TESTOSTERONE'S BUM RAP

Testosterone is secreted by the testes as the final step in the "hypothalamic/pituitary/testicular" axis; it has effects on cells throughout the body (including neurons, of course). And testosterone is everyone's usual suspect when it comes to the hormonal causes of aggression.

Correlation and Causality

Why is it that throughout the animal kingdom, and in every human culture, males account for most aggression and violence? Well, what about testosterone and some related hormones (collectively called "androgens," a term that, unless otherwise noted, I will use simplistically as synonymous with "testosterone")? In nearly all species males have more circulating testosterone than do females (who secrete small amounts of androgens from the adrenal glands). Moreover, male aggression is most prevalent when testosterone levels are highest (adolescence, and during mating season in seasonal breeders).

Thus, testosterone and aggression are linked. Furthermore, there are particularly high levels of testosterone receptors in the amygdala, in the way station by which it projects to the rest of the brain (the bed nucleus of the stria terminalis), and in its major targets (the hypothalamus, the central gray of the midbrain, and the frontal cortex). But these are merely correlative data. Showing that testosterone *causes* aggression requires a "subtraction" plus a "replacement" experiment. Subtraction—castrate a male. Do levels of aggression decrease? Yes (including in humans). This shows that something coming from the testes causes aggression. Is it testosterone? Replacement—give that castrated individual replacement testosterone. Do precastration levels of aggression return? Yes (including in humans).

Thus, testosterone causes aggression. Time to see how wrong that is.

The first hint of a complication comes after castration, when average levels of aggression plummet in every species. But, crucially, not to zero. Well, maybe the castration wasn't perfect, you missed some bits of testes. Or maybe enough of the minor adrenal androgens are secreted to maintain the aggression. But no—even when testosterone and androgens are completely eliminated, some aggression remains. Thus, some male aggression is testosterone independent.*

This point is driven home by castration of some sexual offenders, a legal procedure in a few states.[1] This is accomplished with "chemical castration," administration of drugs that either inhibit testosterone production or block testosterone receptors.* Castration decreases sexual urges in the subset of sex offenders with intense, obsessive, and pathological urges. But otherwise castration doesn't decrease recidivism rates; as stated in one meta-analysis, "hostile rapists and those who commit sex crimes motivated by power or anger are not amenable to treatment with [the antiandrogenic drugs]."

This leads to a hugely informative point: the more experience a male had being aggressive prior to castration, the more aggression continues afterward. In other words, the less his being aggressive in the future requires testosterone and the more it's a function of social learning.

On to the next issue that lessens the primacy of testosterone: What do individual levels of testosterone have to do with aggression? If one person has higher testosterone levels than another, or higher levels this week than last, are they more likely to be aggressive?

Initially the answer seemed to be yes, as studies showed correlation between individual differences in testosterone levels and levels of aggression. In a typical study, higher testosterone levels would be observed in those male prisoners with higher rates of aggression. But being aggressive *stimulates* testosterone secretion; no wonder more aggressive individuals had higher levels. Such studies couldn't disentangle chickens and eggs.

Thus, a better question is whether differences in testosterone levels among individuals *predict* who *will be* aggressive. And among birds, fish, mammals, and especially other primates, the answer is generally no. This has been studied extensively in humans, examining a variety of measures of aggression. And the answer is clear. To quote the British endocrinologist John Archer in a definitive 2006 review, "There is a weak and inconsistent

association between testosterone levels and aggression in [human] adults, and . . . administration of testosterone to volunteers typically does not increase their aggression." The brain doesn't pay attention to fluctuations of testosterone levels within the normal range.[2]

(Things differ when levels are made "supraphysiological"—higher than the body normally generates. This is the world of athletes and bodybuilders abusing high-dose testosterone-like anabolic steroids; in that situation risk of aggression does increase. Two complications: it's not random who would *choose* to take these drugs, and abusers are often already predisposed toward aggression; supraphysiological levels of androgens generate anxiety and paranoia, and increased aggression may be secondary to that.)[3]

Thus, aggression is typically more about social learning than about testosterone, and differing levels of testosterone generally can't explain why some individuals are more aggressive than others. So what does testosterone actually do to behavior?

Subtleties of Testosterone Effects

When looking at faces expressing strong emotions, we tend to make microexpressions that mimic them; testosterone decreases such empathic mimicry.*[4] Moreover, testosterone makes people less adept at identifying emotions by looking at people's eyes, and faces of strangers activate the amygdala more than familiar ones and are rated as less trustworthy.

Testosterone also increases confidence and optimism, while decreasing fear and anxiety.[5] This explains the "winner" effect in lab animals, where winning a fight increases an animal's willingness to participate in, and its success in, another such interaction. Part of the increased success probably reflects the fact that winning stimulates testosterone secretion, which increases glucose delivery and metabolism in the animal's muscles and makes his pheromones smell scarier. Moreover, winning increases the number of testosterone receptors in the bed nucleus of the stria terminalis (the way station through which the amygdala communicates with the rest of the brain), increasing its sensitivity to the hormone. Success in everything from athletics to chess to the stock market boosts testosterone levels.

Confident and optimistic. Well, endless self-help books urge us to be precisely that. But testosterone makes people *over*confident and *overly* optimistic, with bad consequences. In one study, pairs of subjects could consult each other before making individual choices in a task. Testosterone made subjects more likely to think their opinion was correct and to ignore input from their partner. Testosterone makes people cocky, egocentric, and narcissistic.[6]

Testosterone boosts impulsivity and risk taking, making people do the easier thing when it's the dumb-ass thing to do.[7] Testosterone does this by decreasing activity in the prefrontal cortex and its functional coupling to the amygdala and increasing amygdaloid coupling with the thalamus—the source of that shortcut path of sensory information into the amygdala. Thus, more influence by split-second, low-accuracy inputs and less by the let's-stop-and-think-about-this frontal cortex.

Being fearless, overconfident, and delusionally optimistic sure feels good. No surprise, then, that testosterone can be pleasurable. Rats will work (by pressing levers) to be infused with testosterone and show "conditioned place preference," returning to a random corner of the cage where infusions occur. "I don't know why, but I feel good whenever I stand there."[8,9]

The underlying neurobiology fits perfectly. Dopamine is needed for place-preference conditioning to occur, and testosterone increases activity in the ventral tegmentum, the source of those mesolimbic and mesocortical dopamine projections. Moreover, conditioned place preference is induced when testosterone is infused directly into the nucleus accumbens, the ventral tegmentum's main projection target. When a rat wins a fight, the number of testosterone receptors increases in the ventral tegmentum and accumbens, increasing sensitivity to the hormone's feel-good effects.[10]

So testosterone does subtle things to behavior. Nonetheless, this doesn't tell us much because everything can be interpreted every which way. Testosterone increases anxiety—you feel threatened and become more reactively aggressive. Testosterone decreases anxiety—you feel cocky and overconfident, become more preemptively aggressive. Testosterone increases risk taking—"Hey, let's gamble and invade." Testosterone increases risk taking—"Hey, let's gamble and make a peace offer." Testosterone makes you

feel good—"Let's start another fight, since the last one went swell." Testosterone makes you feel good—"Let's all hold hands."

It's a crucial unifying concept that testosterone's effects are hugely context dependent.

Contingent Testosterone Effects

This context dependency means that rather than causing X, testosterone amplifies the power of something else to cause X.

A classic example comes from a 1977 study of groups of male talapoin monkeys.[11] Testosterone was administered to the middle-ranking male in each group (say, rank number 3 out of five), increasing their levels of aggression. Does this mean that these guys, stoked on 'roids, started challenging numbers 1 and 2 in the hierarchy? No. They became aggressive jerks to poor numbers 4 and 5. Testosterone did not create new social patterns of aggression; it exaggerated preexisting ones.

In human studies testosterone didn't raise baseline activity in the amygdala; it boosted the amygdala's response and heart-rate reactivity to angry faces (but not to happy or neutral ones). Similarly, testosterone did not make subjects more selfish and uncooperative in an economic game; it made them more punitive when provoked by being treated poorly, enhancing "vengeful reactive aggression."[12]

The context dependency also occurs on the neurobiological level, in that the hormone shortens the refractory period of neurons in the amygdala and amygdaloid targets in the hypothalamus.[13] Recall that the refractory period comes in neurons after action potentials. This is when the neuron's resting potential is hyperpolarized (i.e., when it is more negatively charged than usual), making the neuron less excitable, producing a period of silence after the action potential. Thus, shorter refractory periods mean a higher rate of action potentials. So is testosterone causing action potentials in these neurons? No. It's causing them to fire at a faster rate *if* they are stimulated by something else. Similarly, testosterone increases amygdala response to angry faces, but not to other sorts. Thus, if the amygdala is already responding to some realm of social learning, testosterone ups the volume.

A Key Synthesis: The Challenge Hypothesis

Thus, testosterone's actions are contingent and amplifying, exacerbating preexisting tendencies toward aggression rather than creating aggression out of thin air. This picture inspired the "challenge hypothesis," a wonderfully unifying conceptualization of testosterone's actions.[14] As proposed in 1990 by the superb behavioral endocrinologist John Wingfield of the University of California at Davis, and colleagues, the idea is that rising testosterone levels increase aggression only at the time of a challenge. Which is precisely how things work.

The explains why basal levels of testosterone have little to do with subsequent aggression, and why increases in testosterone due to puberty, sexual stimulation, or the start of mating season don't increase aggression either.[15]

But things are different during challenges.[16] Among various primates, testosterone levels rise when a dominance hierarchy first forms or undergoes reorganization. Testosterone rises in humans in both individual and team sports competition, including basketball, wrestling, tennis, rugby, and judo; there's generally a rise in anticipation of the event and a larger one afterward, especially among winners.* Remarkably, *watching* your favorite team win raises testosterone levels, showing that the rise is less about muscle activity than about the psychology of dominance, identification, and self-esteem.

Most important, the rise in testosterone after a challenge makes aggression more likely.[17] Think about this. Testosterone levels rise, reaching the brain. If this occurs because someone is challenging you, you head in the direction of aggression. If an identical rise occurs because days are lengthening and mating season is approaching, you decide to fly a thousand miles to your breeding grounds. And if the same occurs because of puberty, you get stupid and giggly around that girl who plays clarinet in the band. The context dependency is remarkable.*[18]

The challenge hypothesis has a second part to it. When testosterone rises after a challenge, it doesn't prompt aggression. Instead it prompts *whatever behaviors are needed to maintain status*. This changes things enormously.

Well, maybe not, since maintaining status for, say, male primates consists mostly of aggression or threats of it—from slashing your opponent to giving

a “You have no idea who you’re screwing with” stare.[19]

And now for some flabbergastingly important research. What happens if defending your status requires you to be nice? This was explored in a study by Christoph Eisenegger and Ernst Fehr of the University of Zurich.[20] Participants played the Ultimatum Game (introduced in chapter 2), where you decide how to split money between you and another player. The other person can accept the split or reject it, in which case neither of you gets anything. Prior research had shown that when someone’s offer is rejected, they feel dissed, subordinated, especially if news of that carries into future rounds with other players. In other words, in this scenario status and reputation rest on being fair.

And what happens when subjects were given testosterone beforehand? *People made more generous offers.* What the hormone makes you do depends on what counts as being studly. This requires some fancy neuroendocrine wiring that is sensitive to social learning. You couldn’t ask for a finding more counter to testosterone’s reputation.

The study contained a slick additional finding that further separated testosterone myth from reality. As per usual, subjects got either testosterone or saline, without knowing which. Subjects who believed it was testosterone (independent of whether it actually was) made less generous offers. In other words, testosterone doesn’t necessarily make you behave in a crappy manner, but *believing* that it does and that you’re drowning in the stuff makes you behave in a crappy manner.

Additional studies show that testosterone promotes prosociality in the right setting. In one, under circumstances where someone’s sense of pride rides on honesty, testosterone decreased men’s cheating in a game. In another, subjects decided how much of a sum of money they would keep and how much they would publicly contribute to a common pool shared by all the players; testosterone made most subjects more prosocial.[21]

What does this mean? Testosterone makes us more willing to do what it takes to attain and maintain status. And the key point is what it takes. Engineer social circumstances right, and boosting testosterone levels during a challenge would make people compete like crazy to do the most acts of random kindness. In our world riddled with male violence, the problem isn’t

that testosterone can increase levels of aggression. The problem is the frequency with which we reward aggression.

SUMMARY

Testosterone has far less to do with aggression than most assume. Within the normal range, individual differences in testosterone levels don't predict who will be aggressive. Moreover, the more an organism has been aggressive, the less testosterone is needed for future aggression. When testosterone does play a role, it's facilitatory—testosterone does not "invent" aggression. It makes us more sensitive to triggers of aggression, particularly in those most prone to aggression. Also, rising testosterone levels foster aggression only during challenges to status. Finally, crucially, the rise in testosterone during a status challenge does not necessarily increase aggression; it increases whatever is needed to maintain status. In a world in which status is awarded for the best of our behaviors, testosterone would be the most prosocial hormone in existence.

SUMMARY AND SOME CONCLUSIONS

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