertiveness, diminishing his propensity to display the dominant actions associated with high status, and increasing his display of such submissive signs as stooped posture, smiling, or eye aversion (Mazur 1985). Faced with a new dominance encounter, Ego is more likely than before to retreat or submit. On the other side Alter, the winner, experiences the opposite effects: rising T, increased assertiveness, and a display of

dominant signs such as erect posture, sauntering or striding gait, and direct eye contact with others. Alter may seek out new dominance encounters and is bolstered to win them. This feedback between high (or low) T and dominant (or submissive) demeanor would help to explain the momentum often associated with strings of triumphs or defeats: Success begets a high T response which begets more dominant behavior which begets more success.

8. Honor subcultures

Nisbett (1993; see also Nisbett & Cohen 1996) has attributed the historically high violence in the American South, compared to the North, to its "culture of honor" whereby Southern men, when challenged by insults to themselves or their families, are required to defend themselves as virtuous warriors or else lose face. Apparently as a result, Southern men are unusually alert to possible insults, reacting dominantly – sometimes violently – to speech or actions that might not be perceived as injurious in other cultures.

Leaving aside the particular historic roots of the South, there may be a general hypersensitivity to insult in any subculture that is (or once was) organized around young men who are unconstrained by traditional community agents of social control, as often occurs in frontier communities, gangs, among vagabonds or bohemians, and after breakdowns in the social fabric following wars or natural disasters. When young men place special emphasis on protecting their reputations, and they are not restrained from doing so, dominance contests become ubiquitous, the hallmark of male-to-male interaction (Sanchez-Jankowsky 1991; Thrasher 1963).

The leading student of street behavior in America's inner cities, sociologist Elijah Anderson (1994), vividly portrays the importance of dominance contests and their constant presence for poor young black men:

(M)ost youths have . . . internalized the code of the streets . . . which chiefly (has) to do with interpersonal communication . . . (including) facial expressions, gait, and verbal expressions – all of which are geared mainly to deterring aggression.

Even so, there are no guarantees against challenges, because there are always people looking for a fight to increase their share of respect – of "juice," as it is sometimes called on the street. Moreover, if a person is assaulted, it is important, not only in the eyes of his opponent but also in the eyes of his "running buddies," for him to avenge himself. Otherwise he risks being "tried" (challenged) or "moved on" by any number of others. To maintain his honor he must show he is not someone to be "messed with" or "dissed."

The craving for respect that results gives people thin skins. Shows of deference by others can be highly soothing, contributing to a sense of security, comfort, self-confidence, and self-respect. . . . Hence one must be ever vigilant against the transgressions of others or even appearing as if transgressions will be tolerated. Among young people, whose sense of self-esteem is particularly vulnerable, there is an especially heightened concern with being disrespected. Many inner-city young men in particular crave respect to such a degree that they will risk their lives to attain and maintain it. (Anderson 1994, pp. 88–89)

The honor subculture, the defense of one's reputation from insult, has been amply demonstrated by social scientists to be a feature of life for young men in the inner city (Anderson 1978; 1991; Horowitz 1983; Katz 1988).

We know from laboratory and athletic studies that T rises in men awaiting a contest, regardless of the eventual out-

come of that contest. Generalizing to the street, hormone levels should be elevated in young men who are constantly vigilant against assaults on their reputations. Of course, T is also affected by the outcome of the contest, so persistent losers might be hormonally depressed, but most men – those with mixed outcomes or better – should have elevated T.

A caveat: stressors such as weight loss, surgery, or military training sometimes depress T (Booth et al. 1993; Kreuz et al. 1972; Strauss et al. 1985). If *all* stressors depressed T, then the stressful challenges of inner-city street life should lower the hormone, not elevate it. However, not all stressors are the same, and social challenges in particular evoke hormonal responses different from those caused by surgery or weight loss. Indeed, we have already seen that T reliably rises in the face of competitive challenges, even while cortisol (the "stress hormone") goes up as well (Booth et al. 1989; Elias 1981; Gladue et al. 1989; Salvador et al. 1987). Thus, stress effects do not negate the hypothesis that street challenges elevate male T.

We may use this hypothesis to interpret reported racial differences in T. A comparison of black and white boys aged 6 to 18 years, mostly preteens, showed no significant race difference in T (Richards et al. 1992). By adulthood, black males do have significantly higher T levels than white males (Ellis & Nyborg 1992; Ross et al. 1986), possibly reflecting the higher defensive demands on black men during young adulthood.

The data set used by Ellis and Nyborg (1992) came from 4,462 army veterans, ranging in age from 30 to 47, and permits a finer grain analysis (Mazur 1995). Among veterans older than the median age of 37 years – too old to be involved in inner-city honor cultures – the T of blacks is no higher than that of whites. Furthermore, among younger veterans who have gone to college – and thus are unlikely to be inner-city residents – there is no significant race difference in T. Only among *younger veterans with little education* do we find T in blacks to be unusually high, significantly higher than in whites. These younger black men, poorly educated, most of them urban residents, are most likely to participate in the honor subculture, and that may be the reason for their elevated T.

The reciprocal linkage between hormones and behavior suggests that if T levels among young men in the inner city are heightened by their constant defensive posture against challenge, then these high hormone levels in turn encourage further dominance contests. Feedback between challenge and T may create a vicious circle, sometimes with lethal effects.

9. Basal versus reciprocal models: Divorce and marriage

A *basal model* is usually used in describing the causal effects of T on behavior, meaning that each man's T measurements represent short-term fluctuations around his characteristic basal level, which is genetically based, and that by adolescence or shortly afterward, this basal level is more or less consistent from year to year. Consistent with this model, reliabilities from $r = 0.50$ to 0.65 are reported for T measurements taken (at the same time of day to control for circadian variation) over periods ranging from a few days to 6 years (Booth & Dabbs 1993), showing that men with relatively high T at one time tend to be relatively high at

other times, too. On the assumption that basal hormone levels are consistent, they necessarily predate any post-adolescent behavior and so cannot be a consequence of that behavior. Furthermore, because basal levels are stable, it follows that they can be adequately measured at any time, whether before or after the behavior, and therefore can be adequately assessed in a cross-sectional study. Going further, basal hormone level is regarded as a *prima facie* cause of any postadolescent behavior that it predicts, especially if the effect persists after controlling for alternate explanations.

We contrast the static basal model with a dynamic *reciprocal model* in which T and status competition influence one another, going up or down together. The observed reliability of a man's T measurements from year to year may reflect his stable social position rather than his genetically determined basal level. Current data are insufficient to choose one model over the other, so we regard both as viable and heuristically useful.

The power of the basal model is illustrated by its ability to predict behavior from T measured at a single point in time. It suggests, for example, that men with high basal T tend toward dominating or antisocial behavior that disrupts family functioning, leading eventually to divorce. Pursuing this reasoning, Julian and McKenry (1989) found in a small sample of men that T levels are negatively related to marital satisfaction. A more extensive analysis of data from 4,462 former military servicemen in their 30s and 40s showed that males with higher T (measured once) are less likely to marry and more likely to divorce (Booth & Dabbs 1993). The likelihood of never marrying is 50% higher for men whose T is 1 standard deviation above the mean compared to those 1 standard deviation below the mean. Similarly, among men who have married, those at the higher level of T are 43% more likely to divorce than those at the lower level. Once married, men with higher T are 31% more likely to leave home because of a troubled relationship with their wives, 38% more likely to have extramarital sex, and 13% more likely to report hitting or throwing things at their spouses. In addition, high T men are more likely to report a lower quality of marital interaction. The occurrence of these behaviors increases continuously with T; it is not limited to men with exceptionally high T.

Using the same sample of men, correlations between T and education, and between T and income, are significantly negative but small in magnitude. Dabbs (1992) coded the status of the occupations of these men, using U.S. Census categories, and showed a correlation with T of -0.11 ($p = 0.001$). Professional and technical workers had lower levels of T than service and production workers. The unemployed had the highest level of T. There was no evidence of a threshold effect.

The men with higher levels of T are more likely to be arrested for offenses other than traffic violations, to buy and sell stolen property, incur bad debts, and use weapons in fights (Booth & Osgood 1993). Those with a T level 1 standard deviation above the mean are 28% more likely to engage in criminal behavior than those one standard deviation below the mean. Again, no evidence of a threshold effect was observed. In addition, those who were delinquent as juveniles were more likely to commit crimes as adults if they had higher levels of T.

An analysis of factors that predict exposure to military combat reveals that T increases the likelihood of exposure

(Gimbel & Booth 1996). It is unclear whether high T individuals take an active role in seeking out combat or if those in command recognize behaviors that make the individual a better combatant and assign him accordingly. It is also possible that high T individuals are antisocial enough to get combat assignments as punishment. In any case, the basal model shows impressive predictive ability.

Unfortunately, these findings, based on data measured at a single point in time, cannot tell us whether the men with marital and other difficulties always had relatively high T, as assumed in the basal model, or if discord surrounding their problems produced elevated T, which in turn exacerbated the discord, as assumed in the reciprocal model.

An unusual opportunity to compare the two models is presented by a panel study of 2,100 male Air Force veterans who received 4 physical examinations, roughly 3 years apart, over a decade (Mazur & Michalek, in press; Wolfe et al. 1990). Correlations between T levels measured in any 2 exams range from $r = 0.47$ to 0.61 , showing the expected consistency across years.

There was little behavioral measurement in this study, but marital status was determined at each examination. T, as measured four times during the decade, could accordingly be correlated with marital status at each exam. Among the 16 possible correlations, 10 were significantly positive, replicating Booth and Dabbs' (1993) association of high basal T with divorce. However, we find that T measured *right after* the divorce is the best predictor, giving a regression coefficient roughly twice as large as when T is measured five years away from the divorce. This higher T with proximity to divorce indicates that the reciprocal model is also at work.

Furthermore, men who divorced during the decade of the study had elevated T in the examinations just before and after their breakups, compared to examinations further removed in time. The T of men who married during the decade fell as they made the transition from bachelor to husband, and T remained low among stably married men. Thus, T is highly responsive to changes in marital status, falling with marriage and rising with divorce.

These results have an easy interpretation in the reciprocal model. Normal marriages are secure and supportive, more free from stress than single life, consistent with the relatively low cortisol found in married Air Force veterans. Single men are more likely than married men to face confrontations and challenges and, lacking the social support of a spouse, they are more likely to face situations where they must watch out for themselves, acting defensively and adopting protective postures. These are precisely the kinds of situations in which T rises. The abrupt act of marriage is the culmination of a longer and more gradual period of courtship and engagement, in which a man accepts the support of his partner, removing himself from the competitive area in which he has operated with his fellows. It is for this reason, we suggest, that T declines with marriage.

Similarly, a divorce is discrete in time but the breakup of a marriage is a process usually spanning years both before and after the legal announcement (Booth & Amato 1991). Typically it is accompanied by arguments and confrontations, the kinds of events associated with high T, both as cause and effect (Booth et al. 1985). We suggest that most men undergoing this level of challenge, unless persistently defeated, will experience rising T, which in turn encourages

further confrontation with their estranged wives. Reciprocity is thus an appealing model here, but we also need the basal model to explain why men initially high in T have more propensity to divorce.

10. Summary and conclusions

Perinatally and during puberty, the effects of T on behavior appear to work primarily through long-term reorganizations of the body and neurohormonal system, and only secondarily through short-term activation. By the end of puberty, usually around age 16 years, the body is nearly at its adult form, so behavior is affected primarily by the level of T circulating in the bloodstream, which can activate steroid receptors.

We share doubts expressed by Archer (1991) and Albert et al. (1994) that circulating T directly affects human aggression – the intentional infliction of physical injury. We favor instead the hypothesis that high or rising T encourages dominant behavior intended to achieve or maintain high status (implying power, influence, and valued prerogatives). Usually humans express dominance nonaggressively. We leave as an important but subsidiary question why men sometimes dominate with intent to harm.

When military, school, or legal authorities require the behavior of subordinates to conform to rigid norms or laws, those people in subordinate roles who are motivated to act dominantly are likely to do so by breaking these norms or laws. In such settings, high or rising T encourages actions conventionally regarded as rebellious, antisocial, or even criminal.

Studies using various paper-and-pencil self reports of aggressive/hostile moods or personalities have not been generally successful in demonstrating relationships to T, nor have we found such instruments reliable in our own research. Using more direct indicators or inventories of behavior, studies in both prisons and free settings fairly consistently show significant correlations between T and dominating behaviors (with or without aggressiveness), and between T and diverse antisocial or rebellious actions. Although we regard the correlation between T and dominant or antisocial behavior as well supported, heightened T has not been established as a cause of these behaviors. Attempts to appraise hormonal causation by evaluating the use of castration or chemical androgen suppressers on prisoners or patients, or the illicit use of anabolic steroids, have not been helpful because of methodological difficulties. We are just beginning to see proper double-blind experiments testing the effect of T on dominant behavior as measured with established laboratory procedures.

There is strong correlational and experimental evidence that T responds in predictable ways both before and after competitions for status. First, T rises shortly before a competitive event, as if anticipating the challenge. Second, after the conclusion of competition, T in winners rises relative to that of losers. T also rises after status elevations, and it falls after status demotions. These effects require the presence of appropriate mood changes – elation or dejection – accompanying the status changes. Limited evidence suggests that this pattern of T responses is specific to men.

People in face-to-face groups form themselves into fairly consistent status hierarchies. Usually ranks are allocated cooperatively, but sometimes people compete for high rank in dominance contests where each contestant tries to out-

stress the other until one concedes, accepting the lower rank. We propose that high or rising T, by encouraging dominant behavior, induces men to compete for high status. The experience of winning or successfully defending high rank boosts T, which in turn encourages more dominant behavior. The experience of losing depresses T, encouraging a switch from dominant to deferential behavior. This mechanism explains the momentum associated with winning or losing streaks.

“Honor subcultures” are communities in which young men are hypersensitive to insult, rushing to defend their reputations in dominance contests. Challenges are pervasive and have the effect of elevating T among those who participate in them (unless they are persistently defeated). Heightened T may in turn encourage more challenge behavior, producing a vicious circle.

This *reciprocal model* implies feedback between T and dominance, each reinforcing the other. It contrasts with the customary *basal model* in which an individual's basal level of T is presumed to be a fairly stable trait that predicts his behavior. Most studies cannot distinguish between the basal and reciprocal models because their data are collected at one point in time. An exception is a study of marital status among 2,100 male Air Force veterans who received 4 medical examinations over a 10-year period (Mazur & Michalek 1995). Among these men, T levels fell and remained low with marriage, and rose with divorce, rather than remaining constant. These results, although limited in scope, favor the reciprocal model over the basal model. The basal model, on the other hand, better explains the propensity for divorce among men who were initially high in T. We tentatively regard both models as viable. The basal model has the pragmatic advantage of predicting behavior when T is measured at a single point in time.

The reliable association of high T with antisocial behaviors, including marital disruption and violent criminality, raises an interesting puzzle. These negative behaviors foster downward social mobility. Under the basal model, which assumes T level to be a persistent trait, we should expect an accumulation of *high-T* men in the lower ranks of society. Indeed, as we have noted, correlations between T and various measures of socioeconomic status (occupation, income, education) are significantly negative. But they are slight in magnitude. Thus, leaving aside honor subcultures, we find little concentration of men with high T in the lower classes. Why not? One possibility is that the downward flow of high-T men who are antisocial is nearly balanced by an upward flow of high T men who are prosocial. This hypothetical stream of prosocial high-T men remains invisible to us, so far, perhaps because past studies have used as subjects mostly working class men or convicts, who have limited opportunities for legitimate advancement.

The nearly uniform distribution of T across social classes is less puzzling under the reciprocal model, which regards T as malleable rather than a stable personality trait. Again excepting honor subcultures, where challenges are exceptionally common, dominance contests probably occur nearly as frequently among elites as in the working class, as often in the boardroom as on the shop floor. Therefore, T responses to challenge, and to winning and losing, should be distributed fairly evenly across classes. Under this reciprocal model, we would expect little accumulation of T at the bottom levels of society.

The applicability of one model or the other would be

elucidated by studying the relationship of T to behavior among upper class men who have favorable social opportunities and strong incentives for prosocial behavior.

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Problems with the concept of dominance and lack of empirical support for a testosterone–dominance link

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Abstract: Mazur & Booth fail to consider the conceptual complexities of dominance; it is unlikely that there is a motive to dominate in animals. Also, the lack of empirical evidence for a causal link between testosterone and dominance is obscured by the narrative reviewing procedure, which is prone to bias.

Mazur & Booth's (M&B's) target article is another attempt to make sense of the confusing and contradictory research on testosterone (T) levels and measures related to human male aggression. Their argument that there is a causal link between T and dominance, and not between T and aggression, can explain only a limited part of the evidence. There are conceptual and empirical problems with M&B's analysis. The conceptual one concerns the discussion of dominance. Considering dominance in animals and children, I have described three different levels to which the concept has been applied (Archer 1992): the group structural (as in "dominance hierarchy"), dyadic or interpersonal, and individual levels. At the individual level, *dominance* is a descriptive term, although it could also be conceived as a personality variable. In animal studies, dominance has generally been used at the dyadic or group level. M&B appear to have moved from dominance as a description of individual actions to assuming that animals must be motivated to strive for dominance. Dominance is therefore elevated to an intervening variable for individual behavior, a tendency which has clouded the analysis of the term throughout its history.

M&B's extraordinary statement that "It is not obvious why there would be selective advantage in aggressiveness per se" (sect. 1) ignores the very obvious advantages of aggression in competing for resources, in protecting young, and in defence (Archer 1988). Over half a century's ethological and psychological research on animal aggression shows that animals fight for a variety of proximate reasons, such as invasions of territory, response to pain, or thwarted goals (Archer 1988). In view of the potential costs of losing a fight, the assessment of cues associated with the likely outcome occurs during the social exchanges that precede damaging physical contact (Parker 1974), and animals readily learn the fighting abilities of former opponents (Barnard & Burk 1979). Out of this process arises what an outside observer may refer to as one animal dominating another, but it does not follow that one animal has a motive to dominate, or that it is attempting to "outstress" the other, as M&B suggest. Dominance is therefore a description of a pattern of social relations arising from the consequences of unequal aggressive encounters, which are themselves triggered by well-understood external cues.

Human concepts such as status, respect, and power depend on being able to articulate these perceptions of inequality among individuals. Ultimately, human status and power are based on the ability to provide a credible threat of physical force, as is the case in the animal world. It is therefore unlikely that at a conceptual level dominance is the appropriate characterisation of whatever aspect of aggression-related behavior, if any, is influenced by testosterone.

Turning to the evidence, I agree that there is consistent support for the conclusion that some psychological variable that is increased following success in status-related competition must be producing a rise in testosterone levels among human males. But the reverse link, from testosterone to behavior motivated by status-striving, is less consistently supported by the evidence than is a causal link between testosterone and aggression (Archer 1994). A major problem with evaluating M&B's hypothesis arises from the narrative form of their review. Where possible, meta-analytic techniques should be used to evaluate hypotheses. Meta-analysis eliminates the possibility of selective presentation of data as well as impressionistic conclusion forming; that is, the conclusions become less prone to bias.

The only human study M&B cite that relates directly to their hypothesis is a small-scale study by Ehrenkranz et al. (1994). It should be noted that in this study the aggressive group showed higher T levels than the socially dominant group. Overall, it is difficult to tell from M&B's narrative review whether null findings occurred elsewhere. There is also no systematic assessment of whether measures of dominance are more closely related to T than variables such as aggression or impulsiveness. A link with aggression *has* been found in previous research, but it is an inconsistent link (Archer 1994). The large-sample study described in the target article showed an *association* (small in magnitude) between T and a constellation of impulsive behaviors, including aggressiveness and responses to challenge, greater variety and less stability of sexual relations, and occupational instability. I have suggested (Archer 1994) that such data are best viewed in terms of a developmental model; any influence of T interacts with the current disposition, which is in turn a product of developmental history, including influences throughout childhood when T levels were low. The constellation of dispositions described above can be viewed as one of two contrasting developmental pathways that have evolved: high T is associated with low parental investment, more overt intermale competition, and more sexual partners; and lower T with high parental investment, less intermale competition, and fewer sexual partners.

Androgens and human behaviour: A complex relationship

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Abstract: The claimed link between dominance and free testosterone is an intriguing one but problems remain in attempting to link this single hormonal measure to human behaviour. These include the heterogeneous nature of dominance, the precise nature of the correlation(s), and whether only testosterone is important.

The basic thesis of the Mazur & Booth (M&B) target article is that free testosterone in human males is much easier to relate to the concept of "dominance" (or, more exactly, success in competitive situations) than to "aggression." This seems to have some basis in fact. There is no doubt that we have moved a considerable distance since the simplistic claim that androgens "cause" human violence. Even in nonhuman mammals, aggression is clearly a heterogeneous phenomenon (the various tests having offensive, defensive, or even predatory components) and is only occasionally influenced by dramatic changes in testosterone levels produced

via castration and/or application of the hormone (Brain & Haug 1992). Brain (1994) suggests that, in our own species, androgens, though not having a simple causal influence on aggression and violence, do seem to alter several factors, including aggressive feelings, self-image, and social signalling, that predispose individuals to carry out actions that can receive these labels. In this sense, the relation between the hormone and the response is not very different from the apparent relation between alcohol and human violence; Brain 1997a). Although it is true that there are even greater difficulties in relating plasma testosterone levels to human aggression, the basic questions that remain for the testosterone–dominance link are:

(1) Is human male “dominance” any less heterogeneous than “aggression”?

(2) What is the nature of the relationship(s) between plasma testosterone level and dominance?

(3) Is the association(s) a result of cause or effect?

In nonhuman animals, it is well known that dominance measured in different ways results in different rankings (see, e.g., Benton et al. 1980). It is interesting that having previously been a winner enables a rodent to recover from the effects of subsequent defeats much more quickly than do animals who lack this positive experience (Brain & Kamal 1989). The plethora of situations studied (athletic and competitive contexts, computer assignments of winning or losing in laboratory reaction time tasks, medical examinations, assessment of male behaviour by female companions, estimations of “toughness” by other prisoners, etc.) suggests that the concept of dominance is going to be no less problematic in our own species. Perhaps winning in a competitive situation is a more appropriate description?

Plasma testosterone provides a very inexact link with expressed behaviour or environmental circumstances. Free testosterone levels fluctuate, and it seems more important to know what is happening at a variety of binding sites in a variety of tissues than simply measuring free testosterone (this partially accounts for the recent use of salivary measures of the hormones in such studies). It is clear that this androgen will change emotions, self-image, and the social signals individuals direct to each other and that these modifications are produced in different targets (sometimes by different metabolites of the “parent” hormone such as oestradiol and 5 α -dihydrotestosterone). The roles of other androgens also remain to be elucidated.

M&B’s account strongly suggests that the association between free testosterone and behaviour is a reciprocal one. Rather than testosterone producing dominance, winning and losing (especially if continued) lead to reliable changes in male sex hormone. These changes modify the probability that one will behave in a particular fashion on a subsequent occasion. Winning competitively (but not as a consequence of chance, as in a lottery) generally augments levels of circulating androgens in adult male men, whereas losing has the opposite effect. The roles of other hormones are likely to be important in this equation. Some of the very profound effects of “victimization” (which includes defeat) have been reviewed recently (Brain 1997b). Brain & Susman (1997) have incorporated this information and have further suggested that the subtle impact of androgens on neural architecture might not be limited to the developmental stages of life. Given this, one can find an even more sustainable link between androgens and competitive human behaviours.

Testosterone and dominance: Between-population variance and male energetics

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Abstract: The testosterone–dominance model is noteworthy but should incorporate the ecological factors that often underlie variability in basal testosterone. This is evident in the ethnic testosterone differences discussed in the target article (sect. 8). The significance of acute changes in testosterone levels in response to competition is also poorly understood. Significant metabolic effects have been reported, suggesting that other physiological explanations should be explored, independent of potential behavioral or social factors.

Mazur & Booth’s (M&B’s) review of the possible relationship between dominance interactions and basal testosterone (T) levels in men is thorough and informative. If anything, the target article exposes the importance of research within the fascinating and provocative area of behavioral endocrinology. Their model of dominance–testosterone interactions, however, could be enhanced by considering the growing body of data showing significant interpopulational variation in basal T levels. Furthermore, dominance and competitive interactions might be better understood with the incorporation of environmental and ecological factors, such as energy usage and availability.

M&B suggest that basal T levels are genetically based. Although chronic T levels exhibit some heritability, studies of monozygotic twins have shown that approximately 40% of the variation in basal T levels between individuals is the result of environmental factors (Meilke et al. 1987). Variability is also evident at the population level. Nonwestern populations show a consistent pattern of low chronic T levels compared to U.S. males; this underscores the importance of understanding the range of human variation (Beall et al. 1992; Bribiescas 1996; Christiansen 1991; Ellison et al. 1989; Ellison & Panter-Brick 1996).

Interpopulation variation in chronic T levels suggests that the ecological and energetic conditions of a population have considerable influence on mean adult T levels (Bribiescas 1996; Ellison & Panter-Brick 1996). Given the importance of establishing baseline means in determining the relationship between dominance and T, the effect of ecological variables on basal levels should receive greater consideration. Booth et al. (1993) have illustrated this in the context of competition; they reported T decreases (instead of the expected anticipatory rises) in fasting male wrestlers compared to competitors without dietary restrictions (Booth et al. 1993).

M&B’s discussion of honor subcultures (sect. 8) is thought-provoking; however, alternative hypotheses should be considered. Although African-American males seem to exhibit significantly higher T levels than European-American males (Ross et al. 1986), dietary factors might underlie these differences. For example, fat intake, which is higher in many poorer populations, has been linked with high T levels (Hämäläinen et al. 1984; Rose & Connolly 1992). In fact, it has been suggested that dietary and other environmental factors underlie ethnic differences in androgen levels as well as hormonally based pathologies such as prostate cancer (Schröder 1996).

Beyond the incorporation of populational variation and environmental factors into the determination of mean basal T levels, the interpretation of T responses to competition should be considered in the context of energy availability. Short-term changes in T levels in response to dominance interactions may involve physiological processes that have not yet been considered. Acute fluctuations in T levels in response to competition may be an adaptive response to modulate muscle metabolism in the context of energy availability (Bribiescas 1997).

Tsai and Sapolsky (1996) have acknowledged the robustness of T responses to competition. However, they also noted that the physiological significance, if any, of short-term changes in an-

drogen levels remains unclear. To determine whether exposure to T has any discernible effect on metabolic rates, they explored the immediate effect of exposure on the metabolic rate of muscle cells *in vitro*. They reported that T exposure significantly increases the metabolic rate of muscle cells *in vitro* within a period as brief as 1 minute (Tsai & Sapolsky 1996). The authors suggest that, if this response is analogous to short-term responses *in vivo*, T responses to competitive interactions might have an adaptive metabolic function independent of neurological effects (Tsai & Sapolsky 1996). Perhaps the apparent sensitivity of muscle cells to acute increases in T is an adaptive response to optimize physical performance during physically competitive interactions. However, M&B note that T responses to nonphysically competitive interactions require a more refined explanation that may incorporate neurological effects on mood and behavior.

Mazur & Booth's review and model of the possible relationship between dominance interactions and T responses are useful contributions to our understanding behavioral endocrinology. However, although it is important to consider the behavioral effects of T, it is equally crucial to consider more proximate sources of T variation.

Primacy of organising effects of testosterone

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Abstract: A test of a biosocial model is reported in which we found no impact of circulating testosterone on either status-seeking or aggression. The fact that sex differences in competitiveness and aggression appear in childhood strongly suggests that the major impact of testosterone is organisational. Whereas dominance and resources are linked among males, female aggression may be a function of pure resource competition, with no element of status-seeking.

Mazur & Booth (M&B) argue that testosterone (T) is directly related to dominance-seeking in men and only indirectly to aggression. We recently tested a very similar model (Campbell et al. 1997). Specifically, we proposed that basal levels of circulating T would correlate with competitive status-seeking and that this in turn would correlate with aggression in younger men only. In addition, we proposed that men who scored highly on the aggression measure would tend to describe their actions in justificatory, instrumental terms.

Three aspects of the study are most relevant to M&B's position. First, we measured dominance directly with the Masculinity Scale of the Personal Attributes Questionnaire. This scale is composed of self-descriptors such as "independent" and "competitive" and is highly correlated with the dominance dimension of Wiggins's circumplex model (Wiggins & Holzmuller 1978). Second, M&B give some weight to ethnographic descriptions of young men's way of construing their aggressive actions. In previous research, we have referred to this form of accounting as an instrumental representation of aggression. Its main features include a belief that aggression is a legitimate form of social control over others' misbehaviour and that interpersonal challenge requires an aggressive counter-response (Campbell 1993). M&B treat these sub-cultural accounts as veridical estimates of the mundane likelihood of challenge and view increased T as a response to this threatening environment (sect. 8). We took the view that an instrumental social representation is a way of justifying aggression that may operate *ex post facto* or prospectively (Campbell et al. 1996). Third, M&B (sect. 1) state that "it is harder to identify instances of aggression devoid of a dominating motive." In fact, our work on social representations suggests that there is another frequently voiced motive for aggression, which we call an *expressive social represen-*

tation. Its main features are a belief that aggression is caused by a sudden and temporary loss of self-control, that the aim is to discharge anger, and that aggression, far from being an honourable behaviour, is guilt-inducing. In the structure of our measuring instrument, subjects are invited to select either an instrumental or an expressive response to a set of 20 questions. Subjects' total scores indicate the extent to which they regard their aggression as instrumental vs. expressive (Campbell et al. 1992).

Despite M&B's scepticism about trait inventories, we found that the Buss and Perry Aggression Questionnaire (1992) was very significantly correlated with self-reported acts of aggression in our sample. Salivary T, however, was unrelated to status-seeking or aggression. There were significant correlations between aggression, age, and social representation of aggression, with younger men indicating greater involvement in aggression and holding a more instrumental (rather than expressive) representation of it. We cannot yet say whether instrumental beliefs are a cause or a consequence of aggression among young men. Published work on the T-aggression link generally demonstrates small effects, with significance often appearing only on post hoc analyses of the data. Even this conclusion must be tentative, because it is likely that many null findings remain unpublished.

This is not to suggest that T is unimportant in understanding dominance, aggression, and other sex differences. Infants demonstrate visual preference for same-sex photographs at age 10 months (Lewis & Brooks 1975), yet they cannot accurately sort photos by sex until about 3 years of age. They demonstrate preference for sex-congruent toys at 14 months, well before they can identify the sex for which the toy is appropriate (Blakemore et al. 1979). Differences in aggression begin at 2 years of age (Koot & Verhulst 1991), before children can reliably sort pictures of themselves into the correct gender group. In short, behavioural sex differences predate cognitive abilities that are identified by gender-schematic processing accounts; this suggests that sex-limited genetic effects have already taken place *in utero* or shortly after birth.

Although aggression occurs in women as well as men, M&B note that female T levels are not responsive to anticipated or successful status competition (sect. 6). Whereas M&B cannot envisage any selective advantage to aggression apart from its dominating function (sect. 1), Campbell (1996) has argued that, among females, resource disputes can occur without necessary consequences for status. Among many species of primates, female resource competition is frequent but confined to low-level bickering. In accounting for these data, Smuts (1987, p. 402) suggests that, among females, "the outcome of a single interaction rarely leads to large variation in reproductive success because female reproductive performance depends mainly on the ability to sustain investment in offspring over long periods of time." For this reason, females may engage in low-risk disputes over food resources but are unlikely to show the male-typical motivation for dominance, which is critical for male but not female reproductive success. Human males show a greater interest in status-seeking both in childhood and in adulthood (Hoyenga & Hoyenga 1993; Weisfeld 1994). This suggests that dominance may indeed be independent of aggression and that the neuroanatomical or neurochemical substrates of men's status-seeking may be laid down very early indeed.

Why is testosterone associated with divorce in men?

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Abstract: There is evidence that in women high levels of testosterone are associated with more sexual partners and more permissive sexual attitudes. If a similar relationship holds true for men, the higher basal testosterone levels of divorced and unmarried men may be caused by this relationship rather than by testosterone's effect on dominance striving.

In this timely and thoughtful target article, Mazur & Booth (M&B) provide abundant empirical support for their claim that testosterone (T) in men both facilitates dominance challenges and rises in response to a successful outcome. Their panel study of marriage and divorce among 2,100 male U.S. Air Force veterans also shows convincingly that the relationship between hormones and marital behavior is reciprocal: men with higher basal T levels are less likely to marry and more likely to divorce, but T levels also increase prior to and following a divorce.

It is not necessarily true, however, that the relationship between basal T and marital history is due to T's effect on striving for dominance. The relevance of the panel study to M&B's topic is based in part on their suggestion that "men with high basal T tend toward dominating or antisocial behavior which disrupts family functioning, leading eventually to divorce" (sect. 9). This may be so, but there are other possibilities.

One is that high T is associated not only with dominance seeking but also with a greater propensity toward sexual variety. This possibility is suggested by two recent studies of women. One study found that women with high levels of T (also androstenedione and estradiol) had more sexual partners and claimed to need less commitment from a man before engaging in sex (Cashdan 1995). The other study found that free T in young women using oral contraceptives was negatively associated with restrictive sexual morality as measured by questionnaire (Bancroft et al. 1991). I know of no similar studies in men (although there are abundant data on T and libido, well summarized in the target article), but if men with high basal T levels are, as is suggested for women, more inclined toward having a variety of sexual partners, it would be reasonable to suppose that they might be less likely to remain married.

As M&B note, findings on hormones and dominance in women are scanty. My reading of the literature is that androgens are associated with assertive and probably dominating behavior in women, but whether or not this enhances (or results from) their dominance status depends on what type of behavior is associated with high status in a particular competitive domain. Although dominating behavior might usually enhance dominance status for men, this is not necessarily the case for women. Our understanding of hormones and dominance in women will require a better understanding of competition among women in domains that are important to them.

Target tissue sensitivity, testosterone–social environment interactions, and lattice hierarchies

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Abstract: The following three points are made. One must consider not only the levels of circulating hormone but the target tissue upon which the hormone acts. Increased testosterone levels alone do not account for differences in displayed intermale aggression, because testosterone and social environment interact in complex ways to influence behavior. A given behavior can be triggered by multiple motivational systems.

This commentary is written from the vantage point of a researcher who until recently has used animal models exclusively to study interactions between gonadal hormones and behavior. There are many subtle and not-so-subtle differences in the nature of these interactions among various species as well as among various strains of a given species. Thus one would not expect one animal strain or species to serve as a perfect model for the nature of the interactions in humans. The different possibilities that exist across strains and species, however, can be instructive when one tries to account for human data. It is in this light that I make the following three points.

First, there is substantial evidence that one must consider not only the levels of circulating hormone but the target tissues upon which the hormone acts. The concept of tissue sensitivity has been used to account for individual, sex, and strain differences and for age-related changes in the threshold amount of hormone needed to activate various behaviors influenced by gonadal hormones (Babine & Smotherman 1984; Chambers 1995; Chambers & Phoenix 1984; Chambers et al., in press; Grunt & Young 1952; Jakobczak 1964; 1967; Larsson 1956; Sengstake & Chambers 1991). The specific mechanisms that determine tissue sensitivity remain unknown, but several possibilities have been suggested: decreases in the availability of testosterone (T) or the active metabolites of testosterone at the receptor sites in the target tissues; decreases in the total available cellular receptors; qualitative changes in the properties of the receptor, such as a decrease in receptor affinity for the hormone or a change in hormone specificity; and changes in the hormone–receptor–nuclear chromatin interaction. For those behaviors that have been studied, differences in tissue sensitivity are due to differences in the availability of testosterone during the prenatal–early postnatal developmental period. Thus, in human males, differences in aggression may be associated with differences in T availability during this developmental period, which then leads to differences in tissue sensitivity to circulating T in adulthood. Androgenization during the perinatal period has been shown to increase intermale aggression in all species that have been studied, including nonhuman primates. It would be surprising if humans were an exception. Although Mazur & Booth (M&B) acknowledge the possible involvement of perinatal gonadal hormones in organizing the brain, they ignore the possibility that differences in aggressive tendencies may be associated with differences in target sensitivity to available circulating T.

Second, there is evidence from other social animals that hormones and social environment interact in complex ways to influence behavior. The authors acknowledge this interaction when they discuss the reciprocal linkage between hormones and behavior (sect. 8). However, in animals, increased systemic T levels alone do not account for differences in intermale aggression but the combined interactions of sufficient T, previous social experience, and present social status do (Albert et al. 1988; 1989; Winslow et al. 1988; Winslow & Miczek 1985). For example, even if two males may have high T levels in the same situation, whether they will display aggression is dependent on their prior social experience. It seems unlikely that circulating T alone will account for differences in dominance-related behaviors in human males either. If, as M&B suggest, T is associated with dominance behaviors in prosocial as well as antisocial men, then one must still account for some men directing their dominance in an antisocial direction in the presence of sufficient T, whereas others do so in a prosocial direction (sect. 10). The answer will probably be found in factors such as history of social learning.

Finally, I think M&B should use a great deal of caution in associating failure to smile with dominance (sect. 6). It is well known that many behaviors are the endpoint of a lattice hierarchy; that is, a specific behavior can be triggered by different motivational systems. I would expect smiling to be such a behavior. There may be stimulus situations in which not smiling represents a dominant stance. However, the smiling that occurs after having won a competition when T levels are high can hardly be viewed as a nondominant stance. T is also an endpoint of a lattice hierarchy.

The mechanism that maintains increased T levels after the winning of a competition is certainly different from the one that maintains increased levels when one is unemployed.

Seductive allure of dichotomies

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Abstract: The basal and reciprocal models of the relationship between androgen secretion and dominance are not mutually exclusive. Individuals may differ in basal levels of androgen secretion, reactivity to experiences, and androgen sensitivity. Early experiences might affect any of these parameters.

Regarding the potential relationship between androgen secretion and dominance, Mazur & Booth (M&B) conclude that the most simple-minded notion – the basal model (that genes/gods/fates give you a certain amount of androgen, then that much androgen results in so-much dominant behavior) – is inferior to the reciprocal view (that experience affects androgen secretion, the androgens affect behavior, the behavioral experience affects androgen secretion, and so on). The latter view is certainly correct, as much research demonstrates, and is often overworked, so we can only approve of the authors' choice between these two alternatives.

However, the technique of presenting two alternatives as if they were mutually exclusive might leave some readers with the impression that there are no individual differences in basal androgen secretion or that any such differences must be dwarfed by the influence of experience. A synthesis of these two models is not only possible but almost certainly gives a fuller explanation of the phenomena. This is not to deny the influence of experience on androgen secretion, but there must be some limit to such influences. If so, then it is possible that basal differences in androgen secretion could also contribute to dominance.

For the most obvious, extreme example, consider the basic sex difference in androgen secretion. There may be some drastic set of experiences (short of administering steroids) that could induce an average woman to secrete male-typical androgen levels for several days, but no one has described such an unlikely case. Similarly, even the most subjugated man, as long as he is gonadally intact, probably secretes more androgen than the average woman. Therefore, at conception, we are fated to have different "basal" levels of androgen secretion, the most significant influence being whether we received an X or a Y chromosome. If there are genetically influenced, individual differences in basal androgen secretion *between* the sexes, it seems easy to imagine that there might be genetic influences on basal androgen secretion *within* each sex. We do not yet know about such genes, but that could easily reflect our present ignorance. For that matter, even among individual males with the same "basal" levels of androgen secretion, it is possible that some men show a more pronounced response (i.e., a greater change in androgen secretion) to a given experience than other men. At the very least, individual differences in the cognitive interpretation of an event must come into play in such instances. These ideas do not contradict the notion that experience also affects androgen secretion. As an amalgam, consider whether some experiences, especially early in life, might affect subsequent basal androgen secretion for many years, even for a lifetime.

The animal literature suggests yet another factor for consideration with these issues, individual differences in *sensitivity* to androgen. There is room for both genetic and experimental influences on androgen sensitivity. Inge Ward and collaborators have demonstrated that stress to a pregnant rat dam can result in reduced masculine behavior in the male offspring. So far, this prenatal stress does not seem to affect later adult androgen secretion. A recent report from this group (Ward et al. 1996)

indicates that males who are both prenatally stressed and exposed to fetal alcohol show severe deficits in male copulatory behavior, despite normal plasma concentrations of testosterone. However, when they are given exogenous androgen, these behavioral deficits are overcome, suggesting that the early experience made these males less sensitive to androgen. We believe, and suspect that Mazur & Booth would agree, that basal and reciprocal relations between hormone secretion and behavior are not mutually exclusive and that a model truly synthesizing these views would be more satisfying than either view alone.

Shaping, channelling, and distributing testosterone in social systems

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Abstract: Culture and social structure may affect the testosterone-behavior link by shaping the way we construe events; by muting, channeling, or amplifying the drives that testosterone produces; and by affecting the distribution and level of testosterone in various parts of the population. Research on testosterone, culture, and social class has produced suggestive results, opening broad areas for research.

Mazur & Booth (M&B) do an excellent job of explaining the testosterone (T) story, showing how it is involved in cycles of dominance and status contests. They also suggest that the issue may be further complicated by considerations of class and culture. These are complications well worth pursuing. Some possible avenues for examining how culture and T interact are described below.

One issue is how cultural construal influences hormonal response. An insult, a threat, or a status challenging move are obviously not the same to all people in all cultures. In our own studies, we compared whites from the South of the U.S., which has a culture of honor, to those from the North, and we examined their responses when another person (actually working with us) bumped into them and called them an "asshole." Through saliva samples taken before and after the insult, we found that southerners and northerners responded differently physiologically as well as behaviorally. Specifically, insulted southerners showed significant increases in their testosterone, whereas insulted northerners did not (Cohen et al. 1996). Although the issue can be discussed in terms of how the southern culture of honor gives meaning to insults and calls forth a response, it can also be discussed in terms of how northern culture produces such an enervated, "unnatural" response (Hill 1997). Either way, it is clear that culture plays a crucial role in interpreting and reacting to "threats" from the environment, and this influence can be seen at very basic physiological levels.

Another important issue is how culture and social structure channel the drives that T produces. It is possible that T leads to antisocial and aggressive behaviors only when the surroundings give these tendencies an opportunity to express themselves. In the analysis by Dabbs and Morris (1990), the authors showed that, among high-socioeconomic-status (SES) veterans, those with high T were no more likely than their peers with normal T to use hard drugs or to have problems with adult delinquency. Among those with low SES, however, those high in T were almost twice as likely as peers with normal T to have such problems. There could be a number of explanations, but a plausible one is that lower SES environments are more fraught with dangers and opportunities for trouble, and individuals with higher T fall into those troubles. Higher SES environments may have fewer dangers and may provide a buffering effect against predispositions that high T produces (Dabbs & Morris 1990; Kemper 1990).

A third issue related to channeling is the way culture may help separate T's influence on status-seeking or dominance from its

influence on aggression. As M&B suggest, testosterone may facilitate successful boardroom maneuvering as much as successful barroom brawling, or it may produce useful creativity as well as antisocial rebellion. To the extent that one can achieve status in a culture or social system for “legitimate” prosocial or creative actions, T’s influence may be sublimated into “higher” purposes. It would be interesting to look at how T might influence (and be influenced by) the behavior of people in a wide variety of sub-populations, such as executives, clergy, artists, scientists, and so on.

Finally, M&B speculate on how different social systems can lead to different levels of T in a population, hypothesizing that living in a culture of honor can produce a population of young men with elevated basal levels of T. Their evidence is contradicted somewhat by our data; the southerners from the study above – who reacted much more aggressively to the insult than did northerners – had basal levels of T no higher than their northern counterparts (Cohen et al. 1996). Perhaps this is so because norms for politeness and deference are strictly adhered to in the South as a way of avoiding potentially dangerous conflicts (Cohen & Vandello, *in press*). If true, this explanation would in fact support the larger point that social systems, customs, and modes of relating to others influence levels of T in a population. It might accordingly be worthwhile to explore T and behavior in various systems, because cultures vary dramatically on many dimensions relevant to issues of dominance, status, and antisocial rebellion.

Thus, some cultures are very “tight” and have severe punishments for violating social norms; others are “loose” and tolerate a good deal of deviance and nonconformity. Some cultures are very hierarchical, whereas others are more egalitarian. Some are more rigid, permitting little mobility in the status hierarchy, whereas others are more competitive, allowing for sudden rises or falls in status. In some cultures, social status is tremendously important for securing other things, such as reproductive mates, whereas, in others, it is less important. Moreover, in some cultures, the basis of esteem is different. Some societies place more emphasis on the individual, valuing self and personal social status, whereas others place more emphasis on the collective, valuing group esteem, harmony, and smooth interpersonal relations (Triandis 1994). Just as honor can be more or less important in some societies, with consequent implications for T and behavior, the dimensions described above may likewise be extremely relevant. We can learn much, of course, from studies of animals, but, if we want to learn more about T in humans, we must go beyond culturally homogeneous samples to see how social systems regulate, mute, channel, or amplify our hormonal drives.

In sum, Mazur & Booth’s target article is a helpful addition to our understanding of T. Perhaps, also, considerations of culture and social structure can further enrich our understanding.

Early organizational influences and social factors: A need for further evaluation

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Abstract: Mazur & Booth’s target article presents strong evidence that social factors influence testosterone; however, the evidence for an effect of testosterone on dominance is considerably weaker. Although social and biological factors may interact, as suggested in the reciprocal model, findings in rhesus monkeys suggest that social factors may predominate. Finally, research is needed to evaluate whether androgens during early life influence later dominance.

This commentary focuses on three issues: (1) the tenuousness of the described relationship between testosterone (T) and dominance; (2) the importance of social factors; and (3) the need to investigate whether early androgens influence dominance.

Mazur & Booth’s (M&B’s) target article reviews evidence across many studies using a variety of dominance measures. The degree

to which each of these variables represents a valid measure specific to dominance is questionable. Several of the studies reviewed could be interpreted as supporting a relationship between mood and T, or stress and T, as much as they support a relationship between dominance and T. In addition, the overall strength of accumulated evidence, especially for a causal influence of T on dominance, is weak. Consequently, it seems premature to accept that a relationship between T and dominance is well established. The issue does, however, warrant additional exploration.

An interesting aspect of the target article is the reciprocal model of T as both a cause and an effect of behavior. Such a model is valuable in its recognition of the complex interaction of social and biological variables. However, the evidence for an influence of social and cognitive factors on T seems much stronger than that for the notion that T influences dominance. M&B propose that this discrepancy in weight of evidence arises because the former type of study is methodologically easier to perform. Although methodological difficulties may exist, an equally plausible explanation is that social effects on T are simply stronger than the reverse. Studies of rhesus monkeys are useful for clarifying the relationship between interacting social and biological factors. As with humans, rhesus have a complex social structure marked by dominance relationships; however, unlike the case with humans, they can undergo more invasive observation and measurement and manipulation of hormones.

The strength of social factors can be seen in rhesus males which were assembled into new, all-male groups. T levels measured before the formation of the new group did not predict eventual rank in the new dominance hierarchy; in contrast, T levels did change in response to the animal’s ultimate rank, with higher ranking males transiently developing higher T (Bernstein et al. 1983). As with humans, the specific cognitive appraisal of the situation appeared to be a critical influence on rhesus T levels. These data suggest that although T may not determine success or failure in dominance contests at least in monkeys, the experience of this success or failure does subsequently alter T. The fact that social interactions alter hormones, perhaps to an even greater extent than hormones alter social outcomes (Monaghan & Glickman 1992), underscores the importance of considering both social and biological variables. At the same time, however, the complexity of these interactions and the perhaps overwhelming influence of social factors suggest that narrowly focused investigations of T effects on dominance in adulthood are limited in power. Effects of relatively small differences in hormones (as seen in normal individuals of one sex) may be overwhelmed by the “noise” of interacting social factors.

Despite the questionable power of investigating effects of adult T on adult dominance, it seems worthwhile to consider whether T or other androgens during early (prenatal or early postnatal) life might relate to adult dominance. In examining T solely during puberty and adulthood, M&B do not address this possibility. During early critical periods, androgens influence the development of selected brain systems. If these include systems related to dominance, then adult levels of T, although perhaps contributing to dominance, might not be the most crucial factor. T’s capacity to activate adult dominance behavior may depend largely on, or be limited by, individual differences in early organizational effects. Tentative support for a role of early androgens comes from studies of play in monkeys. Juvenile rhesus males show higher levels of dominance-related play than do females, including behaviors such as play-fighting (Symons 1978) and nonreproductive mounting (suggested to establish dominance; Goy & McEwen 1980). Juvenile play is not truly aggressive, and injury rarely occurs; rather, it appears to be a way to “seek advantage” (Symons 1978, p. 90), that is, to dominate others. Aspects of dominance-related play are influenced by early T exposure; rhesus females androgenized prenatally show increased play-fighting and mounting (Goy & McEwen 1980). Although these behaviors are not identical with versions of dominance seen in adulthood, they bear an obvious

similarity and potentially could involve related brain mechanisms. Because these behaviors are observed in juveniles, when circulating T levels are low, it can be assumed that they do not require activation influences of T, reflecting early organizational effects instead.

Similarly, in humans, boys show higher levels of dominance-related play (more rough-and-tumble activity and selection of toy weapons) than do females (Goldstein 1994), and early androgens appear to influence aspects of human play (Collaer & Hines 1995). Perhaps dominance-related play is organized by androgens during early life to provide a way for juvenile primates (human and nonhuman) to practice and perfect dominance and other social behaviors important for adulthood (see Symons 1978). Additional evidence for a potential early-life influence of androgens comes from females with congenital adrenal hyperplasia who experience elevated prenatal androgens. They show elevated scores on some personality scales that tap aggressive or dominance-related behavior (see Collaer & Hines 1995). In summary, future investigations might fruitfully explore the possibility that human dominance behaviors relate not only to adult levels of T but also to levels during early life.

Dominance and aggression over the life course: Timing and direction of causal influences

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Abstract: Studies of testosterone's effect on dominance are confounded by the effects of dominance experiences on testosterone. Furthermore, antisocial behavior tends to originate prepubertally, when testosterone levels are the same for aggressive males, nonaggressive males, and females. It seems more parsimonious to view variation in testosterone as an effect of dominance-related mood states than to invoke a reciprocal model.

Mazur & Booth (M&B) have done a great deal over the years to encourage the field to move forward, away from the model of a simplistic causal relationship between testosterone (T) and aggression in man. Their own studies demonstrating the effect of dominance status on testosterone (D → T) have been more compelling than studies suggesting the effect of T on dominance (T → D). The T → D studies cited in the target article generally attribute less than 5% of the variance for dominant or aggressive outcome to T. Because elevations in T occur in anticipation of dominance events and can last for days afterwards, T → D studies involving one-time samplings of T are confounded by the fact that more dominant, violent, or aggressive individuals are more likely to have engaged recently in dominance experiences that have boosted their T levels (especially in settings where the base rates of stressful dominance-related encounters are high, such as in prisons, in the inner city, or in what M&B describe as honor subcultures). Furthermore, T → D studies have been inconsistent about which psychological outcomes are associated with T. For example, Kreuz and Rose (1972) demonstrated a correlation between T and age at first violent offense, but not with observable prison behavior; Ehrenkranz et al. (1974) found T related more closely to aggressiveness than to social dominance; Dabbs and Morris (1990) found that high T was more predictive of hard drug use than other self-report measures of antisocial behavior, and it is possible that correlations between hard drug use and other antisocial behaviors explain some of the weaker associations of T with those other behaviors; Monti et al. (1977) found no association between T and self-reports of drug use or aggressive behavior.

This brings up the question of what the dependent variable represents in T → D studies. Laboratory paradigms for domi-

nance (such as those used in D → T studies) are far cleaner than real-life dominance relationships in humans. Particularly among impulsive individuals, perceived threats to safety or autonomy are often responded to with affective outbursts that blur the distinction between dominance behavior and aggressive behavior. In a study involving nonhuman primates, Higley et al. (1996) demonstrated that elevated cerebrospinal fluid (CSF) testosterone levels predicted socially assertive behaviors, including those exhibited in response to threat, whereas low CSF 5-hydroxyindoleacetic acid (5-HIAA) levels predicted impulsivity and severe unrestrained aggression; elevated CSF testosterone augmented the rate and intensity of aggression among animals with low 5-HIAA. There was no correlation between plasma T and CSF T in that study, suggesting that future T → D studies should utilize samples of CSF rather than plasma. Although many of the pathognomonic behaviors of antisocial personality disorder (ASPD) are perceived by M&B as manifestations of dominant behavior, Constantino et al. (1997) found that, in humans, genetic liability for ASPD correlated inversely with levels of newborn CSF 5-HIAA.

The problem with distinguishing aggression from dominance in real-life human situations is not new. One of the more disappointing attempts to do so comes from the child psychiatric literature, in which attempts to differentiate conduct disorder into socialized and undersocialized types has failed to result in any improved ability to predict outcome. From what is known so far, antisocial development is better predicted by age of onset than by type of conduct disorder, earlier age of onset being associated with poorer outcome (Moffitt 1993). This has direct relevance to the target article insofar as the strongest predictor of antisocial development and aggressive propensity in adulthood is conduct disorder in childhood (Robins 1966). Although the gender ratio for aggressive deviance is identical in children and adults, life-course-persistent patterns of aggressive behavior tend to have their origin prepubertally, at a time when T levels are the same for males and females and when there are no differences in T between aggressive and non-aggressive males (Constantino et al. 1993). If T is a cause of these patterns of behavior, interindividual variations in T activity in the central nervous system (CNS) should exist before or during the time when those patterns of behavior develop (childhood). Although male behavior may be more reactive to T after puberty, the expression of adult antisocial behavior depends not so much on T as on whether or not that pattern of behavior developed before puberty.

Thus, from the data available, it seems more parsimonious to view variation in adult T levels as an effect of dominance-related mood states than to invoke the existence of a reciprocal model. The next generation of T → D studies should involve specific measures of androgen activity in the CNS, such as CSF T levels and, if possible, assessments of interindividual variation in the sensitivity of CNS T receptors. Until this time, support for the T → D half of the reciprocal model in humans will be missing, and studies that link plasma T fluctuations with complex human events involving both dominance and aggression (such as divorce or gang-related behavior) will be very difficult to interpret meaningfully.

Prenatal testosterone exposure, left-handedness, and high school delinquency

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Abstract: Prenatal exposure to high levels of testosterone may lead to increased probability of left-handedness. Extrapolating from arguments by Mazur & Booth leads to a prediction of increased incidence of antisocial behavior among left-handers. Six hundred ninety-four males were tested for seven indicators of delinquency in high school. Left-handers were more likely to display such behaviors, providing indirect evidence for the hypothesized behavioral effects of testosterone.

Mazur & Booth (M&B) have offered the hypothesis that there is a link between testosterone (T) levels in men and the likelihood of

dominant, aggressive, criminal, and antisocial behaviors. The measurement of T levels in an individual usually requires direct physiological intervention, making it difficult to assess the validity of these predictions without special laboratory facilities. However, there is an indirect marker for early T exposure that may prove useful in testing these predictions.

Geschwind and Galaburda (1987) have proposed a theory that links the probability of left-handedness to prenatal exposure to T. They argue that high levels of T during gestation will alter normal neural development in the fetus. These high levels of prenatal T should be associated with sinistrality because T slows neuronal growth in the left hemisphere, hence weakening its relative control. The result is right hemisphere dominance, which is manifested in left-handedness (see Habib et al. 1990, for a review of this hypothesis). An example of the operation of this theory is based on the fact that male fetuses are exposed to higher levels of prenatal T in utero. This occurs because, in addition to being exposed to T from maternal ovaries, adrenal glands, and fat, male fetuses are also exposed to T produced by their own developing testes. This has been used to explain the observation that males are less likely to be consistently right-handed than females (cf. Coren 1993a; 1995).

If the Geschwind and Galaburda theory is correct, then left-handedness could serve as a soft sign of a history of higher prenatal T exposure. If we combine this with M&B's arguments, then we should be able to predict a greater number of antisocial behaviors on the part of left-handers. There have been some sporadic reports that this holds true (see Coren 1993b, for a review of these suggestions).

An opportunity to test these predictions comes from some ongoing research in my laboratory. A sample of 694 men (mean age 26.6 years) were tested using the handedness scale of the Lateral Preference Inventory (Coren 1993b). This is a four-item scale that assesses the hand used to throw a ball, to draw, to use an eraser on paper, and to lift the top card when dealing playing cards. Experiments have demonstrated a 96% concordance between self-reports on these items and direct behavioral performance testing on these actions (see, e.g., Coren et al. 1979). The sample was dichotomized using the stringent criterion of consistent right-handers (RH), with all four index behaviors right-handed vs. nonright-handers (NRH) with any of the behaviors left-handed (Coren 1993a). There are indications that this criterion for dichotomizing handedness is more sensitive to factors associated with lateralization than simply scoring right- versus left-handed (Coren 1994). The present group included 70.6 RH and 29.4 NRH, which is typical for similar samples using this scoring procedure.

In addition to the handedness measures, each subject who was also asked to recall his own high school history and to indicate whether it included any of seven indicators of antisocial or delinquent behaviors. Specifically these were: whether he had been in any fights in high school that involved physical violence, been penalized with many detentions, ever been suspended for disci-

plinary reasons, ever violated school smoking prohibitions, associated with friends who were frequently in trouble, skipped class frequently, or had been in trouble with teachers often. The handedness and high school delinquency data were then cross-tabulated to produce Table 1.

If higher prenatal exposure to T leads to both left-handedness and a life-long predisposition towards dominant and antisocial behaviors, then we ought to find more delinquent acts associated with the NRH group. As Table 1 shows, in five of the seven comparisons this prediction is supported at conventional levels of statistical significance. If we give Mazur & Booth the benefit of direction prediction (hence a one-tailed test), all seven measures are significant.

Obviously, use of left-handedness as a marker is an indirect measure of T levels. However, to the extent that we can believe the theory that high levels of prenatal T exposure lead to left-handedness, these data seem to support the suggested link between T effects and antisocial behaviors among males.

Testosterone and the concept of dominance

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Abstract: Testosterone is related to dominance, but in a broader sense than Mazur & Booth suggest. Dominance need not be competitive. It can arise from strong personal characteristics that produce admiration and deference in others. To understand the testosterone–dominance relationship fully, we must examine behaviors that affect ordinary social encounters. Baseline testosterone levels may be more important than testosterone changes in predicting everyday dominance.

Since 1849, when Berthold transplanted testes of roosters into capons and found that the capons “crowed lustily, often engaged in battle with each other and the other cockerels, and showed the usual reactions to hens” (Berthold 1849), researchers have emphasized aggressive correlates of testosterone (T). Mazur & Booth (M&B) would shift the emphasis from aggression to dominance. This is admirable, because identifying T with aggression is an idea whose time has come and gone. It would be useful to carry their effort even further, examining a wider range of dominance behaviors and the concept of dominance itself.

Dominance has several definitions. Dictionaries define it as a commanding position in an order of forcefulness. M&B define it as action intended to enhance status. The action they focus upon is competitive, where one gains at the expense of another, but there are many ways in which one can dominate or control others. Sometimes dominance benefits the others. For example, strong leaders help themselves and their followers. Flamboyant politi-

Table 1 (Coren). Indicators of delinquent or antisocial behaviors in high school as a function of consistent right-handedness versus non-right-handedness based on a sample of 694 males^a

Behaviors	Consistent right-handed	Non-right-handed	Significance (<i>p</i> less than)
Fights	35.9	49.0	0.01
Many detentions	20.4	31.9	0.01
Suspensions	9.6	15.7	0.05
Violate smoking prohibitions	14.9	26.2	0.001
Friends in trouble	26.1	38.1	0.01
Skip class frequently	38.0	45.1	0.05 (one tail)
Trouble with teachers	50.0	57.4	0.05 (one tail)

^aThe data reported are the percentage of subjects indicating that they had engaged in these behaviors or experienced these events.

cians bring rewards to their constituencies. Heroic altruistic individuals risk their lives for others. All these persons are dominant, in different ways, and future research might well show that they are all high in T.

M&B make intention a central part of their definition of dominance, but intention may be of secondary importance. The main point is being dominant, not wanting or trying to be dominant. Any act that produces deference in others can make one dominant. The act may be planned, as when one puts on a performance or chooses appropriate dress for an important meeting (Mark Twain said, "Clothes make the man; naked men get little or no respect in our society"). It may be unplanned, as in the way a charismatic individual naturally walks, talks, socializes, and captures the attention of a crowd. It may come from violent displays of bad temper or exuberant displays of good nature and optimism. It may come from wealth, strength, learning, experience, audacity, or cunning. Many of the noncompetitive aspects of dominance may be related to T, and it would be shortsighted to focus only on competition.

M&B emphasize changes in T level, but baseline levels might be more important. Changes in T associated with winning and losing tend to be short-lived and modest in size. Among fans watching the 1994 World Cup finals in soccer, winning produced powerful feelings and led to increases in T in almost all the fans of the winning team (Bernhardt et al. 1997). However, the mean increase was less than 20%, smaller than the standard deviation in a normal population (Dabbs 1990). We do not know the relative importance of chronically high and temporarily high levels of T. We know little about changes in behavior that follow changes in T level, and focusing on these changes draws us away from a broader view of dominance. For example, the drop in T around marriage and the rise around divorce reported by M&B, as with the drop in T around fatherhood reported by Worthman, Stallings, and Gubernick (1991), bears no clear relation to dominance. It might be more useful to study differences among individuals in their mean baseline T levels than to study changes in T across time.

Although dominance helps in achieving certain goals, dominance is not desirable per se. It is costly, especially when it involves competition, because competition brings the possibility of loss and defeat. Male birds and lizards injected with T are more likely to be injured or die during the coming months, apparently because they more often fight, travel, and expose themselves to predators (Dufty 1989; Marler & Moore 1988). We need a theoretical framework to help us understand when dominance is especially useful and worth the price individuals have to pay for it.

Such a theory relating T to dominance comes from evolutionary thinking about the reproductive needs of men and women. Each sex has its own needs, and males differ from females in needing mates who will carry, bear, and nurse their offspring. Males compete for females as a limited resource, and dominant males can better acquire mates (Buss 1994). This theoretical orientation explains certain aspects of dominance beyond those considered by M&B. T could contribute to activities that range from defeating or killing other males to charming or raping females. Given the complex nature of dominance, we should consider new ways of studying it. We should examine the behavior of high-T and low-T individuals. We need data more than theory, including data on conversational patterns, how individuals approach others, what makes them pleased or angry, how they resist influence from others, where they go and what they think about in day-to-day life.

Of mice and men: Androgen dynamics in dominance and reproduction

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Abstract: In the animal literature, the concept of dominance usually links status in intermale encounters with differential reproductive success. Mazur & Booth effectively review the human literature correlating testosterone with intermale competition, but more profound questions relating this to male–female dynamics have yet to be addressed in research with humans.

Mazur & Booth (M&B) have provided a fine review of recent studies correlating testosterone (T) levels with ongoing social behavior in human males. The development of new assay procedures, particularly those involving saliva, has led to very substantial progress in this area.

These data complement earlier findings from rodents and nonhuman primates suggesting that there is substantial conservation among mammals in the relationships of social dynamics to gonadal hormones. The most comprehensive data exist for house-mice, in which dominance or subordination in intermale encounters can transform the animal's neuroendocrine state and alter subsequent behavioral initiative (see Brain & Benton 1983). In competitive situations, repeated defeat results in a decline in luteinizing hormone and androgen levels (Eleftheriou & Church 1967; McKinney & Desjardins 1973). Victorious male mice become more assertive, initiating new attacks, and other males are more passive. Studies of rhesus monkeys suggest some comparable patterns in the relationship of T levels and changes in social dominance (Bernstein et al. 1983).

As M&B acknowledge, the definition of *dominance* in humans is complex and is often divorced from aggressive behavior. The main focus of the studies cited is ranking among males in competition. We believe that this neglects a critical dimension of social dominance, that of reproductive success. The animal literature shows that supremacy in intermale encounters is linked to access to females. This issue has profound evolutionary implications. Dominant males gain more access to females and have more offspring than do subordinates (Dewsbury 1982). For example, when given free access to receptive females, male house mice that have previously won in aggressive encounters are more likely to initiate mating than are subordinate males (deCatanaro & Ngan 1983). In baboons, males with higher rank within an established group have the most sexual opportunities with females that are in full estrus (Hall & DeVore 1965).

In animals, several strategies allow dominant males to impregnate females successfully. Dominant males prevent their rivals from mating through agonistic means, or they can sexually pre-occupy a female when competitors are present. Male mice become highly aggressive toward one another when they are briefly exposed to sexually receptive females (deCatanaro 1981). Male mice secrete androgen-dependent chemicals that prevent implantation of ova in females inseminated by other males (deCatanaro et al., 1996) and they may also kill pups sired by other males.

Although M&B cite research demonstrating that fluctuations of T are not directly involved in men's sexual behavior (sect. 3), this may dismiss a complex issue prematurely. In laboratory rodents, exposure to novel females, with or without physical contact, results in increased levels of T (Batty 1978; Bliss 1972; Macrides et al. 1975). Following ejaculation, T levels decrease, and mice show a refractory period, during which sexual responses cannot be elicited for hours or even days (Batty 1978; Bliss 1972). Have M&B considered that sexual satiation or sexual frustration might account for the human data they discuss concerning marital satisfaction and divorce (sect. 9)?

Testosterone is non-zero, but what is its strength?

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Abstract: Mazur & Booth have shown an association between testosterone and dominance behavior, but the strength of the relationship is not given. In addition to being statistically significant, it is also necessary that testosterone account for a meaningful proportion of the variance; a multivariate model is probably necessary. A cautionary tale from the animal literature is related.

Given the considerable difficulty in studying the relationship between testosterone (T) and social behavior in human populations, Mazur & Booth (M&B) are to be commended for daring to venture into what is clearly an academic minefield. Unfortunately, they have made their task more difficult by listing five unpublished papers in their references.

None of the unpublished manuscripts are cited in section 4, which reviews the literature on dominance and aggression in adulthood and makes a strong case that there is a positive relationship between T levels and dominance. This is a qualitative statement, however, and we are never given any information about the strength of the relationship. No means or standard errors are presented, so we know nothing about the effect sizes of the reported significant group differences. M&B state that in other research, significant correlations were found, but they do not let us know the values, with the exception of one r of .11 ($p < .001$), which they acknowledge is small in magnitude. We are informed that, in their sample of 2,100 male U.S. Air Force veterans, 10 of 16 correlations were significant and positive. However, with 2098 degrees of freedom, a correlation of .043 is significant at the .05 level (two-tailed test). Thus, it is possible that they have significant correlations that account for a trivial percentage of the total variance.

Until the strength of the relationship between T and dominance is known, it is impossible to evaluate the relevance of T for an understanding of dominance. The information needed to characterize strength of relationship (effect size and power) can often be derived from data in the original publications, and I hope M&B have an opportunity to summarize those data in their Response.

Given the modest reliabilities for test-retest T values (.50-.65), it is unlikely that T will account for a sufficient amount of the criterion variance (dominance behavior) to warrant debating a basal versus a reciprocal model. Instead, a multivariate approach is needed, measuring a number of variables related to T and/or the criterion measure. Once a reasonable amount of variance is accounted for, theoretical considerations can be entertained.

Let me close with a cautionary tale from the animal literature. The C57BL/10J male mouse is noted for its aggression against a conspecific. Three decades ago, we compared the fighting behavior of C57 mice reared by their mothers from birth to weaning (controls) to that of experimental mice that had experienced identical conditions except that a nonlactating female rat (called an *unt*) was also in the cage with the mice during the lactation interval. See Denenberg (1970) for a review of these studies. The experimental mouse pups received milk from their mouse mother, but they were cared for by the rat aunt who built their nests, carried and retrieved the pups, huddled over them, and groomed them. At weaning, the mice were placed into separate cages, where they remained until adulthood, when nonsibs from the same treatment group were placed into a "fighting box" and their aggression was observed. Forty-three of ninety-six pairs of control mice fought (44.8%), whereas within the rat-aunt group only 3 of 71 pairs fought (4.2%). The point of this tale is that, though T was important (the control males did fight), a social variable (the presence of an aunt caretaker between birth and weaning) was powerful enough to reduce intraspecific fighting by 90%. In the experimental group the variance accounted for by the social variable was vastly greater than the variance accounted for by the

hormonal variable. If this is true in mice, it is highly likely to be true in man.

Evolutionary functions of neuroendocrine response to social environment

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Abstract: The human neuroendocrine system is highly sensitive to the social environment. Hormones such as testosterone and cortisol are released in response to a wide variety of social stimuli. The evolutionary functions of this sensitivity are not well understood. Longitudinal monitoring of hormones, behavior, and social environment is a promising research paradigm for solving these evolutionary puzzles.

Our behavioral biology is usually meaningless outside the context of the social factors and environment in which it occurs.

Sapolsky 1997, p. 158

We view the human neuroendocrine system as a complex set of mechanisms designed by natural selection to communicate information among cells and tissues. A key research objective is to understand the evolutionary functions of this chemical language. Our methodology emphasizes longitudinal monitoring of hormone response, behavior, and social context in the natural environment. In agreement with Mazur & Booth (M&B), data from our studies indicate substantial intra- and interindividual variability of hormone levels, with particular sensitivity to social environment.

Androgens such as testosterone (T) affect, and are affected by, a wide range of somatic processes, including glucose metabolism, muscle growth, thought, and immunity (Mooradian et al. 1987). The actions and reactions are modified throughout ontogeny. Binding globulins, receptor densities, and other hormones mediate effects of T and complicate analysis based on hormone levels.

The baseline and reciprocal models explored by M&B illuminate the "cause and effect" phenotypic dance (cf. Dabbs 1992). T is associated with divorce among U.S. Air Force veterans from whom saliva was collected during four physical exams at a military base over a 10-year period.

One explanation is that T *causes* or influences behavior – the detailed minutiae of helping wash the dishes, a kind word or touch, a temper tantrum – in such a way that marital relationships are affected. High-T individuals are prone to divorce because some cell receptors for T are bound more frequently, affecting neural actions (see, e.g., Kendrick & Drewett 1979) that eventually translate into behavioral activities, broken hearts, and legal paperwork. Some studies suggest that such behavioral effects are unlikely (e.g., Bhasin et al. 1996). T is posited to have a "permissive effect" within a broad range of hormone quantity, but not to fine tune behavior to specific T levels.

Alternatively, a veteran's T levels may be an *effect* of his environment. T may be higher in the environments of an unstable marital relationship and post-divorce bachelorhood. A large and convincing research literature supports the "effect" hypothesis for a variety of social environments (e.g., McCaul et al. 1992). This presents a paradox, however, insofar as the benefits of hormone response to environmental conditions are uncertain, given the lack of knowledge about the behavioral consequences of such hormonal changes. Why should natural selection have designed the human neuroendocrinological system to be so sensitive to social factors, if this has little real effect on behavior?

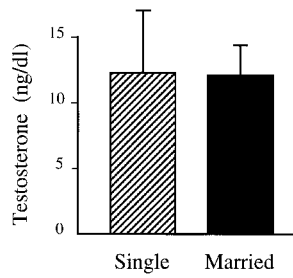


Figure 1 (Flinn et al.). Testosterone and marital status in a Caribbean village. T levels of married and single men are not significantly different. Study collected 534 saliva samples from 30 adult males resident in a rural village on the island of Dominica (Decker 1993). Samples were excluded from this analysis if sex, alcohol use, tobacco use, or other extraneous factors had occurred during prior 8-hour period.

More complex still, the association between T and divorce might be a spurious effect of common links to a third variable, such as personality traits or early childhood experiences. How to tease apart this tangle of hormones, axons, dish throwing, lawyers, and potty training?

Using a research paradigm pioneered by Robert Sapolsky (1990a), we have collected longitudinal information about hormone levels, behavior, and social context in normal, everyday environments. We find that individuals have different cumulative average levels of hormones and that these hormone levels are associated with a variety of social factors (Flinn & England 1997; Flinn et al. 1996). For example, among adult males in a Caribbean village, there is no association between T and marital status (Fig. 1), but males ranked high in status by their peers have higher T than those ranked low (Fig. 2). Divorce was too infrequent to allow for analysis.

Individual differences in the patterning, or "profiles," of hormone response to environmental conditions provide additional data for testing hypotheses about hormone-behavior-environment relations. As with Sapolsky's baboons, we find that male social position (partially mediated by personality) is associated with hormone response to social events. For example, an adult male in a Caribbean village ranked low by his peers responds to a social challenge (a court appearance) with low T (Fig. 3) and high cortisol (C) levels. Experienced bike racers in Missouri respond to races with elevated T and diminished post-race C, whereas less experienced racers usually have moderate T and high post-race C (Figs. 4, 5).

These context-dependent responses make sense: dominant males are more likely to benefit from elevated T levels during

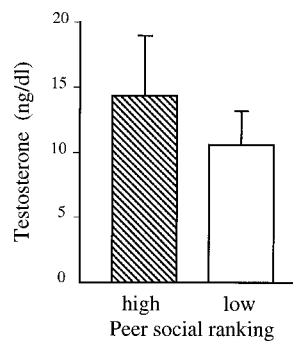


Figure 2 (Flinn et al.). Testosterone and peer-ranked status. High ranking males have higher T than low ranking males (one-tailed t-test, $p < .05$). Study and samples are as described for Figure 1.

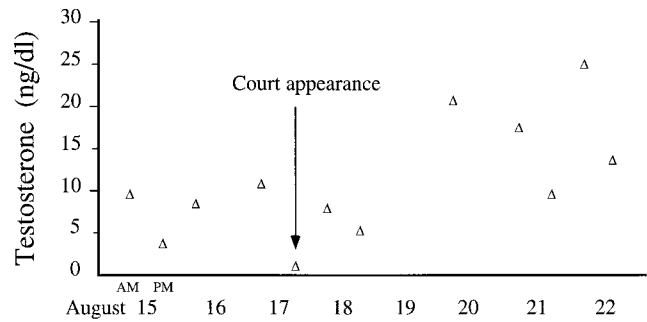


Figure 3 (Flinn et al.). Testosterone levels of a 43-year-old male. T was exceptionally low on the afternoon of a court appearance for minor theft. Saliva samples were collected twice daily (morning and late afternoon). Study and samples are as described for Figure 1.

social challenges, if high T affects cognitive or other neural processes in ways that encourage facing down the competition. Conversely, subordinate males might be best served (e.g., avoiding injury) by a more conservative, inhibited behavioral response (Sapolsky 1990b). Some social environments have long-term effects on hormone response. Males in a Caribbean village raised without resident fathers have lower T and higher C as adults than males with resident fathers during childhood (Flinn et al. 1996). We suspect, however, that these response patterns are contingent on population-specific social conditions, such as mating opportunities determined by kinship networks.

Some of our current research focuses on the ontogeny of individual differences in neuroendocrine response. Hourly, daily, weekly, and yearly monitoring of hormones, behavior, and social conditions (Fig. 6) provides data on longitudinal patterns of neuroendocrine response (cf. Dabbs 1990; Valero-Politi & Fuentes-Arderiu 1993). Understanding such patterns may be important; hormones such as C and T have major effects on immune function and, hence, may provide clues about relations among childhood social environment, psychological stress, and health (Weiner 1992; Flinn, in press).

Hormonal responses to social events present a number of fascinating unresolved biological puzzles. The development of salivary immunoassay techniques for reliable, noninvasive monitoring of hormones and other endogenous substances provides a new window into the workings of the human mind and body under

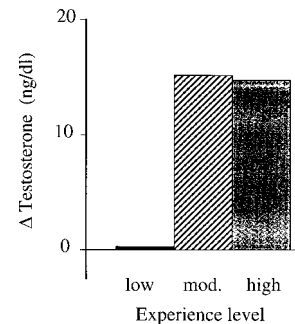


Figure 4 (Flinn et al.). Change in testosterone levels from immediately (5–10 minutes) before to immediately (5 minutes) after off-road bicycle races. Experienced racers (*low* includes U.S. Cycling Federation racer categories 5 and 6; *moderate* includes category 4; *high* includes categories 2 and 3) have greater elevation of T than inexperienced racers. Study collected 264 saliva samples from 17 adult male bike racers (Baerwald 1998).

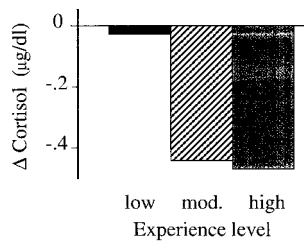


Figure 5 (Flinn et al.). Change in cortisol levels from immediately (5 minutes) after to 1 hour after bike races. Experienced racers have greater reduction of C levels than inexperienced racers. Study and samples are as described for Figure 4.

natural, everyday conditions (Ellison 1988). Why, indeed, is T associated with divorce? And how – what are the details of the processes – does it happen? Frequent (daily) temporal monitoring of T and other hormones from individuals experiencing divorce may provide useful insights. For example, T might drop in response to the blow of being dumped, or rise in response to a favorable legal negotiation. Mazur & Booth, along with Dabbs, Ellison, Sapolsky, and

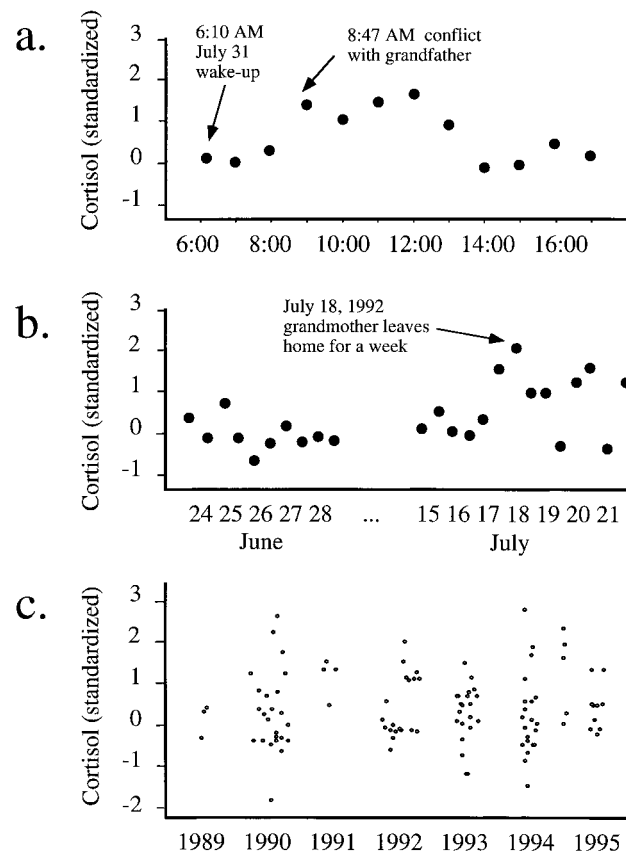


Figure 6 a,b,c (Flinn et al.). Longitudinal monitoring of cortisol levels of a girl (born 1984) hourly for one day (a), twice-daily for two weeks (b), and twice-daily for a few weeks each year for seven years. Study conducted over a ten-year period (1988–1997) collected 22,562 saliva samples from 267 children resident in a rural village on the island of Dominica.

others are pioneering great new opportunities for connecting Tinbergen’s (1963) why and how questions about behavior, mechanisms, and evolution.

Testosterone and the second sex

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Abstract: Because the reciprocal theory of Mazur & Booth dominates the static basal model, given the evidence they present, it is worth considering the implications for women’s equality, supposing it true. Testosterone might well give males a competitive edge, and hence higher status, creating an inequality that mere social legislation would be ill-suited to address. Further research on the role of testosterone is needed.

Mazur & Booth (M&B) masterfully bring to light some extremely interesting and important data concerning testosterone (T). Their theory, the reciprocal theory, bests the static basal model given the evidence the authors present. Although this evidence is not decisive, let us consider the consequences for women’s rights if their central contention is true: that T encourages behavior intended to dominate and enhance status.

There have been many arguments designed to show that men (or, less commonly, women) have some native superiority over women (or men). The motive for such arguments is seldom explicit, but it is typically this: unequal abilities justify unequal rights. Parents, for instance, have the right to tell their children how to behave, because they are better able to judge how to behave. It is granted by all but the most radical feminists that males are innately stronger physically than females, but, in modern societies running on brain power rather than muscle power, the skills that dominate at the Olympic games provide no basis for superior rights. Proponents of male superiority have expanded the scope of testosterone to include intellectual prowess as well, and have proposed that males are innately better at mathematics. [See Benbow: “Sex Differences in Mathematical Reasoning Ability in Intellectually Talented Preadolescents” BBS 11(2) 1988; Geary: “Sexual Selection and Sex Differences in Mathematical Abilities” BBS 19(2) 1996.] These arguments are invariably buttressed by supposition when the evidence fails, as fail it must, for the simple reason that infants have scant mathematical skills and those are equally shared according to gender. Mathematics is a recent, socially imparted skill of this species, and it is not credible that evolution has already linked to the Y chromosome brain structures supporting mathematical skills. Battle of the sexes aside, who would have supposed mathematicians to be superior breeders?

The contention of M&B, by contrast, is evolutionarily sound. The role of male dominance in reproductive success is clear not only in this species but in those from which it evolved, right down to the roots of sexuality in the evolutionary tree. Dominance takes on another dimension in social species such as the wolf, lion, and human being. Social organization requires leaders and followers. The alpha wolf must be a wily killer and must, like the king of beasts or the King of England, organize those below, and sire heirs. Evolution must have provided some innate mechanisms facilitating social organization, and M&B’s reciprocal theory outlines some roles of T: to encourage contests between males, to reinforce winners with euphoria to further contests, and to discourage losers and thus establish some stability in the hierarchy. The fact that the contests may range from prison yard fights through chess matches shows that the human T mechanism is, as with humans in general, extremely adaptable to changing environments.

In this view, T also spells trouble for women in their struggle to gain equality with men. There are two main difficulties. First, human societies are largely meritocratic. Those who get to fly the airliner, teach mathematics, or sit in judgement in the courtroom have shown themselves to be better at that activity than others who

vie for the same position. The ubiquity of competition in meritocratic organization is no mere right-wing ideology or phallogocentric fetish but an engine of adaptation and improvement, rooted in evolution itself. T would seem to provide an advantage insofar as it encourages competitive behavior and rewards success. Any advantage, even if small, will have an effect, and bearers of high T will be more numerous than females in socially dominant positions. Men need not have any innate mathematical superiority to do better at mathematics, but merely the extra boost T gives to compete in such a socially important field. A small competitive advantage in a population will show up disproportionately at the extremes of success and failure, and this is all that is needed to explain the predominance of males at the highest levels of mathematical achievement, or other areas.

The second problem testosterone poses for women's rights is that equal-rights legislation will be ineffective or worse. Where meritocratic principles are left intact, the mere fact of women's having a right entrenched in legislation will not automatically result in its having any value for them. It is one thing to have the right to travel, but it is another thing to afford the fare. We all have the right to run for office, but very few can provide the motivation and money to enjoy this right. Therefore, we must distinguish in general between the mere possession of a right and its value. When we do, we see that women will never achieve real equality with men, despite having equality of rights under the law, if testosterone gives males a competitive edge in the exercise of their rights.

Of course, what often goes under the name of equal rights legislation is really a reversal of meritocratic principles: the strength requirements for firemen may be set lower for females than for males, for instance. This unlevelling of the playing field must result in a general lowering of competence: more property and lives lost to fire. So if M&B are right about testosterone, then the rights-legislation approach to women's equality may face a destructive dilemma: either inequality of status under nominal legal equality, or else a general lowering of the quality of life.

This is indeed a gloomy picture, but let us not despair. The testosterone picture remains unclear despite the clarifications of Mazur & Booth. Maybe a competitive spirit is not always an advantage, particularly where persistent concentration, or continued cooperation, is required. In the Greater Victoria School District in 1996–1997, among 109 secondary school scholarships, 71 went to girls, and only 38 to boys. Boys, on the other hand, led girls in suspensions by a ratio of 78% to 22%. If the will to dominate, and thus testosterone, explains the greater tendency of males to misbehave and thus be suspended from school, it may also explain their poorer academic performance. Testosterone may be a mixed blessing, if a blessing at all. However, with so much at stake, the need for more study is obvious.

Testosterone is not alone: Internal secretions and external behavior

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Abstract: Using testosterone alone as a measure of dominance presents problems, especially when *dominance* is loosely defined to include a range of behaviors that may arise from multiple causes. Testosterone should be examined in relation to other hormonal and neurotransmitter factors, such as serotonin. Various hypotheses about the relationship between high and low levels of testosterone with serotonin and with impulse control are suggested for future study.

Mazur & Booth (M&B) have unquestionably done a great service both by bringing together all this material on testosterone (T) and by concentrating our attention on its effects on dominance as opposed to aggression. They also underline the important distinc-

tion between general life-cycle effects, such as the absolute rise in basal T in males at puberty, and variable adult interindividual effects. Also important is their distinction between basal and reciprocal models. If other hormones and neurotransmitters are any guide, then the reciprocal model would be the better description of reality. Even if basal rates are good *predictors*, this does not necessarily establish a simple cause-and-effect relationship.

A major problem with the findings, however, is that what is or is not “dominance behavior” seems so often to be a matter of judgment. Wide arrays of behaviors are labelled “dominant” and correlations with T are sought. When they are found, the hypothesis is declared confirmed; when they are not, some rationalization is sought. Thus “antisocial” behavior – “childhood truancy, troubles as an adult on the job and with the law, marital disruption, drug and alcohol abuse, violent behavior, and military AWOL” (sect. 4) – are all labelled as “assertive norm breaking” and hence “dominance” behaviors. But clearly the behaviors on this list could result from a multitude of causes, including poor impulse control, genetic alcohol addiction, generalized anxiety, low intelligence with frustration, and even timidity and fear of others. That all these show positive correlations with T could mean that even the most timid person, for example, one seeking to go AWOL from boot camp, has to work up some measure of determination to carry it through. T could therefore be a basic measure not of “dominance behavior” per se but of “determination” even in nondominant behavior. We simply do not know how to assess such a wide range of behaviors, and lumping them all under “dominance” threatens to beg the question. It also introduces circularity if we are going to define *any* high-T-correlated behavior as “dominance.” One needs a true independent definition and measure of dominance, not a loose, fuzzy category that is largely impressionistic.

Another problem arises from multiple causation. That T correlates highly with certain behaviors does not necessarily mean that there is any direct causal relationship. How does one know that T is not simply an indicator, that is, that T correlates highly with the true causative factor? This possibility can be eliminated only by looking at several such factors. Let us take serotonin (S), because its relationship to aggression and dominance is also well established. To enthrone T as the cause, as opposed to S, we have to show that they vary independently. If high T is always associated with high S, then we cannot rule out S as the cause (or effect in a reciprocal model).

Insofar as the studies have not been performed in this way, it is impossible to verify this now, but the speculation can provide us with models for testing hypotheses. Since we know that *low* S correlates with aggressivity, and *high* T does the same, several possible combinations suggest themselves (Table 1). Thus, the first case (high S, high T) should produce individuals who are both dominant and aggressive, whereas the second (high S, low T) should produce those low in aggression but high in dominance, achieved perhaps by words, body language, charisma, and so forth. The third case (low S, high T) would be one of out-and-out aggression with a low dominance component, and the last (low S, low T) would be one of “trulent submission,” that is, submission but with a high aggressive potential: “passive aggression” perhaps, or the army’s “dumb insolence” so infuriating to drill sergeants.

I have suggested above that poor impulse control (IC) might be relevant, so let us look at some profiles in which such IC is seen in conjunction with T (Table 2). There is no need to spell the connections out. One can see easily that, for example, there is a huge difference between high T combined with high IC, high IC combined with low T, and so on. If one throws in serotonin, the profiles become more complicated, but productive of more varied outcomes matching real empirical alternatives. And we haven't even started on adrenalin, cortisol, lactic acid, endorphins, or any of the other numerous internal secretions associated with external behavior.

Initial explorations may of course have to consider only two or three variables at a time, but the results, though still difficult to pin down, may give a more plausible account of the actual behavior-

Table 1 (Fox). Possible connections between testosterone (T) and serotonin (S)

Level	S	T	S	T	S	T	S	T
High	+	+	+			+		
Low				+	+		+	+
Related behavior	Aggressive dominance		Nonaggressive dominance		Aggression/violence		Aggressive submission	

Table 2 (Fox). Possible connections between testosterone (T) and impulse controls (IC)

Level	IC	T	IC	T	IC	T	IC	T
High	+	+		+	+			
Low			+			+	+	+
Related behavior	Dominance		Rebelliousness		Caution		Erratic submission	

hormone interaction than the use of a simple measure of T, however worthy this is as a first approximation. Perhaps M&B know of studies in which both T and S have been measured against variable behavioral outcomes. If so, then perhaps this should be the next step in their important synthesis of ongoing work.

Dominance runs deep

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Abstract: Seen in its historical context, Mazur & Booth's (M&B's) target article may come to be viewed as a turning point in the study of the biological basis of human behavior in general, and dominance in particular. To facilitate further research, suggestions are offered for making the definition of dominance more precise. From an evolutionary point of view, the testosterone-dominance link may be as important in women as it is in men.

Mazur & Booth's (M&B's) target article marks a confluence of several research streams. The major one, flowing along for at least 2,000 years, concerns the relationship between temperament/personality and bodily attributes or physiology (Galen's humours, Kretschmer's typology (1925), Sheldon's varieties of temperament (1925), Eysenck's introversion/extraversion (1967)). Tributaries relating to dominance began flowing in the 1940s, when personality psychologists considered dominance to be one of three major personality dimensions (Cronbach 1949, p. 313). In 1970, Russell and Mehrabian demonstrated how three and only three dimensions (level of arousal, positive vs. negative affect, and dominance) were both necessary and sufficient to describe all human emotions. In 1980, White showed how dominance/submission is one of only two "universal conceptual schema produced by the interaction of innate psycholinguistic structures and fundamental conditions of human social life."

Another research stream arose with the study of dominance in animals (see, e.g., Maslow 1940). By the late 1960s, animal behaviorists, seeking biological rather than environmental explanations of behavior, began following a hunch that hormones were relevant to dominance. In 1971, Rose et al., in a major contribution, published a paper entitled "Plasma testosterone, dominance rank and aggressive behavior in a group of male rhesus monkeys."

This paper might have opened the way for a major research surge, but it did not because by that time social scientists were deeply mistrustful of explanations that incorporated a biological component. Even though A. H. Buss (1985) showed how dominance was one of only five personality attributes that humans share with animals, very few researchers were willing to explore this area. Those who did (Ehrenkrantz et al. 1974; Ellis 1986; as well as Mazur, Booth, and others) were working against the Zeitgeist.

Over the last decade, two more streams have contributed. The first is the technological one, best exemplified in the work of Dabbs (1987; 1988); it is now possible with radioimmunoassay and other techniques to measure both saliva and serum testosterone (in all its forms) with a high degree of accuracy. The other contributing stream is the rise of evolutionary psychology, which provides the context for this research, especially the ultimate explanations, which complement the proximate ones. In this area, D. M. Buss (1991) has described the evolutionary role for dominance and Sadalla et al. (1987) have demonstrated it. Although M&B do not appear (in this paper, anyway) to appreciate the evolutionary significance of their work, they have provided a concise and cohesive description of the relevant findings.

Viewed historically, the very fact that this paper is being published in *Behavioral and Brain Sciences* marks renewed acceptance of the validity of explorations into the biological bases of human behavior. Insofar as the dominance-testosterone link appears strongly established, and because it is central to both survival and reproduction, one would expect a new wave of interest in this area in particular.

My second point concerns the definition of *dominance*. More precision is needed. Dominance is a core personality attribute. (Status-seeking and out-staring are only two of a large number of behaviors that might, in some settings, discriminate a dominant from a nondominant individual.) In this area it is likely that psychologists' definitions will be helpful. In particular, Fiske's (1971) definition provides a solid base: "The core of dominance," he said, "can be identified as acting overtly so as to change the views or actions of another" (p. 98). This imposing of one's own views or goals on others is likely to be the essential ingredient. The research of Sadalla et al. (1987) showing the evolutionary importance of dominance in males was based on a meticulous discrimination between *dominant* and the related but irrelevant descriptors *domineering* and *aggressive*. The group of words the authors used to define the core elements in dominance are "powerful, commanding, authoritative, high in control, masterful and ascendant," whereas *domineering* means "overbearing, oppressive,

bossy, dictatorial, arrogant and high-handed” and *aggressive* means “hostile, belligerent, quarrelsome, argumentative, angry and violent” (p. 735).

Thus, between them, Sadalla et al. (1987) and Fiske (1971) have given the most useful definitions of dominance to date. However, I think there is still something missing, and the clue to this comes from the work described by M&B. In summarizing the findings from a series of studies, they indicate that testosterone is more likely to be related to “rebelliousness and assertive norm breaking” (sect. 4). Fiske’s “acting overtly so as to change the views or actions of another” does not show us this other side of dominance. The definition might thus be improved by adding “and being unwilling to change one’s own attitudes or behavior merely (i.e., without explanation) at the instigation of others.” Such an extension to the definition would encompass virtually all the behaviors subsumed under *dominant*. In particular, it would include those who rebel against following apparently arbitrary orders, especially in settings such as prison, the military, or school.

Although their limitations and shortcomings are well known, I think it is premature to dismiss self-report tests of personality. If the definition of *dominance* were more accurate and self-report tests were designed to avoid easily identifiable themes and contamination by social desirability factors, then such tests might again prove useful.

Finally, a comment on dominance and testosterone in women. If the dominance–testosterone link is of central importance in the evolution of human male behavior, is the female equivalent a simple vestige, or might it have some importance in its own right? My view is that it is just as important in women as it is in men, but for a completely different reason. In a series of studies, I have shown that women who are more dominant in personality than other women are more likely to conceive sons (Grant 1994a). In addition, dominant mothers of sons interact with their newborn infants qualitatively differently from the way mothers interact with daughters (Grant 1994b). These sex-of-infant differences in mothers’ behaviors appear to ensure that higher dominance is passed on, via mothers, to sons rather than to daughters, thus both ratifying and perpetuating psychological sex differences in this area.

Adult testosterone levels have little or no influence on dominance in men

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Abstract: There is substantial evidence that psychological factors influence human testosterone levels, but little support if any for an influence of circulating testosterone on dominance in men. Persistent interest in testosterone as an explanation of behaviors such as dominance and aggression might reflect the influence of cognitive schemas regarding race and sex rather than empirical evidence.

What most surprised me about Mazur & Booth’s (M&B’s) review was how little evidence could be mustered to support an influence of circulating testosterone (T) on dominance in human males. T does not relate reliably to dominance-related behavior assessed using paper-and-pencil inventories, nor do the massive changes in T at puberty appear to have any direct effect on dominance behavior. Instead, hormone–behavior relationships are thought to reflect social responses to hormone-induced physical changes that accompany puberty. Finally, high doses of anabolic steroids do not increase dominance behaviors, despite producing other psychological changes.

M&B do report correlations between T and antisocial or delinquent behavior (e.g., substance abuse, job and relationship problems, military AWOL, stealing) and interpret these to support a T–dominance relationship. However, these behaviors are not typical

of dominant individuals, nor do they produce dominance. Instead, antisocial behavior is associated with nondominant persons and causes a decline in dominance. M&B argue that dominance relates positively to antisocial behavior, but they do not cite any data to support their argument, and it is the opposite of what has been observed by others. Even if the argument were accepted, the relationship between T and antisocial behavior is extremely small. In large studies, T typically accounts for 3% or less of the variance in antisocial behavior.

What remains as supporting data is a reported correlation between T in four male physicians on a 2-week holiday boat and dominance/assertiveness as ranked by three women on the boat, and a report that six men showed more aggression in a laboratory situation when given T than when given placebo. This weak support is further diminished because, although this is unmentioned by M&B, the correlation between T and dominance/aggression in the physicians on the holiday boat was not evaluated statistically. It was not apparent at week 1 and unlikely to be significant at week 2. According to the original report, “the correlation between rank score [for dominance/aggression] and plasma prolactin and testosterone at the end of the first week was not marked, but at the end of the second week . . . the higher ranking pair had higher testosterone levels, whereas the least dominant pair had lower levels.” (Jeffcoate et al. 1986, p. 219). The data are perhaps described in pairs rather than individually, because the top-ranked man had lower T than the man ranked second.

Evidence for psychological influences on T is stronger than evidence that T influences dominance. T rises before competitions, and rises further following victory, but only if mood is elevated by the win. T also rises with divorce and falls with marriage. These effects are impressive but do not necessarily relate to dominance. Winning a competition may be a form of dominance, but it seems inappropriate to view divorce as dominant or somehow similar to a mood-elevating win. Stress is another psychological factor with marked hormonal consequences. Could relationships between T and life events such as divorce relate to stress or life cycle correlates of the life event (e.g., drinking, drug use) rather than dominance?

Much of M&B’s review is not data based but instead describes theory and speculation on topics such as “dominance contests” and “honor subcultures.” Without data, these are difficult to evaluate. When data are presented, they are notably unresponsive of the hypothesis that T influences dominance in adult males. Why then does theorizing about circulating T as a cause of dominance or aggression persist? One possibility involves issues of sex and race that are implicit in M&B’s review. People have well-developed cognitive schemas about sex and race that function to allow conclusions based on limited data (see, e.g., Martin 1991). A typical schema regarding sex might include the elements that men compared to women have more T, tend to be dominant, and are more likely to be aggressive and to engage in antisocial behavior. Although people are usually unaware of their schemas, these can exert powerful effects. We generally notice and remember information that is consistent with our schemas and fail to notice, misremember, or distort inconsistent information. One consequence is overemphasis on research findings consistent with a schema (e.g., six subjects in a single supportive study) and discounting inconsistent evidence (e.g., numerous questionnaires showing little or no support for a T–dominance relationship), distortion of information to fit the schema (e.g., construing divorce or antisocial behavior as dominant), or misremembering information as supporting the schema (e.g., recalling the study of physicians on holiday as demonstrating a testosterone–dominance relationship).

Cognitive schemas also function in such a way that, when one element in a schema is activated, other elements are activated as well. This produces the perception of links between elements that may in fact not be causally related; a person with the cognitive schema described above is likely to associate T’s dominance, aggression, and antisocial behavior whether or not supportive data exist. Because scientists, as with other people, bring cognitive

schemas to their research and its interpretation, it is easy for erroneous conclusions to seem obvious based on limited data. Consequently, work in these areas benefits from being particularly data-bound. Otherwise, the gaps between small bits of evidence are in danger of being filled by assumptions based on race and gender schemas, rather than fact.

Signalling via testosterone: Communicating health and vigour

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Abstract: Our commentary summarises the current understanding of how testosterone can be used as a mechanism to link quality to external traits potentially used in sexual signalling, particularly female choice. Testosterone-dependent traits may reveal male's status to rivals and immunocompetence to females. We highlight some interesting unanswered questions and suggest that cross-disciplinary collaboration would help solve them.

The target article by Mazur & Booth (M&B) refers to two models for the control of testosterone (T) levels in males, the "basal" and the "reciprocal" (also known as the "challenge hypothesis" [Wingfield et al. 1990]) models. The two models are not incompatible, insofar as varying levels can be superimposed over heritable differences. Both models pose questions of evolutionary stability. We comment on the communicational implications of T-dependent traits, properties evolved to serve as signals that modify the behaviour of other individuals (Grafen 1990; Pomiankowski 1987; Zahavi 1975; 1977).

M&B address the signalling implications of dominance contests that are solved cooperatively, such as staring, a conventional form of contest. Evolutionary stability is involved, because, in theory, if most of the population behaves conventionally (i.e., settles dominance disputes by staring endurance), a mutant with staring endurance disproportionate to its fighting ability would initially gain undeserved dominance ranking, leading to a devaluation and demise of the convention. Staring should then be evolutionarily unstable unless some check exists, such as a cost of being "found out" in a proportion of cases. Occasional detection might explain the stability of the communicative role of T-dependent traits in male-male interactions (Rohwer 1975). However, the signalling role of T in female choice is more problematic.

The target article reports work in which males with "dominant" facial features claimed to copulate earlier than their "wimpish-looking" counterparts. Assuming that this is not due to such males' simply being more boastful but to females' preferences for features such as larger beards and deeper voices (Barber 1995), the question is, why should females use such traits to assess males? what qualities are being displayed? and why are these qualities reliably linked to T level?

The prevalent theoretical view of signalling in evolutionary biology can be summarised as follows. Say that a female benefits by picking males with high rank in some hidden property "x." Because x is hidden to female observers, males must signal it. Males then benefit by signalling that their x ranking is the highest, but, if the signal is arbitrary, males can make boastful claims and females will grow indifferent to their signals. Unless, that is, the ability of males to signal bears a forced correlation to their true x, a condition imposed in the case of male-male contests by the occasional fight with a sceptic. What, then, could make signals of male quality reliable in the context of female choice?

One evolutionary scenario in which a signaller may be obligately truthful is when x is important for male survival and the intensity of the signal imposes a loss in it. When costly signals are used, the signaller is in a quandary: a stronger signal increases the receiver's

estimate of x, but it costs the sender some x. Under appropriate assumptions about the functions involved, such systems may be evolutionarily stable. The signal itself handicaps the subject, a feature that is captured in the "handicap principle" (Grafen 1990; Zahavi 1975; 1977). Now, what might x be in the case of T-dependent signals affecting sexual attractiveness?

A likely candidate is disease resistance, because females may prefer males with higher ability to fight pathogens (Hamilton & Zuk 1982). Folstad and Karter (1992) suggested that T links parasite resistance with intensity of sexual signalling through counterbalancing effects, enhancing secondary sexual characters and simultaneously suppressing the immune system. The authors proposed that males who can withstand the immunosuppressive effect of high T levels can afford to develop a high level of T-dependent characteristics that are attractive to females. Males highly susceptible to prevalent pathogens cannot afford large amounts of immunosuppressive hormones, and are forced to emit smaller signals. They called this "the immuno-competence handicap hypothesis" (Folstad & Karter 1992).

An immunosuppressive action of T is compatible with the finding that females have stronger immune responses (Paavonen 1994) and suffer lower parasitism (Schalk & Forbes 1997) than males. Experimental evidence of the immunosuppressive effects of T in humans includes work by Kanda et al. (1996) in which T inhibited the production of immunoglobulins (antibodies) by immune cells in vitro and by Cutolo et al (1995) in which T was found to be useful for its therapeutic effects on the autoimmune inflammatory disease rheumatoid arthritis. In some instances, T seems to have a stimulating effect on the immune system, but the consensus is that androgens generally down-regulate rather than enhance immune function.

This picture faces some difficulties. One is that it must account for the persistence over evolutionary time of variance in fitness-related traits. If high-T, high-resistance males are preferred and consequently have more offspring, high-quality genes are "creamed" from the genetic pool by female choice itself, homogenising the gene pool and thus removing the benefit that females might obtain from choosing (a form of the so-called Lek paradox; Borgia 1979). There is evidence that genetic variance persists in the presence of choice, and there are mathematical models that can account for this, but the issue is far from settled (Pomiankowski & Møller 1995). Another problem is the arbitrariness of immune suppression.

It is not clear whether immune suppression caused by T would be an evolutionarily unavoidable link or whether it has a separate adaptive function. In other words, why hasn't natural selection favoured mutants that control secondary characteristics without the cost of immune suppression? Such mutants (thick-bearded men with low T or with high T but uncompromised immune systems) should invade the population's genetic pool and lead to devaluation of, say, beardedness as a signal. The vast knowledge of T action from the clinical endocrinology and immunology literature together with the stubborn questioning of the conditions for stability by evolutionary biologists should be recruited to solve these puzzles.

Fantasy, females, sexuality, and testosterone

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Abstract: (1) Mazur & Booth do not explain precontest rise in testosterone. Anticipatory T rise may result from fantasized dominance scenarios. (2) Mazur & Booth conclude that females do not experience the dominance-T rise effect. The data are insufficient for this judgment. (3) Mazur & Booth misstate my position on T and sexuality. I offer an emendation and correction.

(1) Mazur & Booth (M&B) report the quite robust finding that, at least among males, testosterone (T) rises prior to both physical and

nonphysical competition, “as if in anticipation of the competition.” However, they neither offer explanation nor propose any mechanism for why this should be so. I hypothesize that the precontest rise in T may be explained by fantasy rehearsals of the anticipated conflict, marked by vivid cognitive enactments of actions and responses that end in victory or success for the anticipator, thus achieving a dominance T surge by mental means alone. Such mental rehearsal may be considered a normal anticipatory response to a significant challenge, a coping response to master anxiety about the outcome. Supporting this view is the result obtained by Mazur et al. (1992) that losers, that is, the less able chess players, had significantly higher pretournament (day-before) rises in T than did winners. Low-ranked tennis players (Booth et al. 1989) also had higher cortisol levels than did high-ranked players who were consequently “more relaxed” (p. 561) and less in need of precontest fantasies of victory.

There is evidence that cognitive activity, such as imagery of muscular activity, excites to a measurable degree the muscles whose motion is being visualized (Suinn 1993, pp. 493–94). [See also Jeannerod: “The Representing Brain” *BBS* 17(2) 1994.] There is also some evidence that T can rise in situations of vicarious dominance, that is, strong identification with a winner (Fielden et al. 1994). I hypothesize that intense fantasies likewise can have physiological and endocrinological effects. Thus T can rise in response to anticipatory fantasies of decisive victory. A formal application of anticipatory fantasies is well grounded in U.S. sports and is programmed by many coaches and players to make up a significant aspect of training. Discussed mainly under the heading of “imagery” or “visualization,” such training tends to concentrate on specific cognitive and motor actions that mimic those that will be required during the sports event, and evidence generally supports the view that such rehearsal is beneficial (Suinn 1993). Owing to the relative youth of the research tradition in this area, there is little standardization with respect to how much affective or “psyching up” material (i.e., victory fantasy), as opposed to purely motor performance, should be included in mental rehearsal programs.

(2) I believe that M&B dismiss too easily, on the basis of two unpublished studies, the possibility of a parallel relationship between dominance and T in women and in men. We are living in a time of extraordinary social transformation of gender roles, when women seek and attain occupational and political positions that, in men, would be deemed to result *from* or to result *in* high T. Although nature works in mysterious ways, the parsimonious hypothesis is that, when the effect is the same, the cause is the same, and vice versa. Females do secrete T, and there is at least as much evidence as M&B rely upon to reject the dominance–T relationship in women as there is that female dominance and/or aggression is accompanied by high T (M&B cite some of this evidence in sect. 6, para. 1; more can be found in Kemper 1990, pp. 137–44, 152–56). Nor does the effect of T in females depend on fetal or perinatal organization of the central nervous system and target receptors. The animal studies by Allee et al. (1939) and Bouissou (1983) reveal that low-status adult females injected with T move up in the status hierarchy through newly acquired aggressive or assertive behavior. Indeed, it would be puzzling if T served in a unisex manner to foster dominance, but was not sex-blind after dominance attainment. M&B write that “the recent availability of studies including thousands of men have expanded our knowledge greatly.” Scientific discretion would warrant some hesitation in rejecting the dominance–T relationship in females until we have more data than we do now. An extremely important biosocial issue is at stake.

(3) M&B attribute to me the idea that “a normal man’s temporal fluctuations in T substantially affect his sexuality, with heightened T especially causing an increase in libidinous feelings and tendency to masturbate.” They reject this notion (quite properly; it is not my position either). M&B seem to have misconstrued my view of how T relates to sexuality. In Kemper (1990), I offer the following (with additional interpolations on M&B):

Five heuristic propositions to organize the rather ambiguous data. . . . First, within the normal range, T is not related to the physiological aspects of sexual activity per se, with or without a partner. It does not rise in anticipation or desire for such activity, nor does it rise afterward because of sexual activity. Second, T is related to dominance/eminence. [M&B have contributed significantly to the validation of this hypothesis.] When elevated social rank is attained to a significant degree, T rises; when it is lost, T declines. Third, surges of T after the attainment of dominance/eminence enhance libido and perhaps attractiveness to potential sexual partners. In this way, rise in T can precede sexual activity. [M&B acknowledge that dominance “would have evolutionary advantage in helping an individual acquire valued resources, especially in competition for mates” (sect. 1). This links dominance to sexuality. The authors themselves are among the foremost researchers to link dominance to T. It requires only the link from T to sexuality, for which there is ample evidence, to complete the theoretical formula I propose.] Fourth, when the sexual activity itself constitutes an attainment of dominance or eminence, T will rise. . . . In this way T rise can follow sexual activity. Fifth, fantasy attainment of dominance/eminence can also produce T elevation. [I would include in fantasy both self-initiated as well as externally presented erotic scenes in which the self can be inserted in a dominant or eminent position, which can include any sexual position, with or without partner.] (p. 48)

In sum, what matters much more in the sexuality–T relationship than has been recognized in current work is the *social* dimension of sexuality. Social victory (dominance) or status attainment (eminence), whether in actuality or fantasy, stimulates T, which, I believe, heightens libido. Whether or not this will result in higher sexual activity – intercourse or masturbation – depends on circumstances (Kemper 1990, pp. 42–43) and attitudes toward sexual practices.

Testosterone’s role in dominance, sex, and aggression: Why so controversial?

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Abstract: Testosterone’s connection to sex differences and key evolutionary processes arouses controversy. Effects on humans and other species, though, are not robotically deterministic but are parts of complex interactions. We discuss the societal implications of these findings and consider how the naturalistic fallacy and the person–situation dichotomy contribute to misunderstandings here.

What makes testosterone (T) so fascinating? Consider, in contrast, adrenaline, a hormone with powerful behavioral effects, boosting arousal and facilitating a broad range of responses. Adrenaline affects rats, monkeys, and humans similarly, but people do not stay up at night arguing about it. T, on the other hand, is a topic that gets people’s adrenaline up. On the negative side, social scientists who happily accept cross-species findings on adrenaline growl at the suggestion of a hormone affecting social behaviors, particularly behaviors such as aggression, sexuality, and dominance. Some worry that acknowledging T effects could be used to justify male violence and rape or exclusion of women from high-status positions. On the positive side, evolution-based researchers get excited about T’s role in a tight nomological network – sexual selection by females leading to increased competition and sexual proceptivity among males. Testosterone fits in at the proximate level: produced in massively greater quantities in males, linked in the short term to assert sexual and competitive behaviors and in the long term to morphological differences (larger muscles, bigger horns, etc.).

Is there solid evidence? Although T’s effects on sexual behavior are robust, Mazur & Booth (M&B) note that effects on other behaviors are not always clear in humans. This could be due to

unreliability of T measures or behavioral indices or to a “true” small effect size. Nevertheless, the findings are rarely reversed, and, in the cleared lenses of a meta-analysis, one would probably see a robust effect of bloodstream T on male dominance and aggression. Even without all those data in, we cannot ignore the longer term lifespan effects on morphology and behavior. Across the range of human societies, adult males grow larger and engage in more competition and violence, all the markings of a species in which females exerted the standard sexual selection pressures on potential mates (Daly & Wilson 1983).

Although many studies find that women are attracted to dominant men, they are not attracted to aggressiveness, but seem to prefer men who are dominant in nonaggressive ways (Jensen-Campbell et al. 1995; Sadalla et al. 1987). This research has typically examined college students. Within a different social group, where subsistence is a daily challenge, females might prefer partners with the physical ability and behavioral tendency to aggress. It is more likely, however, that aggressiveness is not directly selected by female choice but is a byproduct of intramale competition for status. As implied by M&B, aggression might be necessary only among desperate males, whose paths to status and resources are otherwise blocked (see also Wilson & Daly 1985).

Does the evidence excuse social problems? What do we admit by allowing that some human sex differences are linked to sexual selection and that T mediates those differences, developmentally and behaviorally? Does it counsel the exclusion of women from high-status positions (such as a senate or parliament)? No. That interpretation succumbs to the naturalistic fallacy. The findings might elucidate why males proliferate in such positions, but it could be argued that we should choose modern leaders for cooperativeness rather than traits selected during the Stone Age.

Could such findings justify crimes such as homicide or rape via a “not guilty by reason of testosterone poisoning” defense? No, again. Consider other factors that social scientists already admit as vectors affecting aggression. Excessive heat, for example, increases hostile behaviors from horn-blowing to assault (Anderson 1989; Kenrick & MacFarlane 1986). Likewise, the presence of guns fuels aggressiveness. Such vectors from the external environment are not considered sufficient excuses for violence, and there is no logical reason why we should treat internal vectors, such as enhanced irritability, arousal, or status strivings, any differently (regardless of which hormones affect those internal vectors).

Are we puppets of our hormones? Acknowledging a testosterone-behavior link does not imply that males are blindly driven by hormones. A change in T level may lead to a motivation to act, but not necessarily to action. In keeping with M&B’s point, there are potential costs associated with heightened T in the short and long terms. Given those potential costs, situational reactivity of T might well vary according to the likelihood of a positive outcome. Just as we ignore hunger unless there is relatively accessible food nearby, men might suppress their motivation to dominate another male or copulate with a female unless success is likely.

M&B’s discussion of basal versus reciprocal models brings up the perennial person-situation controversy. For years, psychologists debated the relative merits of “trait” versus “situational” approaches to explaining behavior (Kenrick & Funder 1988). As we now realized, internal factors are inextricably linked to environmental inputs, and environmental effects depend on the organism’s responses. M&B suggest that basal T levels cannot be separated from interactions with the environment. Likewise, people in the environment respond to behaviors affected by basal T level, and so on, in a continuing cycle. Just as natural selection always involves traits of organisms dynamically adjusting to ecological constraints and opportunities, so it is for adaptation at the level of individual lives and days in those lives.

Testosterone-aggression relationship: An exemplar of interactionism

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Abstract: Mazur & Booth provide life scientists with an example of the multilevel biopsychosocial approach. Research paradigms have to become more flexible and multidisciplinary if we are to free ourselves from the nature-nurture dichotomy that we have long agreed was simplistic and shortsighted. I point out a variety of kinds of interactions that may be the next frontier for behavioral scientists.

Mazur & Booth (M&B) are at the forefront of a small cadre of sociologists (including, in addition, Udry, Dabbs, Mueller, Machalek, and Ellis) who have gone beyond the rhetoric of the nature-nurture debate to truly embrace interactionism in its various forms. I have identified in the target article reference to no fewer than four kinds of gene-environment interactions, three kinds of feedback loops, and three kinds of evolutionarily stable strategies for maintaining population variability.

Gene-environment interactions. M&B’s review documents at least four kinds of interactions we might call gene-environment interactions. First, there is *age limitation* and *sex limitation* of both the organizing and activating effects of testosterone (T). The fact that the physiological environment of T-influenced cells, tissues, organs, and circuits differs across age and sex, and that the expression of T covaries with these differences rules out simplistic “genetic vs. environmental” explanations of behavior.

A second complication is the phenomenon sometimes referred to as *reactive heritability* (Tooby & Cosmides 1990), whereby genetic differences in one variable (such as age of pubertal increase in T) elicit different social responses from others (such as differential aggressiveness, deference, or sexual interest), which, in turn, provide differential reinforcement and punishment for other behaviors (such as bullying, petty criminality, or “womanizing”). As a result, early maturers or “dominant-looking” individuals may find themselves in a social environment different from that of their age-mate peers, with significant effects on later life-history trajectories (Berry & Landry 1997; Moffitt 1993; Mazur et al. 1994; Thornhill & Gangestad 1994; Zebrowitz et al. 1992). Behavior geneticists have demonstrated that, within normal ranges, the most important environmental factors influencing the variance in adult phenotypes are the rather idiosyncratic social experiences that are not shared by siblings; many of these “environmental” experiences have genetic “causes” (Plomin & Daniels 1987; Scarr & McCartney 1983).

Next, there are those *gene-environment correlations* resulting from the nonrandom assortment of individuals of different geno-/phenotypes into different physical environments (Neale & Cardon 1992). Some of this assortment is a “voluntary” form of self-selection, for example, the different career choices of individuals with varying T levels (Dabbs et al. 1990; Purifoy & Koopmans 1980), although some may be “involuntary,” for example, the differential upward and downward mobility of people with different T levels (Dabbs & Morris 1990). In addition, some gene-environment correlations – such as those relating to racial segregation – may covary with other gene-environment interactions (as described in the target article’s example of honor subcultures).

Fourth are the effects of *assortative mating*, which may or may not be the result of some of the gene-environment correlations described above (Neale & Cardon 1992). Particularly when the phenotypes in question are age- and sex-limited (which T-related phenotypes are), assortment at the phenotypic level may or may not result in assortment at the genotypic level; alternatively, nonrandom mating might actually increase genotypic assortment when a single genotype has more than one manifestation (see, e.g., Harpending & Sobus 1987).

Aggressiveness and dominance

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Other interactions not mentioned by M&B include the *epistatic interactions* among the alleles and products of an individual's genome and *gene–environment interactions* of the classical statistical kind that result when individuals of different genotypes respond differently, or develop differently, in relation to variation in the environment.

Feedback loops. Basal T level is regulated by a *physiological feedback loop* operating between the hypothalamus and the Leydig cells of the testes. On top of this is the more dynamic *physiological–behavioral loop* M&B discuss in section 5 on “reciprocal causation.” On top of that may be a longer-term *physiological–psychological loop*, the workings of which M&B briefly hint at in the last sentence of section 7 on dominance contests. M&B's alter ego scenario need not be considered so hypothetical; the loop connecting psychological state with T levels is mediated by adrenal steroids and serotonin, which, like T, fluctuate in response to psychosocial stressors such as dominance contests (McGuire et al. 1983, Raleigh et al. 1991). Nesse (1991) discusses the evolutionary advantages of a loop between “success” and “mood”; others (e.g., Price et al. 1994) go even farther, postulating that clinical depression (and the individual symptoms associated with it) is a long-term consequence of repeated “failure” in social dominance contests.

Evolutionarily stable strategies. There are at least five ways in which an evolutionarily stable mix of phenotypic differences might be maintained in a population (Mealey 1995). One is that individual differences might be *genetically based*; that is, phenotypes might vary in direct relation to genotype regardless of environmental conditions; in this scenario an individual's phenotype is said to be “obligate.” A second is that individual differences might be *developmentally contingent*; that is, each individual has an initial potential to realize every phenotype but becomes fixed after exposure to certain environmental stimuli in the course of development (e.g., during a critical period). In this scenario an individual's phenotype is said to be “canalized.” A third is that phenotypic differences might be *environmentally contingent*; that is, every individual can exhibit every phenotype and does so in relation to immediate circumstances. In this scenario an individual's phenotype is not a stable trait and is said to be “facultative.”

As an explanation, the first scenario might be thought to reflect pure “nature” and the second pure “nurture.” The third scenario is not really a model of individual differences; all individuals will behave predictably in relationship to current circumstances regardless of any individual differences in genotype or developmental history. A fourth scenario, which is probably more realistic (though admittedly difficult to disentangle), involves one or more gene–environment interactions in a complex mixture of nature and nurture. M&B do not address these evolutionary issues directly (for this, see Daly & Wilson 1988; Wilson & Daly 1985), but we can see, in their report of sex differences, chromosomally based obligate phenotypes; in their recounting of the honor subculture, a form of developmental canalization; and in their report of longitudinal, environment-related changes in T, a kind of pan-specific, flexible, facultative response.

By considering a wide variety of methods and paradigms, M&B have been able to approach a full understanding of a complex topic better than can anyone who relies on a single theoretical tool. I hope their successes will encourage their fellow sociologists to also become behavioral and brain scientists.

Abstract: Aggressiveness is a vital component of dominating behavior. We must distinguish adaptive from nonadaptive aggression and must control for skills, intelligence, appropriate context variables, and – most important – whether the aggression displayed was actually suitable for improving a subject's social status. If we do, we may find a consistent positive correlation between adaptive aggressiveness and testosterone.

Mazur & Booth's (M&B's) is a brilliant and knowledgeable review, which will serve as a standard reference in this field for years to come. It does, however, show certain difficulties in organizing the vast amount of observational and experimental data on aggressive and dominant behavior it presents. In the opening section of their paper, M&B write “We . . . frame . . . dominating . . . behavior as being theoretically prior to aggressiveness, leaving it as an important but subsidiary question why men sometimes dominate with intent to harm” and then go on to write about the relation between aggressiveness and testosterone (T) in the rest of their target article. In fact, this question, as well as the question of why aggressiveness often fails to help in gaining high status, is by no means subsidiary; it is absolutely essential for an understanding of the intricate relation between T and behavior.

M&B correctly place dominant behavior together with antisocial behavior in one category: competitive behavior aimed at achieving and maintaining high status – privileged access to physical resources and mates. They distinguish this from aggressive behavior – behavior aimed at inflicting physical harm on a conspecific. They also point out correctly that it is the social context that determines whether a given behavior is eusocial “dominant” or antisocial “rebellious.”

There is a sizeable game theoretical literature on the endogenous evolution of cooperation (starting with Freedman 1971; 1977; Axelrod 1981; 1984 to this date; see also Mueller 1987) that demonstrates unequivocally that nice (start cooperatively), retaliatory (if hit, eventually hit back), and forgiving (if the opponent stops hitting, so do you) strategies are the most successful ones for being accepted in a high-status position by less fortunate players. Strategies of unconditional confrontation in most contexts do less well, whereas strategies of unconditional niceness are a recipe for disaster. That is, high status cannot be achieved if aggressive behavior is never an option.

Aggressiveness, that is, the threat and, if necessary, the actual application of physical violence against competitors, is an equally indispensable qualification for high status, whether the going is easy or tough. At the same time, the more skillful an aspirant to or current holder of high status, the less frequently and the less directly he will actually have to carry out that threat. Quite often, overt aggression is the mark of the untalented and unsuccessful, frustrated by their lack of success. On the other hand, men who are incapable of direct aggression (or at least organizing direct aggression) even if seriously challenged do not have the qualifications for dominance.

Thus, the relation between T and aggressive behavior (and all the risks associated with it) lies at the core of the relation between T and competitive behavior. There is adaptive aggressive behavior, usually reactive, calculated, rare; and there is nonadaptive aggressive behavior, often unprovoked, overreacting, not calculated, frequently displayed.

From the results presented in sections 7–9 of M&B's target article, the absence of high T levels in institutionalized individuals with a record of unprovoked physical violence should come as no surprise. This may simply be the result of a T decline because of the sanctions following the violent acts. If an act of violence puts you in jail, this aggressiveness was obviously unsuitable for improving your social status. As a practical consequence for research,

in experiments as well as in field studies, subjects' social integration (and especially social status gains as a consequence of acts of violence on the one hand and social skills and general intelligence on the other) should be controlled so that we can distinguish between the adaptive and nonadaptive, that is, the smart and the dumb kinds of aggressiveness. Perhaps then we will observe a positive correlation between measured T and smart aggressive behavior, just as there is a positive correlation between T and adaptive (successful) competitive behavior.

Placebo-controlled manipulations of testosterone levels and dominance

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Abstract: Mazur & Booth present an intriguing model of the relationship between circulating testosterone levels and dominance behaviour in man, but their review of studies on testosterone-behaviour relationships in man is selective. Much of the evidence they cite is correlational in nature. Placebo-controlled manipulations of testosterone levels are required to test their hypothesis that dominance levels are testosterone-dependent in man. The changes in testosterone level that follow behavioural experience may be a consequence of stress. Testosterone levels in man are determined by a wide variety of factors, and a multivariate approach is required.

Mazur & Booth (M&B) propose a reciprocity between testosterone (T) and dominance behaviour in man. The emphasis on "bidirectionality" (Hatch 1981) is to be applauded. However, their review of the literature is highly selective. They refer extensively to positive findings that do not appear to have been subject to the normal peer-review process necessary for publication in scientific journals (e.g., Booth & Dabbs 1995; Dabbs & Hargrove, in press; Fielden et al. 1994; Mazur & Michalek 1995; Mazur et al., in press), and they neglect to cite published negative findings. For example, O'Carroll and Bancroft (1984) reported a placebo-controlled study in which circulating T levels were manipulated in endocrinologically normal men, and no change in aggressive mood state was observed. In a further study of men with low circulating T levels, elevation of their T levels, in a placebo-controlled manner, resulted in a reduction in self-rated aggressive and irritable mood, if anything (O'Carroll et al. 1985). Finally, in a placebo-controlled single-case study, O'Carroll & Bancroft (1985) described the case of a mentally handicapped young man who had been castrated traumatically in a road accident in childhood. He required T injections in order to stimulate epiphyseal closure (cessation of long bone growth). However, the nursing staff demanded that the injections should be stopped as they were apparently causing hyperaggressive behaviour. When varying doses of oral T were evaluated using a placebo-controlled, double-blind design, nurse ratings failed to detect any significant effect on aggressive behaviours. Such experimental designs, although difficult, are required in order to determine hormone-behaviour relationships in man.

Aggressive behaviour is clearly not "one thing"; it is likely that only some aspects of aggression may be related to T levels. Response to provocation or threat appears to be a promising candidate, worthy of further investigation, particularly insofar as positive results have been obtained from a variety of sources: adolescence (Olweus et al. 1980; 1988), the laboratory (Kouri et al. 1995), and sporting behaviour (Scaramella & Brown 1978).

M&B propose in section 1 that it would be "naively behavioristic" to deny our ability to read people's intentions. However, particularly in relation to aggressive behaviour, we must acknowledge that people often misperceive the social signals and inten-

tions of others (Navaco 1986). Aggressive men often misperceive. For example, an innocent glance may be construed as a challenging gaze (inferred malevolence where none exists), thus leading to challenges and overt aggression.

In section 1 it is proposed that dominance mechanisms have clear evolutionary advantage. It is interesting to note recent claims for the opposite viewpoint, for example, that submissiveness as a personality trait is associated with protection from coronary artery heart disease or that submissiveness not dominance confers survival advantage (Whiteman et al. 1997).

M&B correctly point out that T levels in man fluctuate markedly (sect. 2). This fact makes interpretation of correlational studies extremely difficult, particularly in that most studies have relied on single-sampling methodology. M&B cite reliability values in the region of $r = .5$ as proof of within-subject consistency of T levels across years (sect. 9). This is not particularly impressive as a reliability figure; T level at time 1 predicts 25% of the variance in T level at time 2, leaving 75% of the variance unexplained. Given this degree of within-subject variation, claiming hormone-behaviour relationships based on single-sample correlational methodology may not be warranted.

In their discussion of reciprocal causation (sect. 5), M&B propose that a precompetition boost in T level would make individuals more "sensation seeking" and willing to take risks. In support of this view, they cite Daizman and Zuckerman (1980), who described a correlation between sensation-seeking behaviour and gonadal hormone level. M&B fail to cite O'Carroll (1984), however, who showed that placebo-controlled manipulations of circulating T levels in groups of both eugonadal and hypogonadal men had no effect whatsoever on any measure of sensation-seeking behaviour.

Much is made of reductions in circulating T levels following adverse experience (sect. 5), and the hypothesis is proposed that these changes reflect changes in dominance levels. However, surely the most parsimonious explanation (as M&B admit in their caveat in sect. 8) is that these changes are due to stress effects, not status loss. The seminal study in this field, cited in support of the dominance theory, is in fact entitled "Suppression of plasma testosterone levels and psychological stress" (Kreuz et al. 1972).

Much is made of dominance contests as well. I for one remain unconvinced that normal day-to-day social interaction is filled with such confrontations (sect. 7). The examples given (e.g., length of stare leading to stress in the recipient) would surely be expected to lead to alterations in the hypothalamic-pituitary-adrenal axis rather than the gonadal steroid level.

It is rather worrying that a number of sweeping generalisations are made without supportive evidence, for example, the claim of elevated T levels in black males "possibly reflecting the higher defensive demands on black men during young adulthood" (sect. 8) and the claim that "normal marriages are secure and supportive, more free from stress than single life" (sect. 9).

The evidence regarding divorce, marriage, and T (sect. 9) is particularly difficult to evaluate. The U.S. Air Force data to which M&B refer is supported by two references, one unpublished and one in *JAMA*. M&B describe 2,100 U.S. Air Force veterans, yet the cited *JAMA* paper describes 995 veterans who were exposed to herbicides during aerial spraying of "Agent Orange" in Vietnam versus 1,299 comparison subjects. M&B report significant correlations between T level and marital status, claiming that 10 of 16 correlations were "significantly positive" and that T levels are highly responsive to marital status. However, T levels were apparently taken every 3 years, hence a man may have been divorced nearly 3 years prior to his T measurement and a multitude of life events and biological and psychological stressors may have occurred in the intervening period, all of which could conceivably have a significant effect on his endocrinological status. M&B claim that "T measured right after the divorce is the best predictor." What does "right after divorce" mean – some time within the preceding 3 years? If there is an association between high T and recent divorce, could this not perhaps reflect elevation of circulat-

ing T level following cessation of prolonged marital stress? As M&B state, the break-up of a marriage usually spans years, “accompanied by arguments and confrontations” (sect. 9). Hormone levels are multiply determined, and choosing a single crude demographic measure such as marital status (“because there was little behavioral measurement in the study”) and looking for endocrine associations is unlikely to lead to significant advances in our knowledge of endocrine–behaviour relationships in man.

In conclusion, the link between T and aggressive and sexual behaviour in lower animals (e.g., rodents) is clearly established. However, as we ascend the phylogenetic ladder to humans, this relationship becomes less clear. This is not to deny that such a relationship exists, but the complexity of human social behaviour suggests that both behaviour and endocrine status are influenced by a wide variety of biological and psychological variables, and a multivariate approach is required. Furthermore, as a consequence of the pulsatile variability in circulating T levels in man, significant error variance is introduced into single-sample correlational studies. Definitive evidence is likely to come from placebo-controlled, double-blind experiments in which circulating T levels are manipulated and appropriately reliable and sensitive assays of behaviour are taken.

Of fish and men: A comparative approach to androgens and social dominance

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Abstract: Four aspects of Mazur & Booth’s target article are discussed from a comparative perspective using teleost fish as a reference: (a) the relationship between aggression, dominance, and androgens; (b) the interpretation of the data in light of the challenge hypothesis; (c) the potential role of testosterone as a physiological mediator between social status and the expression of male characters; and (d) the fact that metabolic conversions of testosterone may be important in its effect on aggression/dominance.

As a fish biologist interested in hormones and behavior, I was fascinated to find myself to some extent on very familiar ground while reading Mazur & Booth’s (M&B’s) target article on dominance and testosterone in humans. However, insofar as testosterone (T) in particular and androgens in general are an essential part of the conserved vertebrate reproductive axis (i.e., hypothalamus–pituitary–gonads), one would expect some parallels between teleosts and mammals, including humans, in the relationships between sex hormones and social behavior (although M&B neglect to acknowledge the comparative literature on androgens and dominance in nonprimate vertebrates). Here I will comment on four issues raised by M&B in the light of this comparative approach, using the teleosts as counterpoint. Teleost fishes are the most diverse of living vertebrate taxa and represent a very successful lineage of recently evolving organisms (Nelson 1994). It would accordingly be very interesting to compare hormone–behavior systems in these two successful vertebrate lineages.

Dominance, aggression, and androgens. In the target article, M&B point out that dominance in humans may be exerted nonaggressively and that T is related primarily to dominance and not to aggression per se, except when dominance is asserted aggressively. They go on to suggest that nearly all primate studies linking T to aggressive behavior can also be seen as linking T to social dominance.

In fish, castration lowers both androgen and aggression levels but not social dominance (Francis et al. 1992). These results can be explained by the fact that aggression is an individual attribute, whereas social dominance is a relational one, which can vary with the social context into which the individual is placed (Bernstein

1981; Francis 1988). [See also Bernstein: “Dominance Relationships and Ranks” *BBS* 3 1981.] Moreover, the underlying mechanisms involved in dominance relationships may differ according to the number of individuals involved. In dyads, dominance may be more directly related to aggression, because the two individuals are competing directly, whereas, in triads, other phenomena may be involved, such as prior experience, individual recognition, bystander effects, or transitive inference. It would accordingly be expected that, in cases in which dominance is assessed in a dyad, T can be more easily related to aggression. Nevertheless, T is also known to be related to attention/cognitive mechanisms (Hampson & Kimura 1992), which might also be involved in status-assessment processes; thus T could still be linked to dominance in this scenario. The findings linking T to aggression but not to social dominance in fish can thus be explained as a resilience effect of the dominance relationship previously established between each pair of tested individuals. It would therefore be instructive to pay more attention to the context in which the data are collected and to the possible underlying mechanisms involved in status acquisition, in considering the relationship between T and dominance.

The challenge hypothesis. Wingfield (1984) has proposed that the androgen levels of a given individual will respond in the short term to the social interactions in which the animal has participated, which will result in an adjustment of the readiness and intensity of the agonistic behavior according to changes in the social environment into which the animal is placed. In this view, variation in T levels may be more closely associated with temporal variations in aggression than with basal reproductive physiology. According to the challenge hypothesis, baseline breeding levels of T are sufficient for normal reproductive function and temporal patterns in T levels may differ between species according to the mating system of the population. In monogamous species, T levels should rise above the baseline breeding level only in periods of social challenge, so that aggression will not interfere with parental care and pair bonding, whereas, in polygynous species, T levels should increase to near the maximal level and remain high, because this will facilitate aggressive behaviors in male–male competition (Wingfield et al. 1990). As the human species is considered to be monogamous and does not present a breeding seasonality, the challenge hypothesis would predict human male T levels to respond sharply to social challenges. In fact, the data presented by M&B provide further evidence for the challenge hypothesis; T rises in response to a competitive match, as if in anticipation of the challenge. This precontest rise in T might have the function of preparing the individuals for confrontation by increasing readiness to fight and improving the cognitive capabilities required by a competitive situation.

Again, there are parallel data for teleosts. Socially isolated males show low levels of both aggression and plasma androgens; these levels increase very rapidly after visual exposure to a territorial male, which acts as a challenge stimulus (Hannes & Franck 1983; Heiligenberg & Kramer 1972). Territorial males have higher androgen levels than nonterritorial males, and recently established territorial males undergo a large increase in androgen levels. After territory establishment, androgen levels drop to the territorial male baseline. Furthermore, simulated territorial intrusions promote an increase in androgen levels in resident males (Barnett & Pankhurst 1994; Cardwell & Liley 1991; Oliveira et al. 1996). This link between androgens and social status has also been shown to be a function of the number of territorial intrusions and of population density (Pankhurst & Barnett 1993). These data suggest that short-term increases in circulating androgens are a response to intense social competition during territory establishment. It must be of high adaptive value to react to the presence of a male intruder with a quick rise in agonistic motivation, which might be achieved by high androgen levels. Subordinate individuals should adjust their aggressive behavior to a level that maximizes their reproductive success without promoting excessive confrontations with dominant males. This trade-off may be regulated by social modulation of androgen levels.

Androgens, social dominance, and sexual selection. Androgens may play a very important proximate causal role as mediators between social status and the expression of male secondary sex characters, both morphological and behavioral (including aggressive behavior), which might serve as cues to both males and females. Indeed, increasing evidence shows that androgen levels are strongly affected by social factors such as the outcomes of social interactions in which the individual participates (see Oliveira et al. 1996, for references). On the other hand, the expression of many male secondary sex traits is under androgen control (for teleosts, see Borg 1994). Together, these results suggest a model in which androgens would rise in response to social status and would in turn activate both the expression of male reproductive behavior, including aggression, and the expression of male secondary sex characters. Dominant males, by signalling their status both morphologically and behaviorally, may reinforce their social status by a positive-feedback mechanism. This causal chain has been demonstrated for a cichlid fish by our group (Oliveira & Almada 1995; 1997; Oliveira et al. 1996). Thus, the expression of phenotypes, such as armaments and ornaments that are thought to evolve as a result of sexual selection, may be influenced by the social environment to which the individual is exposed, a fact that is usually ignored in genetic models of sexual selection.

Again, there are some human data to support this model. M&B provide some data in their target article (sect. 1) concerning the advantages of human dominance, which include mate attraction and earlier sexual activity (which could increase fitness). Moreover, M&B also suggest that “around puberty, the effect of T on behavior works primarily through long-term reorganization of the body, including increased size, muscle mass, and the appearance of secondary sexual characteristics” (sect. 3). It would thus be very interesting to know whether more dominant men reach puberty earlier and whether androgens are also implicated as mediators between social status and the expression of male secondary sex characters in humans, which might serve as cues available to other individuals too.

Testosterone: A hormone or a prohormone? M&B give an oversimplified picture of vertebrate androgens and their relationship to behavior. T has received considerable attention as a proximate factor regulating aggression and social dominance in vertebrates; however, an increasing body of evidence shows that, in the so-called higher vertebrates (i.e., birds and mammals), T has to be converted to an estrogen (E) metabolite for it to be effective in influencing behavior (Balthazart & Foidart 1993; Hutchison 1993; Schlinger & Callard 1990). For example, it has been shown in rats that administering an aromatase (the enzyme complex responsible for the metabolization of T into E) inhibitor together with T inhibits the demonstrated effect of T in promoting aggression (Brain et al. 1988).

In fish, the most potent androgen is a T metabolite, 11-ketotestosterone (11-KT), which is unique to fish and to urodeles (Kime 1987). Interestingly, in a study of steroid metabolism, it was demonstrated that keeping fish in high densities inhibits territorial and aggressive behaviors and also blocks the conversion of T to 11-KT. In the same study, Leitz (1987) showed that dominant males had a higher production of 11-oxy-androgens than subordinates. In another study, it was found that, when male groups were created, 11-KT increased in fish that became territorial but showed no change in nonterritorial fish, suggesting that one physiological consequence of subordinate status would be to block the enzyme that converts T into 11-KT (11 β -hydroxylase), leading to a reduction in 11-KT production and an accumulation of T (Oliveira et al. 1996).

It is interesting that in humans there is also some evidence that metabolic conversions of hormones are important in their effects on aggression and/or dominance. In a study on androgens and different components of aggression in men, Christiansen and Knussmann (1987) found that interest in sexual aggression was not correlated with salivary or circulating levels of T but was negatively

correlated with an index of conversion of T into one of its metabolites, dihydrotestosterone (DHT). Because the available evidence linking T to aggression and dominance in humans is mainly correlational, future research should also consider the role of T metabolism in the activation of aggressive and dominant behaviors.

I hope to have drawn attention to the fact that fish and men share a number of mechanisms underlying the hormone-behavior system of dominance and aggression, suggesting a conserved ancestral mechanism across all the vertebrate taxa. A comparative approach can contribute to a better understanding of the reciprocal relationship between hormones and behavior.

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The nurture of nature: Social, developmental, and environmental controls of aggression

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Abstract: Evidence from many species suggests that social, developmental, and cognitive variables are important influences on aggression. Few direct activational or organizational effects of hormones on aggression and dominance are found in nonhuman primates. Female aggression and dominance are relatively frequent and occur with low testosterone levels. Social, cultural, and developmental mechanisms have more important influences on dominance and aggression than hormones.

Does testosterone (T) have a direct role in dominance and aggressive behavior in men? Much of the evidence presented is correlational and many of the correlations, though statistically significant, have small effect sizes, explaining a minuscule amount of variance. Two important sets of contrary data have been ignored: (1) Several studies of human and nonhuman animals indicate that social, environmental, and cognitive variables influence aggression to a greater degree than hormonal levels. (2) Females of many species, including humans, display a capacity for aggression at least equal to that of males despite much lower levels of T; there is also evidence that female reproductive success benefits directly from dominance.

Testing conditions often influence the outcome of dominance contests: Castrated male woodrats fight as vigorously as intact males in neutral arenas (Caldwell et al. 1984). In mice, castrated males with no previous fighting experience do poorly, but castrated males with fighting experience prior to castration show normal levels of aggression (Scott & Fredericson 1951). Bernstein et al. (1983) demonstrated that T levels in rhesus macaques changed in response to winning or losing a dominance contest, in parallel with results on humans reviewed by Mazur & Booth (M&B), but they found no change in T levels when monkeys were provoked to attacks against a human holding two infant monkeys over a much longer time period than the dominance contrast. Bernstein et al. (1983) suggest that a cognitive interpretation of an encounter may have more influence on hormones than the actual amount of aggression expressed. [See also Bernstein “Dominance” *BBS* 3 1981.]

Wallen (1996) reviewed 30 years of research on hormonal and social influences on behavior in rhesus macaques and concluded that social environments had a more important influence on the expression of dominance and submissive behaviors than did hormonal environment. The presence or absence of mothers and the sex composition of peer groups influenced all sexually dimorphic behaviors. Rough-and-tumble play was the only behavior found in high levels in males across all rearing conditions, but even this was

modulated by social variables. Wallen (1996) concluded that behavioral sex differences result from hormonally induced predispositions that are shaped by specific social environments and interactions. If social environments, prior experience, and testing conditions influence the expression of aggression in a variety of nonhuman species, then it seems simplistic to relate human dominance and aggression to T alone.

The finding of high levels of aggressive behavior in females with much lower levels of T than males argues strongly for additional mechanisms. Until recently it was thought that there was little variance in female reproductive success, making dominance contests among females of little consequence. However, there are several species of cooperatively breeding mammals in which one or two females reproduce while the remaining females do not. In at least one of these species, the golden lion tamarin, high levels of aggression have been reported between parents and offspring and between siblings. Although the rate of aggression was equal for both sexes, two independent studies have reported that female–female aggression is often lethal, whereas male–male aggression is not (Kleiman 1979; Inglett et al. 1989). De Waal (1982) has described sex differences in aggression among chimpanzees: Males frequently engaged in dominance interactions but were readily reconciled. Female chimpanzees, although they were observed to engage in dominance interactions much less often, showed little tendency to reconcile when they did fight, and were more likely to harm each other during a fight. Recent analyses of long-term field data show that dominant female chimpanzees have greater lifetime reproductive success, with more total offspring and daughters reaching reproductive age sooner (Pusey et al. 1997). Thus, for tamarins and chimpanzees, dominance contests are of critical importance.

In many species females are dominant over males (e.g., spotted hyenas, Frank 1986; hamsters, Floody 1983). Pygmy marmoset females do not show as much aggression toward their mates at ovulation as they do during the rest of the cycle (Converse et al. 1995). When unbiased epidemiological studies are performed on human pairs, females are more likely to initiate aggression than males. Magdol et al. (1997) studied all members of a birth cohort in New Zealand at age 21 years and found that 37% of women and 22% of men reported that they initiated aggression in the home. Severe aggression was initiated by 18.6% of the women but by only 5.7% of the men. Men who committed severe aggression were more likely to be deviant on social and mental health measures, whereas highly aggressive women were normal. These data contradict our popular beliefs about human aggression, but most previous studies have used selective samples of those who seek treatment at a hospital or those found in courts. The results can be explained in terms of social norms and expectation. Men are reared to avoid being aggressive toward females and know they are more likely to be prosecuted by courts if they do act aggressively. Women do not have these constraints and will be held less accountable by society and the legal system.

Much aggression expressed by human and nonhuman species appears to be influenced more by social, developmental, and environmental variables than by current hormonal levels. The high levels of often lethal aggression displayed by females that have measurably low T levels coupled with the relatively small effects and correlational data on T and dominance in men suggest that T plays a very small role in dominance and aggression in humans. We will reach a better understanding of dominance and aggression by looking for social, developmental, environmental, and cognitive mechanisms rather than relying on a simple hormonal mechanism.

Honour subcultures and the reciprocal model

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Abstract: Tests of models of reciprocal interactions of testosterone and behaviour patterns in honour subcultures, if based on adult samples measured at a single point in time, would be aided by measures of behaviour in such samples that indirectly index basal testosterone levels at earlier developmental ages, for example, hand preference and other measures of cerebral dominance. Such models raise questions about the social preconditions of honour subcultures, and their indirect effects on health.

Mazur & Booth (M&B) make a convincing case for the involvement of testosterone (T) in male dominance-seeking behaviour and for the reciprocal nature of the interaction. More detail on the possible mechanisms involving T in the mobilization of physiological and cognitive resources would be useful. (Isn't it significant that increased T can rapidly elevate rates of cellular metabolism in muscle tissue [Tsai & Sapolsky 1996]?) One recurrent psychological finding is an effect of elevated T on visual–spatial abilities (Hampson 1995; Janowsky et al. 1994), but its precise nature is controversial. In this respect, the literature on T and dominance seeking in adults has much in common with the literature on fetal T and subsequent adult hand preference. Lefthandedness may be influenced by fetal T levels (Geschwind & Galaburda 1987) and may also be associated with enhanced spatial cognition in adult males (Annett 1992); however, findings from longitudinal studies are inconsistent and hard to interpret in simple terms (see, e.g., Grimshaw et al. 1995).

An indirect test of the hypothesis linking fetal T levels (and thus, by implication, postnatal basal T) with subsequent handedness involves assessment of interactions between hand preference and immune status in children or adults. This follows from the well-known association between elevated T and suppression of immune function in vertebrates generally (Zuk 1996). T is implicated in the development of male secondary sexual characteristics, such as the red comb of the cockerel, and it has been proposed that, despite their immunosuppressive effects, high T levels are maintained in males as a result of female sexual selection for male ornamentation. Other things being equal, we would therefore expect prolonged elevated T levels to be associated with poorer health status even in humans, although the relationship is not a simple one, because some individuals will have compensatingly high baseline levels of immunocompetence.

It follows from this that we would also expect to find, in “honour subcultures,” a suppressive effect of chronically elevated T levels on immune status and thus on health, although, among individuals within the population, great variability may still exist in the strength of any such effect. However, unless the chronically elevated T levels characterised as the product of an “honour subculture” among young adult males in the reciprocal model somehow influence the fetal hormonal environment of their offspring, we would not expect to see atypical patterns of adult male hand preference or other measures of cerebral dominance. If hand preference or any other measures of cerebral dominance were among the measures recorded in either of the large military samples discussed by M&B, then perhaps this further, indirect test of the reciprocal model could be carried out using adult data from a single point in time. [See commentary of Coren, this issue.]

Would M&B elaborate on the social preconditions of honour subcultures? The sample of 4,462 army veterans among whom Mazur (1995) found an apparent effect on T and on behavioural deviance of participation in an inner-city, low-educational-attainment honour subculture is the same sample of 4,462 army veterans among whom Dabbs (1992), Booth and Dabbs (1993), and Booth and Osgood (1993) found correlations between elevated T and low occupational status, marital dissatisfaction, and criminality. These correlations could therefore be due to latent socio-

economic variables (mediated by the interaction of age, race, and educational level, in the terms of the veterans' survey), rather than to the effects of T on behaviour.

Dominance, sexual activity, and sexual emotions

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Abstract: Men's interest in sex partners' status traits and commitment (investment thoughts) declines with number of sex partners and permissiveness of attitudes; women's investment thoughts do not seem to decline. Testosterone, dominance, sexual attractiveness, and number of sex partners are correlated in men but not in women. It is plausible that these sex differences are part of sexually dimorphic feedback systems. This type of feedback is consistent with both reciprocal and basal models of testosterone.

Mazur & Booth (M&B) have made an important contribution to the study of dominance and testosterone (T). Their distinction between dominance and aggression and their comparison of basal and reciprocal models are especially useful. Also noteworthy is the lack of consistent evidence for a correlation between T and dominance or between T and competition in women. Studies of people's interest in their partner's investment potential (Buss & Schmitt 1993) reveal a similar sex difference. Men with more permissive attitudes and sex partners show less interest in target persons' status traits, and report more willingness to copulate with target persons solely on the basis of a visual inspection of physical attributes, than do men with fewer partners and less permissive attitudes (Townsend & Wasserman 1997a).

Women's interest in status traits and reported willingness to copulate on the basis of a visual inspection were not associated with their sexual attitudes or number of sex partners. In an independent study, women were much more likely than men to worry about partners' willingness to invest and to have thoughts about marriage even when they had voluntarily decided not to get emotionally involved with a particular partner. Women's agreement that they had such reactions to casual sexual relations was not associated with their sexual attitudes and number of sex partners. Men's agreement, however, was significantly and negatively associated with their number of partners and permissiveness of attitudes (Townsend 1995; Townsend & Wasserman 1997b). In contrast to these measures, researchers have consistently reported *comparable* correlations for men and women between sexual behavior and conventional measures of sexual attitudes (Simpson & Gangestad 1991; 1992; Townsend 1995).

Thus, if all these measures are valid, compared to conventional measures of sexual attitudes, women's reported concern about partner's ability and willingness to invest may covary less with other factors in women's sex lives. For women, the incidence of investment thoughts as reactions to new and ongoing sexual relationships may be relatively constant, whereas, for men, the incidence of thoughts about partners' potential for long-term relationships appears to be negatively associated with greater numbers of partners (Townsend 1987; 1995; Townsend & Wasserman 1997a; 1997b).

As with most of the research on T and dominance, my studies were cross-sectional, so they cannot establish whether men who report more casual relationships always had more permissive attitudes and emotional reactions to coitus or acquired them as they gained sexual experience. It is likely, however, that the attitudes and thoughts and feelings of men with more experience in casual relations diverge from those of less experienced men (and from those of women) as the former gain familiarity, confidence, and experience. This interpretation is supported by several lines of evidence. First, men's reported willingness to have sex with attractive partners suggests that most men have sufficient desire to lead to multiple casual encounters if opportunity allows (Townsend 1987; 1992; 1993b; 1995; Townsend et al. 1995). Hence, the

crucial determinant of gay men's reporting larger numbers of sex partners than do heterosexual men is arguably a difference of opportunity rather than desire (Bailey et al. 1994; Ellis & Symons 1990; Symons 1979). Second, a study of West German school children indicated that at age 11 both males and females had egalitarian sexual attitudes (Schoof-Tams et al. 1976). As males gained sexual experience, however, they exhibited a greater desire for and acceptance of casual sexual relations. As females gained experience, they increasingly wanted to confine sexual relations to a loving relationship. Third, Benedict's study (1995) of male athletes suggested that their sexual experiences afford them greater confidence, familiarity, and acceptance of casual relations. Benedict (1995) argues that through their multiple sexual experiences with fans, star athletes and other male celebrities become so confident and convinced that women want low-investment sex with them that they misconstrue the cues when women are unwilling. Such celebrities therefore have a high risk of charges of rape and sexual harassment.

Although sexual activity in both sexes correlates with T levels (Udry & Billy 1987), dominance appears to correlate with sexual attractiveness and number of sex partners in men but not women (Mazur et al. 1994; Perussé 1993; Sadalla et al. 1987; Townsend 1993b; Townsend et al. 1995). Kinsey et al. (1953) concluded that men's thoughts, fantasies, and emotions motivated them to engage in low-investment relations with a variety of partners. More recent studies have supported this view (Bailey et al. 1993; Ellis & Symons 1990; Weinrich 1988). Although both sexes can experience lust and love, the desire for love (i.e., investment) tends to be an autonomous, appetitive desire in women but not in men, whereas lust tends to be an autonomous, appetitive desire in men but not in women (Ellis & Symons 1990; Weinrich 1988). If this view is correct, we would expect the feedback that men and women receive when they engage in casual relations to differ. For women, these feelings and memories can be very negative; for men, they are more often positive, and they stimulate men to attempt to repeat the experience (Ellis & Symons 1990; Kinsey et al. 1953; Townsend 1987; 1995; Weinrich 1988). Because of the correlation between T and sexual interest and activity generally, and between T, dominance, and number of sex partners in men, it is plausible that this type of feedback occurs, and reported sex differences in investment thoughts, number of sex partners, and correlations between dominance and T are part of this differential feedback system. This type of feedback would be more consistent with a reciprocal than a basal model of T, but basal levels of T would also be significant predictors.

Authors' Response

Old issues and new perspectives on testosterone research

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Abstract: This Response focuses on the strength of the testosterone (T) dominance relationship, the circumstances under which aggression accompanies dominance, the viability of the basal model, mediators and moderators of the T-dominance relationship, and the research that is needed.

The commentaries on our target article were thoughtful and well-crafted, and extend our thinking about tes-

tosterone (T) and dominance. They can be classified into one or more of five topics around which we will organize our Response: (1) Is the case for the T-dominance relationship overstated? (2) When is dominance accompanied by aggression? (3) Is the basal model a viable one? (4) What mechanisms mediate and moderate the relationship between T and dominance? (5) What research is needed to make significant advances in knowledge regarding T, behavior, and social relations?

R1. Is the case for T-dominance relationship overstated?

Although none of the commentators denied some relationship between testosterone and behavior, several suggested that the case was overstated in the target article because our literature review was selective (**O'Carroll** and **Hines**) and the effects of T are so small as to be insignificant (**Denenberg**).

Although our review was selective, we think our criteria for selecting studies were valid, given the purpose of the target article. We omitted clinical studies because of their focus on people with problems (e.g., hypogonadism): they are likely to involve atypical effects on dominance. Moreover, clinical studies are often based on very small samples; single individuals can accordingly make a great deal of difference in the outcome. We may have missed a hormone study here and there, but we are pleased that no commentator uncovers a body of literature we missed.

We also omitted nonhuman studies except when they were especially pertinent (e.g., **Johnsen & Zuk** 1995). The nonhuman literature is large and instructive and a good source of hypotheses, but it is difficult to extrapolate to humans because of cultural, social, cognitive, and physiological differences. **Oliveira's** comparison of hormone-behavior mechanisms in humans and fish is interesting but takes us outside our area of expertise. We agree with **Oliveira** and with **Kacelnik & Norris** that our reciprocal theory is similar to the "challenge hypothesis" that **Wingfield** and his colleagues have put forward for birds (**Wingfield** 1984; **Wingfield et al.** 1990). These theoretical lines have apparently developed independently (**Mazur** 1976; 1983; 1985), providing an excellent opportunity for students of animal and human behavior to integrate them into a general model that applies across vertebrate species. An important implication is that T-dominance mechanisms and associated status processes must operate in portions of the brain that are far more primitive than the human neocortex (**Mazur** 1973).

As to the argument that the relationship between T and behavior is trivial, we make two points: in the competition studies, which are central to our analysis of the reciprocal model, it is not uncommon to obtain pre-event rises in T upwards of 40%. We do not regard a change of that magnitude to be insignificant, nor would most readers. In the cross-sectional studies integral to our analysis of the basal model, T is typically correlated with dominance-related behavior by coefficients from $r = .10$ to $.30$. Although the amount of variance explained is very small, a correlation that high is not uncommon for a single factor (e.g., T) in large cross-sectional studies, given the number and complexity of factors that affect our behavior and social relationships. What is important is the amount of work done by T. As we illustrate in the target article, the odds of a

person experiencing a divorce are 50% greater in a high T individual than in a man with low T. When an event is relatively rare (e.g., only 5% of marriages dissolve each year), there can be a low correlation but a large effect size. The importance of effect size is illustrated in the widespread use of aspirin to reduce the risk of heart attacks. In a randomized experiment in which over 20,000 physicians across the country received either an aspirin or a placebo, the size of the effect was so great in lowering the risk of heart attacks that researchers terminated the study early because withholding treatment from those in the control group would have been unethical (Steering Committee of the Physicians' Health Study Research Group, 1988). It is interesting that the correlation between treatment and outcome is only $r = .03$ (**Rosenthal** 1994).

One final point in deciding whether the relationship is trivial concerns whether there is evidence that the relationship is ever reversed (i.e., T has a negative relationship with dominance). **Kenrick & Barr** point out that the link between T and dominance is rarely found to be reversed, suggesting that the relationship we propose is viable.

O'Carroll cites low reliability of T as a problem. The fact that we get consistent results from single measures suggests that T's relation to behavior may be more robust than most studies indicate. Fortunately, contemporary studies are collecting two and three measures at a time, which will bring the reliability up to acceptable levels.

A related issue is whether pencil and paper tests adequately measure dominance behavior (**Grant** and **Campbell et al.**). Our view is that they usually do not; we have accordingly discounted several published failures to link T to dominance as measured by pencil and paper tests. Obviously, giving more credence to these tests weakens our case for the T-behavior link.

We all agree that experimental tests are needed to compare the effects of T and placebo on dominating behavior. In our target article we cite one small experimental verification by **Kouri et al.** (1995) that is based on only six subjects. Continuing this work, **Kouri and Pope** (1997) have recently reported results for another 16 subjects. As before, administered T increased "aggressive" behavior in a laboratory task. However, the authors report that conventional rating scales such as the **Buss-Durke Hostility Inventory** appear insensitive to the effects of the testosterone.

Rather than overstating the case, state-of-the-art knowledge reveals that the relationship of T, individual behavior, and social relations is more complex than early researchers realized. Our inquiry, and that of others, is guided by a systems model in which the links among environmental (which in the case of humans is largely social), behavioral, and biological influences are bidirectional (e.g., **Cairns et al.** 1990; **Gottlieb** 1991). Biological functions (in this case, T production) set the stage for behavioral responses to challenges from the environment. Environmental challenges can also alter behavior, which in turn affects hormone production (a point with which **Snowdon** would no doubt agree). An important feature of this model is that hormone-behavior relationships are not always linear. That is, T's ability to set particular behavior into motion may be increased or decreased depending on the nature of the environmental challenges in the immediate or distant past. For example, in the reciprocal model, as exemplified by the competition studies, T will not rise in response to a challenge when the outcome is a certainty or there is little by

way of status or resources at stake. On the other hand, T rises sharply when the outcome is uncertain and the stakes are high. In the basal model, we hypothesize that T-related behavior may be decreased and is rarely accompanied by aggression when there is heavy parental investment early in the individual's life, as suggested by **Archer**. Early parental investment may be a pivotal factor in explaining why many men with high T have successful marriages and careers: they handle challenges with equanimity and prosocial behavior rather than dominance. Part of the reason they are successful is that they read social cues correctly (**Mueller**), a trait related to early parental investment. However, even well-socialized individuals may resort to aggression when they become desperate because their paths to status and resources are otherwise blocked (**Kenrick & Barr, Mueller**). In the systems model we suggest that the effect of T in enhancing or muting dominance may be organizational and occurs perinatally (Campbell et al.), a view shared by **Collaer** as well as **Constantino**.

R2. When is dominance accompanied by aggression?

A number of commentators expressed concern about our distinction between dominance and aggression and several suggested ways to clarify and improve upon our efforts. **Archer** assumes that our definition of dominance removes it from the acts of competing for resources, protecting the young, and defending territory, which he calls aggression because of the accompanying threat of physical force. He is also concerned that dominance must be motivated and that this is somehow connected to a motive "to strive for dominance." The motivational aspect of his argument is never made clear. We assume that most behavior is motivated and we fail to understand its relevance to our argument. Perhaps **Archer** is concerned that a motive to dominate does not carry the threat of physical force. It certainly can, and **Mueller** argues persuasively that this combination is often valuable in achieving or maintaining high status. But we believe that threatening physical force and actually intending to harm a conspecific (our definition of aggression) are quite different things. Acts of dominance may carry the threat of physical force, but the intent to cause harm implies damaging the individual so that they may die. We suggest that physical force associated with dominance is typically ritualized so that no serious harm comes to the dominated individual.

Several commentators, although they did not take issue with our distinction between dominance and aggression, suggested factors likely to influence the expression of dominance and aggression. **Cohen** richly illustrates how the social environment may influence whether aggression accompanies T-related dominance. Environments fraught with threat are more likely to call out aggressive behavior than those which are not (see also **Mueller**). Environments that call for prosocial responses (boardrooms) are more likely to see expressions of dominance not accompanied by aggression than are those for which prosocial responses are not expected (prisons). Cultures that have severe punishments for aggression and those that have resources more equitably distributed may see less aggression accompanying dominance than those which are more tolerant of aggression and provide few opportunities for obtaining food, sexual partners, and other resources. Moreover, soci-

eties that are more individualistic would be more tolerant of dominance accompanied by aggression than societies that are more collective, with a stress on group esteem and harmony. Clearly, these ideas should be incorporated into future research and are consistent with **Chambers's** suggestion that whether or not aggression accompanies dominance behavior is related to social learning; they are also compatible with the **Flinn et al.** research showing that factors which correlate with that basal T differ in a Caribbean society.

Bribiescas suggests that nonwestern populations show consistently lower T levels than American males. Wortheman and Konner (1987), however, report that !Kung hunter-gatherer men have T levels comparable to those established for western populations. **Bribiescas** goes on to suggest that diet may account for the relationship between basal T and dominance in the honor subculture because fat intake is related to higher testosterone levels. If this explained the relatively high T among young, poorly educated black males, we would expect older, poorly educated black males to have higher T than comparable white men, which is not the case.

Constantino suggests that very different biological mechanisms may be involved in the expression of aggression and of dominance. He proposes that serotonin is related to severe, unrestrained aggression whereas T is more related to dominance-related assertiveness. We know of no human data on both neurotransmitters and T, but such studies are certainly warranted. **Fox** also draws our attention to the importance of examining serotonin and T simultaneously to increase our understanding of the activators of dominance and aggression. The neurotransmitter may have a unique influence on impulse control, which could affect whether or not aggression accompanies dominance. He points out that the wide range of behaviors we link to dominance could result from genetic alcohol addiction, generalized anxiety, timidity (both of which may involve another hormone, cortisol), and low intelligence, a view shared by **Collaer**.

Part of the problem in understanding when dominance is accompanied by aggression may be resolved by refining our definition of dominance as suggested by **Brain** and by **Grant**, who suggest that dominance may be best understood as overt behavior intended to change the views or actions of another or as an unwillingness to change one's own attitudes or behavior at the instigation of another.

R3. Is the basal model a viable one?

Most of our commentators believe that behavior and the social environment affect T, but opinions about whether T affects behavior and social relations, as proposed in our basal model, were mixed – some reject the idea outright, others concede the idea has merit, and still others clearly accept the notion. **Hines** rejects the idea that T influences behavior and suggests that anyone who believes otherwise has "cognitive schemas" about race and sex that are not borne out by empirical evidence. **Constantino** agrees with **Hines** that our evidence is weak. The implications of the relationship of T to behavior in women is given thoughtful consideration by **Foss**.

Flinn et al. have concerns about the effect of T on behavior but concede that T may have a generalized "per-

missive effect” on the grounds that natural selection would not have resulted in a system where T is sensitive to social factors if T had no effect on behavior. **Collaer** suggests that whereas T or other androgens may play a minor role in influencing dominance in adulthood, T’s main effect on dominance is in the neurological organization during the prenatal or early postnatal period. **Archer** and **Christensen & Breedlove** echo this view, suggesting that any influence of T is largely a product of developmental or experiential history. We agree that the impact of basal T on adult behavior may be influenced by early social experiences or by T’s neurological organizing properties. The Udry et al. (1995) study of a sample of 351 women in their late 20s also supports such an interpretation. They found that the T level of the mother during the second trimester of pregnancy is as good a predictor of the gendered behavior of her female offspring as the daughter’s own T level as an adult. This finding is consistent with **Christensen & Breedlove’s** argument that if there are genetically influenced differences in T between the sexes, it is logical to believe that there are such influences within each sex. We hope that the extent to which T’s effect on behavior is due to circulating levels, early neurological organization caused by the mother’s or offspring’s T, or a combination of these factors will be clarified by research in the near future. On the basis of existing studies, however, we would argue that basal circulating levels continue to play a role.

Dabbs believes that basal levels are more important in understanding behavior than T change as it relates to day-to-day dominance behavior. He argues that day-to-day changes related to dominance are short-lived and entail minor fluctuations in T relative to the effects of interindividual differences in basal T found in the population. He also suggests that the definition of dominance (gaining and maintaining status) is too narrow, pointing out that dominance may benefit others by conferring status and resources. Moreover, Dabbs alerts us to situations where T appears to be related to factors unrelated to dominance behavior or aggression. For example, he reports a study showing that the father’s T drops immediately following the birth of his child. In many cultures, becoming a father is a sign of achievement, a time when we would expect an increase in T.

We are not convinced by arguments that the basal model is not viable; the reciprocal model simply overlays the basal model. We do not reject the suggestion that perinatal biological factors may play a role in organizing responses to circulating levels of T or in establishing a predisposition to be dominant. In addition, early social experiences may be especially powerful in decreasing or exacerbating the influence of basal T on behavior on a day-to-day basis. Finally, we take to heart **Dabb’s** admonition that we are a long way from understanding all the effects of circulating T on behavior, as far as we are from understanding T’s role in day-to-day competition.

We appreciate the **Kenrick & Barr** explanation for why testosterone research arouses people, while other hormones with equal or greater effects on behavior (e.g., adrenaline) hardly raise an eyebrow. They suggest that people worry that T-behavior relationships may be used to justify male violence and the exclusion of women from high positions. They effectively deal with each of these arguments. We urge the concerned reader to re-read the Kenrick & Barr commentary.

R4. What factors mediate or moderate the relationship between T and dominance?

Perhaps most interesting in the Commentary are the numerous proposals concerning factors that mediate and moderate the relationships of T, behavior, and social relations. Suggestions range from mechanisms by which T rises in anticipation of competition to the role of sexual activity in explaining T’s relationship to divorce.

Kemper proposes that the precompetition rise in T is a result of fantasy rehearsals of the anticipated conflict. We have heard coaches encouraging players to re-enact events or particular plays that resulted in success. Even when coaches do not use this technique, players engage in such mental rehearsals to cope with anxiety about the outcome. A study that taps competitors’ reports on the incidence and nature of such pre-game imagery as it relates to T production would help us understand this potential explanatory factor.

Cashdan suggests that men’s tendency toward domination and antisocial behavior is not the factor that accounts for the relationship between basal T and divorce; rather, it is women’s T which is at work here. She cites evidence that women with higher T levels have more sexual partners and need less commitment from men before engaging in sex. This, coupled with men’s well-known tendency to extramarital affairs (e.g., Smith 1991) may be the reason for the higher divorce rate reported in the target article. A study of women’s T and marital success would help to resolve this issue.

A variation on this view is offered by **Townsend**, who proposes that whereas T is related to interest in sex and number of partners for both men and women, the response to heightened activity would be different for the two sexes. His research indicates that women are less satisfied with relationships that do not entail relationship investment, whereas for men relationship investment is of little concern. Although there is no negative reinforcement for men having multiple partners, T is more apt to be expressed in dominance acts such as rape and sexual harassment.

Christensen & Breedlove report nonhuman studies indicating that maternal stress during pregnancy may moderate the effect of genetic predispositions toward masculine behavior on the part of offspring, despite normal levels of plasma T. In humans this would mean that maternal stress (which is known to suppress T production in humans) during the second trimester of pregnancy may decrease the relation between T and dominance behavior in offspring. **Chambers** reports that prenatal T exposure in nonhumans may reduce circulating T at receptor sites, decrease the number of cellular receptors, or decrease the receptors’ affinity for the hormone – in short, reduce target tissue sensitivity to circulating T. It is reasonable to expect a similar relationship in humans.

Mealey’s commentary illustrates gene-environmental interactions that expand the target article’s thesis and moves thinking away from the simplistic gene-versus-environmental explanations. For example, she indicates that the age at which pubertal T increases varies the social responses of others so that individuals find themselves in a different social environment from peers and friends. The outcome may affect life course trajectories in ways that influence such factors as nonmarital child bearing, participation in a deviant subculture, and other experiences that have a great

impact on life course trajectories and life chances. Her discussion of feedback loops between T and behavior that may provoke the production of adrenal steroids which may in turn influence the onset of depression adds yet another dimension to the overall consideration of methods and paradigms for studying T and dominance.

Steele comments on the implications of the immunosuppressive effects of high T for the health of men in an honor subculture and their offspring. **Kacelnik & Norris** examine the impact of immunosuppressive effects as they relate to sexual signaling. Our reading of the very limited literature on T's suppression of immune function is that the findings are not conclusive. Whereas T may suppress immunoglobulin production, its effect on lymphocytes is very much in question (e.g., see Kanda et al. 1996 and Paavonen 1994, cited in Kacelnik & Norris). Granger et al. (1998), using a military sample, indicate T has a positive relationship with the number of helper/inducer T cells (CO4s).

The suggestion to use handedness as an indirect test of T models is interesting and consistent with **Coren's** finding that left-handedness is associated with delinquency. Other factors that could be at work, such as living in a world of right-handed people, may have an effect that is independent of T. Also, the ease with which T can be measured now may make it less necessary to use surrogate measures.

With respect to **Steele's** query about whether the relationships between elevated T and low occupational status, marital dissatisfaction, and criminality could have been caused by socioeconomic variables mediated by age and race, the answer is no, with respect to occupational status and marital relations. We were able to remove much of the T-criminality relationship, however, by controlling for whether the person was married, employed full-time, and belonged to voluntary organizations. Thus, for some variables, the effects of T appear to transcend the usual social influences on such events.

DeCatanzaro & Spironello speculate that the relation between T and low marital quality and stability may be due to sexual satiation or frustration. This may be true in a few cases, but unlikely overall. Usually people who divorce or have unhappy marriages are troubled in other ways as well. Unstable marriages are apt to be characterized by high levels of conflict, low interaction, problems involving infidelity, drinking, spending money foolishly, and not spending time at home (Amato & Rogers 1997; Booth et al. 1985). Our research indicates that in some men high T is associated with a wide range of problems and that those individuals are the most likely to report low happiness and a greater likelihood of divorce. They are just not good marriage material.

R5. What research is needed to make significant advances in knowledge regarding T, behavior, and social relations?

The commentaries repeatedly illustrate how little we know about T, behavior, and social relations. **Dabbs** proposes that the definition of dominance needs to be refined and elaborated at the same time. It needs to be refined so that we better understand when antisocial behavior, aggression, courting, and risk taking are part of a dominant act and when they are not. The definition needs to be expanded to include a range of behaviors such as conversational pat-

terns, approaching strangers, and resisting the influence of others. Is timidity related to testosterone? or to cortisol, as others have suggested (e.g., Kagan et al. 1988)? Broad-based theory-driven studies on women and children as well as men are clearly needed.

Many commentaries stressed that perinatal T organizes the tendency to exhibit dominant behavior and whether or not dominant behavior is accompanied by aggression. This is important in furthering our understanding of the basal model. We know of no studies on perinatal T's role in organizing dominant behavior. This would require assessing T in mothers during the second trimester, T in children in the first two years of life, and the behavior of children over the first three years of life. Such a study is clearly needed. Also important will be research on early child-rearing practices as they relate to parental and offspring T. These would help assess the role of early experience in determining the T-behavior relationship in children. Booth is now directing a longitudinal study of 400 families in which parents and children are interviewed and given a variety of psychological tests in conjunction with an analysis of saliva samples. Results should be available in about two years.

Research linking T and dominance in women is scant, but there are important reasons to pursue this line of inquiry. **Grant** reports a series of studies showing that dominant women are more likely to conceive sons. Once born, the sons of these dominant women are treated in ways ensuring that higher dominance is passed on, thereby perpetuating the sex differences. There was the contrary suggestion that T was not instrumental in female behavior because women restrict their competition to things (e.g., food) that have no status implications (**Campbell et al.**). Grant's finding is consistent with the Udry et al. (1995) study showing that testosterone is related to gendered behavior in 351 women but Campbell's is not. **Kemper** suggests that we too often dismiss the possibility that women's response to competition may be similar to that of men and cites evidence for this. We agree that judgment must await more research. There are good reasons to expect dominance-seeking in women to be as variable as it is in men. Research on women is needed to gain even a rudimentary understanding of the relation between hormones and dominance behavior in women. Both reciprocal and basal models need to be systematically tested. [See also Fitch & Denenberg, this issue.]

Knowledge about women will inform male models as well. The fact that competing females report higher levels of stress than men (Dohrenwend & Dohrenwend 1976; Mirowsky & Ross 1995) and are more nurturing than men, both within family settings (Thompson & Walker 1989) and outside them (Maccoby & Jacklin 1994), suggests that the role of T in social relations may be more selective. For example, Cashdan (1995) finds that T is positively related to dominance in females but negatively related to status based on being accepted by other women. Furthermore, there is evidence that social controls such as parental permissiveness blunt the relationship between T and risky or nonconforming behavior in females to a greater extent than in males. Udry (1988) has demonstrated that social controls nearly eliminate the relationship between T and sexual activity among adolescent girls, whereas these same controls have little impact on the T-sexual behavior link among males.

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[Note: the letter 'a' before author's initials stands for Mazur and Booth's target article references, and the letter 'r' for Booth and Mazur's response article references.]

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