The Dual-Hormone Approach to Dominance and Status-seeking

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Abstract: This chapter describes the dual-hormone hypothesis, which provides an analytical framework for studying neuroendocrinological contributions to dominance and status-seeking. This hypothesis examines behaviour in terms of the interaction between testosterone and cortisol, endogenous steroids secreted by the hypothalamic-pituitary-gonadal axes and the hypothalamic-pituitary-adrenal, respectively. In particular, we review evidence for the view that the relationship between testosterone and dominance (an association that has received a great deal of popular and academic attention) depends on levels of cortisol. More specifically, several studies suggest that testosterone is positively related to dominance under conditions of low cortisol, but this relationship does not hold under conditions of high cortisol. We discuss this dual-hormone interaction in the context of a range of social behaviours, including, for instance, leadership, risk-taking, and aggression. We provide examples of departures from this typical dual-hormone pattern particularly for anti-social behaviours such as aggression, and also describe potential factors moderating the testosterone × cortisol interaction. We conclude with a discussion of important avenues for future research.

Testosterone is a steroid hormone secreted as the end-product of the hypothalamic-pituitary-gonadal (HPG) axis, and is widely theorised to trigger dominance and status-seeking tendencies that support or enhance reproductive behaviour (Mazur & Booth, 1998). At the biological level, testosterone guides important aspects of male sexual development, including the growth of the testes and penis, spermatogenesis, and the appearance of secondary sexual characteristics. At the psychological level, testosterone is predicted to enhance dominance-oriented behaviours, both in the research community and in popular culture. A central theory that has guided the field of social endocrinology – and the social endocrinology of dominance in particular - has been the challenge hypothesis, proposed by Wingfield and colleagues (1990), which explicitly linked endogenous testosterone concentrations and dominance behaviour in birds. This testosterone-dominance link has now been explored in a range of animals, and has also been proposed for humans (Mazur & Booth, 1998). The idea of a strong testosterone-dominance association is now so entrenched that testosterone is colloquially referred to as the "power hormone", and is believed to trigger dominance, aggression, competitiveness, and risk-seeking.

Certainly, there is an intuitive elegance to a single hormone exerting such widespread and profound behavioural effects. There are several approaches to understanding whether elevations in testosterone are a cause or consequence of dominance. For instance, elevated testosterone may follow the attainment of social dominance. Alternatively, social dominance may follow on high or rising levels of testosterone. A bidirectional relationship has also been proposed (Mazur, 1985), such that that high testosterone levels may facilitate social dominance, which further elevates testosterone levels.

While there are notable positive associations between testosterone and social dominance, especially under situations when status is challenged (Archer, 2006; Beehner et al., 2006; Giammanco et al., 2005; Gould & Ziegler, 2007), there are also a range of weak or

null results that render such a straightforward interpretation untenable (Carré & McCormick, 2008; Mehta & Josephs, 2010; Johnson et al., 2007; Josephs et al., 2006; van Bokhoven et al., 2006). Similar to the weak results for testosterone and dominance, a meta-analysis also did not find more than a weak association between testosterone and aggression (Archer et al., 2005).

In particular, a great deal of research has approached the effect of testosterone on behaviour by – perhaps reasonably - studying only testosterone. Studying only testosterone is theoretically and analytically expedient, as well as more resource-friendly. However, from a physiological standpoint it is more likely that the HPG-axis does not always function in isolation. Rather, testosterone may often exert its effects in concert with – or opposition to – other hormones to jointly regulate cognition and behaviour. Not considering other theoretically relevant hormones may account for several of the weak testosterone-behaviour links that have been noted. To this extent, a recent programme of research (Mehta & Josephs, 2010; Mehta & Prasad, 2015) has adopted a novel perspective on the psychological and social effects of testosterone, based on the principle that hormones do not act in isolation. This dual-hormone hypothesis predicts that the psychophysiological effects of testosterone are moderated by a second hormone – cortisol, an end-product of the hypothalamic-pituitary-adrenal (HPA) axis. Like testosterone, cortisol is a steroid hormone. It belongs to the family of glucocorticoids, and its primary physiological function is to metabolise sugar. Cortisol concentrations rise during experiences of physical or psychological stress (Dickerson & Kemeney, 2004), and also exert several other psychological effects. In the short term, cortisol induces some forms of cognitive impairment, such as weakening retrieval of information from long-term memory (Dominique et al., 2000), though it may also enable effective adaptation to uncertainty (Cueva et al., 2015; Plessow et al., 2017). Over longer periods, however, cortisol exposure can become maladaptive, leading to reductions in approach-

oriented behaviour such as risk-taking or increases in social avoidance (Kandasmy et al, 2014; Roelofs et al., 2009). On the other hand, low levels of cortisol have been linked to lower levels of stress and a general increase in approach-related behaviour and status attainment (Brown et al., 2006; Roelofs et al., 2009; Sherman et al., 2012).

Importantly, the HPA-axis and the HPG-axis are known to co-regulate one another in the brain, with downstream effects on the secretion of cortisol and testosterone (Viau, 2002). Furthermore, cortisol can inhibit testosterone function (Viau, 2002), and may thus be a suitable candidate hormone for a disruptor of the testosterone-behavior link. Within the framework of the dual-hormone hypothesis, then, the effects of testosterone are predicted to depend on concentrations of cortisol. For instance, two individuals who have similarly high levels of testosterone may have very different cortisol levels. According to the dual-hormone hypothesis, high cortisol levels should weaken the capacity of testosterone to influence status-seeking behaviours. Thus, the stereotypical effect of testosterone on dominance and status-seeking should be most likely to occur under low levels of cortisol. Studies that only consider testosterone produce analyses that collapse data across all cortisol levels, essentially diluting high testosterone concentrations in too wide a distribution of cortisol concentrations. This potentially accounts for the noisy, weak, or null testosterone-dominance associations that have repeatedly been observed.

The dual hormone hypothesis has a particular statistical translation – a statistical interaction term representing the product of testosterone and cortisol concentrations. According to this hypothesis, there should be a significant relationship between testosterone and the response variable in the direction of interest (e.g., a positive relationship between testosterone and dominant behaviour), but only under the condition that cortisol concentrations are low. If cortisol concentrations are high, the testosterone-behaviour association is expected to be attenuated. An analysis of the interaction yields a substantial

theoretical payoff in that it enables the generation of predictions that are both richer and more precise in terms of which outcomes will occur under which combinations of endocrine conditions.

The dual hormone hypothesis has been successfully applied to findings in several psychological domains closely related to dominance and social status. In the remainder of this chapter, we offer a brief overview of the evidence that has accrued in support of this hypothesis. We also discuss cases in which there is an interaction between testosterone and cortisol in predicting behaviour, but the pattern of the interaction deviates from the original predictions of the dual-hormone hypothesis (particularly for studies that examine aggressive and anti-social behaviour). We conclude with a discussion of future directions that will help refine and build this emerging literature.

Evidence in Support of the Dual-Hormone Hypothesis

Basal Hormone Profiles

Dominance: An early investigation of behaviour specifically in the context of the dual hormone hypothesis was aimed at understanding dominance (study 1, Mehta & Josephs, 2010). In this experiment, participants (n = 100) were split into same-sex dyads, and were randomly assigned to the role of a leader or a follower (participants later switched roles, such that followers were then observed as leaders). Leaders would give instructions for the followers to complete a standardised psychometric assessment of spatial reasoning. These interactions were filmed, and seven hypothesis-blind judges were later shown the footage and asked to rate the leader on various aspects of perceived dominance (e.g., the perceived dominance scale included terms such as “dominant”, “assertive”, “confident”, and “leader-like”). Aggregation and analysis of the ratings revealed the first evidence of what appeared to be a dual-hormone effect on perceived dominance (see Figure 1): Individuals who had higher baseline testosterone were also judged to be more dominant, but this effect was conditional –

it was apparent only in individuals with low cortisol. This association between testosterone and perceived dominance was not observed in individuals with high cortisol. Furthermore, the pattern was consistent across males and females.

An important feature of this experiment is the response variable: observer ratings of participant behaviour. The results suggest that the dual-hormone profile is *visible,* expressed in an individual's behaviour in forms that can be detected by others. This is an important feature because testosterone and cortisol also exert cognitive and behavioural effects that individuals themselves may not be aware of. For instance, in a study that administered testosterone to female participants, they were unable to introspect on its effects on them in self-reports, even though their behaviour changed (Eisenegger et al., 2010; van Honk et al., 2005). Because the psychological effects of testosterone need not be observable, either to the individual or to others, it is particularly impressive that the dual-hormone profile was discernible by unacquainted strangers at the behavioural level.

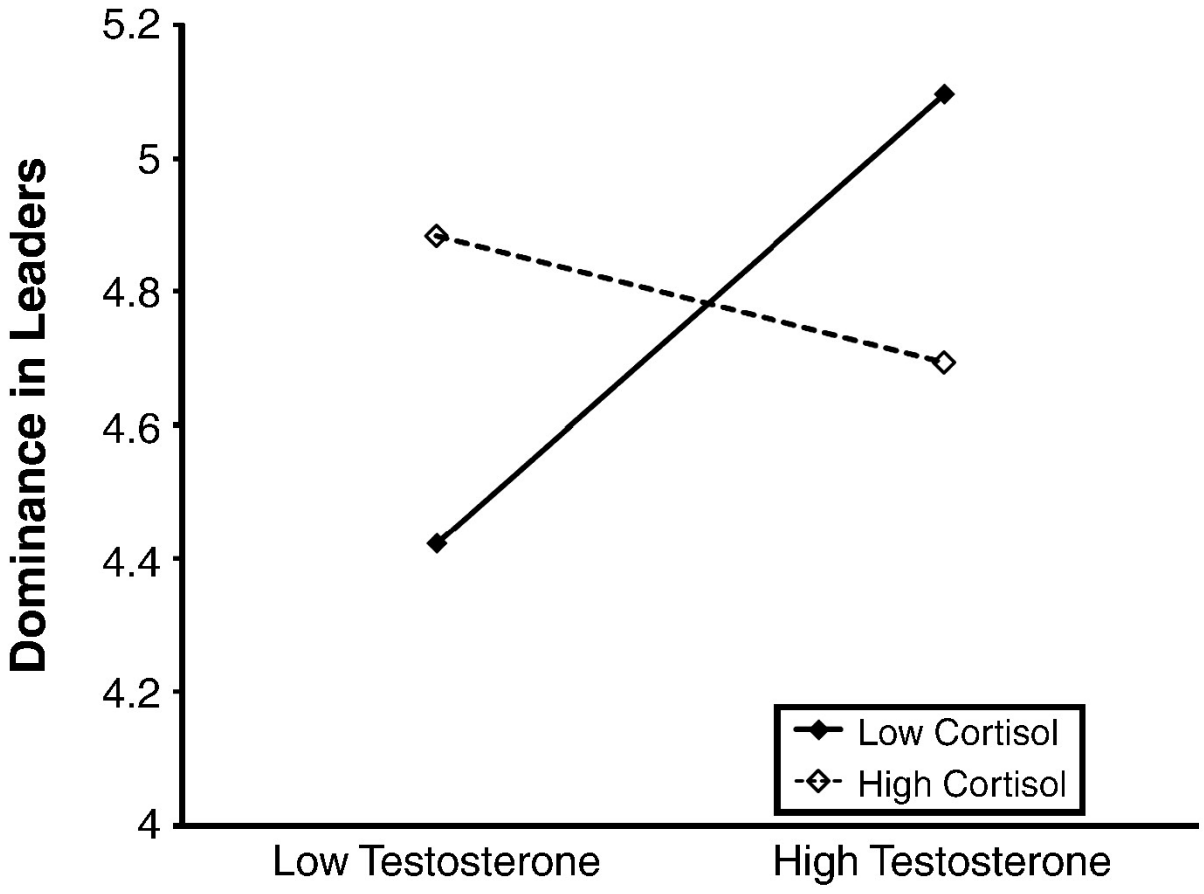

Figure 1: Dominance in leaders (average of observers' ratings on a 7-point scale) as a function of testosterone and cortisol levels. Hormone levels were measured at the beginning of the experiment. Low = 1 standard deviation below mean; high = 1 standard deviation above mean. The intercept and slopes from the multiple regression model were used to plot dominance scores one standard deviation above and below the means for testosterone and cortisol. *Figure and legend used from Mehta & Josephs (2010), with permission.*

Social Status: Ultimately, many testosterone-driven behaviours can be interpreted as means to attain higher social status. For example, there is growing evidence that dominant behaviour is positively related to status attainment (Anderson & Kilduff, 2009; Cheng & Tracy, 2013). Furthermore, status outside of the laboratory builds on a multiplicity of sustained social relationships, quite in contrast to many laboratory-based tests of dominance, which involve only dyadic communications, often between strangers. To that extent, some studies have begun investigating the joint role of testosterone and cortisol in regulating social status outside of the laboratory, accounting for both real-world significance and the fact that an individual who is dominant often exerts that dominance over groups of other individuals.

An examination of sportswomen in competitive collegiate teams revealed that perceived social status varied with basal concentrations of cortisol and testosterone (Edwards & Casto, 2013). In particular, participants (n = 74) were asked to rate other members of their specific teams in terms of perceptions of leadership capability. Consistent with the dual-hormone hypothesis, testosterone levels were positively associated with leadership ratings, but only when endogenous cortisol was low. Therefore, these hormones may regulate perceived leadership within social groups and competitive teams. This study extends the

results described in Mehta and Josephs (2010) by showing the effect of the testosterone × cortisol interaction on social status among individuals who are actually in the same group rather than just strangers in a brief lab setting.

Another indicator of status is the centrality and connectedness of an individual in a social network. A recent study (Ponzi et al., 2016) applied social network analysis to understand the link between network position and hormone levels in a sample of male athletes (n = 44). In a social network, the vertices and edges that form the network acquire particular psychological properties. Each individual represents a vertex in space, and the connections to or from other vertices (other individuals) represent social relationships. Importantly, the connections between vertices possess direction (that is, a connection from *A* to *B* is not the same as a connection from *B* to *A*). Features of these connections, such as their number and direction, are therefore interpretable in social terms. The number of outgoing connections from one vertex to others represents gregariousness. The number of incoming connections to one vertex from other vertices represents popularity. The number of times one vertex comes in between two other vertices represents betweenness. In line with the dual-hormone hypothesis, popularity was positively related to basal testosterone concentrations, but only if cortisol was low. Also consistent with the dual-hormone hypothesis, betweenness (an index of the individual's centrality in the network) was predicted by high basal testosterone and low basal cortisol. Furthermore, the dual-hormone effect for gregariousness was in the same direction for as popularity and betweenness but was not statistically significant (perhaps due to low statistical power). Therefore, the dual-hormone hypothesis is also able to predict – at least to some extent – social status at the level of human social networks.

Further extending the ecological validity of the dual-hormone hypothesis is an examination of male leaders who hold genuine leadership roles in major organisations

enrolled in the executive education programme offered at Harvard University (Sherman et al., 2016). Specifically, participants were senior-level individuals (n = 78), holding positions in the government, defence, law enforcement, and the military. The response variable in this case was a crude but effective marker of rank: the self-reported number of subordinates. Consistent with the dual-hormone hypothesis, testosterone was positively related to number of subordinates, but only if cortisol was low. Furthermore, the participants described by Sherman et al. (2016) are an important example of research participants who are *not* mostly full-time undergraduate or graduate students (in the context of the dual-hormone hypothesis). These participants were fully employed and are significantly older than participants in all of the other studies described here. This difference in age, employment, and general status addresses potential concerns over the dual-hormone hypothesis being restricted to only younger individuals in university settings (a restriction that could have compromised the ecological and external validity of the hypothesis and its predictions).

Overall, it is important to note that the dual-hormone hypothesis has predicted dominance and social status across both sexes, younger and older individuals, and, perhaps most importantly, across various operationalisations of dominance and social status, including observer reports of instruction-giving behaviour (Mehta & Josephs, 2010), leadership ratings provided by team members (Edwards & Casto, 2013), the number and nature of connections in graphs representing social networks (Ponzi et al., 2016), and in the self-reported number of subordinates (Sherman et al., 2016). Future work should aim to extend the repertoire of response variables that measure leadership and dominance.

Risk-Taking: Individuals take risks to gain rewards in the context of significant uncertainty. If unsuccessful, they may be worse off than before. One example of risky behaviour is financial risk-taking, which has been particularly tractable to laboratory investigation, because participants make financial decisions instead of entering into

dangerous situations that may characterise other types of risk-taking. In the context of financial risk, pharmacologically elevated cortisol over several days suppresses financial risk appetite (Kandasamy et al., 2014). On the other hand, endogenous testosterone has been positively correlated with risk-taking behaviour (Apicella et al., 2008; Coates & Herbert, 2008), though this relationship is not strictly positive and null results have also been noted (Zethraeus et al., 2009, Boksem et al. 2013; Buskens et al. 2016).

Two recent studies (Mehta et al., 2015b) have analysed risk-taking in the context of the dual-hormone hypothesis. In the first of these, male and female participants (n = 115) provided self-reports of their own risk-taking tendencies. Participants also nominated informants, who were then requested to rate the participant on their risk-taking tendencies. Consistent with the predictions of the dual-hormone hypothesis, higher testosterone levels predicted greater self- and informant- evaluations of risk-taking, but only in individuals with lower cortisol. This relationship between testosterone and risk taking was not observed in individuals with higher cortisol levels, and there were no differences in the pattern of the dual-hormone interaction between males and females.

In one sense, these results are even more striking than the finding that observers are able to perceive dominance behaviours in participant footage (Mehta & Josephs, 2010), because it suggests that an individual's impressions about his or her friends and colleagues may track their basal hormone levels over time. Because the informants were reporting on risk tendencies from memory, rather than by observing the participants in a risk-taking situation, their memories and judgements of the participants appear to encode the participant's basal hormone profiles as well.

The second study in this sequence examined risk-taking at the behaviour level, using performance on the Balloon Analogue Risk Task (BART; Lejuez et al., 2002). This task has a relatively high degree of construct validity, and predicts risk-taking in real-world situations

(Hunt et al., 2005; Lejuez et al., 2002). Participants are required to inflate digital balloons over a number of trials. Each pump yields a small number of points, and further inflates the balloon. These points are exchanged for cash at the end of the task. The balloon is programmed to burst after a random number of pumps (and the participant is aware of this random bursting). If the balloon bursts, all points earned by inflating that balloon are lost, and the next balloon is presented. The participant may choose to cash in all points on an unburst balloon and move to the next balloon. Every time the participant decides to pump the balloon further is an instance of a risky decision, because the participant does not know whether the next pump will cause the balloon to burst. It is, of course, in the participant's interest to maximize the number of points. In this study (Mehta et al., 2015b), male participants (n = 165) first provided a hormone sample and then completed the BART. As with the self- and informant-evaluations of risk-taking, associations between hormones and BART risk taking were also consistent with the dual-hormone hypothesis – that is, testosterone was positively associated with risk-taking (measured as the number of pumps on unburst balloons) when basal cortisol was low. This association between testosterone and risk taking was not observed in participants who had higher cortisol levels.

A recent pre-registered study (Ronay et al., 2018) that used hair hormone levels provides further evidence of the dual-hormone hypothesis in relation to risk. The researchers found that, in male participants (n = 53 males, with a total of n = 162), hair testosterone was positively associated with risk-taking behaviour, but only when hair cortisol levels were low. Hair provides an index of long-term, cumulative hormone levels (Dettenborn et al., 2012), and is freer of momentary fluctuations that characterise hormone quantifications from blood or salivary samples. Hair can be used to provide estimates of both cortisol and testosterone, though it is used only infrequently in hormone-behaviour research.

Competitive Bidding: In an auction, if an individual offers more money than the estimated value of the object, the individual is said to be overbidding, as it is unlikely one values the object as much as one is willing to pay for it (if the individual truly did value the object as much as they are offering, then it cannot be considered overbidding). A relatively recent study has shown that overbidding in auctions is consistent with the dual-hormone hypothesis (van den Bos et al., 2013). Analysis of saliva samples provided by male participants (n = 26) involved in a small laboratory-based auction study revealed a positive association between testosterone and overbidding when cortisol was low. The association was not observed in participants with higher endogenous cortisol. Although there is no rational economic value to overbidding, it does signal an individual's competitiveness, and perhaps a desire to win at any cost – that is, winning itself is the goal, not the object one is bidding for. Overbidding in an auction (where others are aware of the individual's bids) could also be a channel to increase visibility, again, perhaps, acting as a signal of willingness to compete. To this extent, overbidding affects the social environment and draws attention toward the bidder. From a psychological perspective, the difference between the object's estimated value and the amount that an individual overbids by may, in part, represent the additional utility the individual gains through victory.

Empathy: Empathy has been classically understood as the capacity to transpose oneself into the experiences and emotions of another individual. One large study combining both males and females (n = 469) found that variation in empathy as self-reported on a well-validated psychometric questionnaire (the Interpersonal Reactivity Index; Davis, 1983) was consistent with predictions of the dual-hormone hypothesis (Zilioli et al., 2014). That is, higher basal testosterone concentrations predicted lower empathy, but only under conditions of low cortisol. This association was not apparent when cortisol was high. Indeed, the opposite tendency was observed when cortisol was high: higher testosterone appeared to

predict greater empathy. This positive association between testosterone and empathy is consistent with a recent investigation of 84 males (Vongas & Al Hajj, 2017), where contest-induced increases in testosterone concentrations predicted better emotion recognition in a procedural task; however, this study did not include cortisol measures.

Importantly, although these patterns in Ziloli et al. (2014) emerged in the combined sample of males and females, when the sexes were analysed separately, the dual-hormone interaction was statistically significant only in males. This difference is consistent with some recent work that also reported a significant dual hormone interaction only in males when males and females were analysed separately (Ronay et al., 2018). But it is a departure from several previous comparisons between males and females, where there were no sex differences (e.g., Mehta & Josephs, 2010; Mehta et al., 2015b). Whether this apparent sex difference is a true psychological difference or an artefact of the inevitable loss of statistical power that follows splitting a sample remains to be verified. Because there were over twice as many males (n = 323) as females (n = 146), it may explain why the effect was observed in the former but not the latter. However, even for the smaller group of female participants the sample was fairly large – larger than almost any other study discussed in this chapter (testosterone measurement in females is especially error-prone, providing a potential explanation for null results, Welker et al., 2016).

It should be noted that these findings characterise *self-reported* empathy. The dual-hormone effect did not extend to performance on another widely-used measure of cognitive empathy, the Reading the Mind in the Eyes Test (RMET), which captures the capacity to accurately infer simple and complex emotional states expressed in the eye region of another individual, with no other portion of the face shown (Baron-Cohen et al., 2001). There are also other manifestations of empathy that are behavioural (e.g., prosocial behaviour) and emotional (e.g., the extent to which viewing the emotional experiences of others causes

physiological arousal in the observer). It will be important to examine how these behavioural and physiological aspects of empathy fit within the framework of the dual hormone hypothesis (see also Sollberger, Bernauer, & Ehlert, 2016 for an interesting application of the dual-hormone hypothesis to pro-environmental behaviour, which may be driven in part by pro-social motivation, in a sample of 147 male participants).

Aggression and Punishment: The link between testosterone and aggression is one of the more stereotypical associations that this hormone shares with a psychological variable. In fact, earlier research on aggression anticipated the dual-hormone effect before it was formally theorised. Aggression, especially amongst younger individuals, may also be a behavioural pathway to higher social status (Cillessen & Mayeux, 2004; Vaillancourt & Hymel, 2006). A relatively early study (Dabbs et al., 1991) has linked adolescent aggression and violence to endocrine profiles consistent with the dual-hormone hypothesis. In particular, delinquent adolescent males (n = 113) who had higher basal testosterone and low basal cortisol were also found to have been more violent, received stricter treatment from their parole boards, and also were more likely to break institutional rules. The positive slope between testosterone and behaviour was detected among low-cortisol individuals but not among high-cortisol individuals. A more recent study also found converging evidence in this direction (Popma et al., 2007). Adolescent males (n = 103) on a delinquency diversion programme provided self-reports on their aggressive tendencies. The psychometric test used to measure these tendencies was the Buss-Durkee Hostility Inventory (Buss & Durkee, 1957), which captures both overt aggression (the open expressions of anger and aggression) and covert aggression (unwillingness to freely express anger and aggression). While the researchers did not find significant associations for covert aggression, the relationship between self-reported overt aggression and hormone levels was in line with the dual-hormone hypothesis. In particular, higher scores for overt aggression were positively associated with higher levels of basal

testosterone when basal cortisol was low. This testosterone-behaviour association was not observed for individuals with higher levels of cortisol.

An intriguing recent study (Grotzinger et al., 2018) examined the relationships between adolescent aggression, testosterone and cortisol using hormone estimates hair (n = 460). Consistent with the dual-hormone hypothesis, hair testosterone was a significant predictor of aggression at low levels of hair cortisol.

Antisocial behaviour is not, of course, restricted to aggression and violence. Indeed, there are many kinds of aggression, and many of these are not related to delinquency or delinquent-like tendencies. More recent research has examined antisocial behaviour in economic games, in which participants can opt to punish other players (in the context of economic games, punishment often entails making decisions that will reduce another player's monetary payoffs). Not all forms of punishment are antisocial. If individuals choose to punish individuals who are free-riding on resources in a public goods game, then that is an instance of prosocial punishment. On the other hand, individuals may sometimes choose to punish individuals who invest more than they are expected to in a common resource pool (or indeed, more than the participant). If the participant punishes such individuals, it is an instance of antisocial punishment. In a recent study (Pfattheicher et al., 2014) of healthy male participants (n = 72), testosterone was positively related to antisocial punishment among those with lower basal cortisol, but this link was not observed among individuals with high basal cortisol.

Overall, then, it appears that the dual-hormone hypothesis can predict aggressive behaviour at both the self-report and behavioural levels, and in both clinical and healthy samples.

Group Performance: A recent area of enquiry is the joint influence of testosterone and cortisol on group-level decisions and performance. This is an important subfield of

research both because many financial decisions and risks are executed by groups rather than individuals, and also because the consequences of such decisions extend to multiple individuals. To this extent, a recent study (Akinola et al., 2017) has described a novel endocrine construct – the group-level hormone profile, obtained by aggregating individual hormone concentrations (in this case, testosterone and cortisol) using multi-level modelling (Croon & van Veldhoven, 2007). Male and female participants (n = 370) worked in small groups of three to six individuals to complete a complex logistics and supply chain management problem in which they were required to optimize financial performance. Importantly, there was no "correct" strategy that had to be discovered and implemented. Rather more consistent with decision-making in the real world, there were multiple approaches that could yield successful outcomes, and groups could vary multiple parameters in arriving at an optimal strategy. Consistent with the dual-hormone hypothesis, group-testosterone was positively related to group performance only for those groups low in cortisol but not for those groups high in cortisol. This effect remained even when controlling for the effects of personality and hormonal variation at the group level.

Alongside providing evidence for the dual-hormone hypothesis, these results offer two key advances to the study of hormones in decision-making. First, they highlight the validity of using a hypothetical, collective-level endocrine construct to describe group decision-making. The second advance lies in the task's impressive ecological validity, being a much closer approximation of real-world decisions than many laboratory measures of decision-making. Therefore, these results provide concrete evidence for how endocrine processes can affect business-relevant outcomes.

Hormone Change Profiles

Aside from the effects of basal hormone profiles discussed earlier, a smaller body of research suggests that acute *changes* in hormone levels may also reliably predict behavioural

outcomes. Hormone concentrations change predictably over the course of the day. However, they also change dynamically during social interactions. These intra-situational variations in hormone levels are also of significant theoretical interest in generating an understanding of how the endocrine system regulates behaviour. Two studies have found behavioural effects of changes in cortisol and testosterone concentrations that were consistent with the dual-hormone hypothesis in the context of competitive bargaining (Mehta et al., 2015a).

In the first study, male and female MBA students (n = 70) were assigned to act out a negotiating task in pairs, with the roles of buyer and seller determined at random. Negotiations are interactions that two often competing motives against one another. One motive is to secure a strong financial outcome for oneself or the group one is representing (a monetary motive). A second motive is a social one. Negotiators who experience conflict between financial and social motives often end up with lower financial earnings. For example, an entrepreneur seeking to sell his business may be concerned that proposing too high a price to potential buyers could reduce social rapport and undermine his social reputation. As a result, he may offer a lower price and thus negotiate a worse financial deal. for himself. The results of this study of seller-buyer negotiations were broadly consistent with the dual-hormone hypothesis. Individuals who experienced an increase in testosterone alongside a decrease in cortisol secured economically stronger bargains (a financially adaptive hormonal profile), while financial outcomes for individuals experiencing an increase in testosterone alongside an increase in cortisol were significantly weaker (a financially costly hormonal profile). Furthermore, individuals who perceived the monetary and social motives of interactions to be in conflict also showed the financially costly hormonal profile (a testosterone increase combined with a cortisol increase), while those who did not perceive monetary and social motives to be in conflict showed the financially profitable hormonal profile (a testosterone increase combined with a cortisol decrease). Importantly, the effect

was specific to individuals assigned to act as the sellers in the bargain. This moderation by social role (buyer or seller) was not originally hypothesised, but was noted to be consistent with previous findings that the seller is typically the individual who has greater influence over the outcome of the negotiations (Amantullah et al., 2008).

In the second study, the authors further examined the idea of hormones acting as a proxy for social and financial concerns in the context of an ultimatum game in which males and female participants (n = 115) were involved. In the ultimatum game, a participant must decide whether to accept or reject a portion of money offered by another individual. The individual making the offer (the proposer) receives a fixed sum (e.g., $10) and can allocate this money between himself or herself and the other player in any ratio they please. The receiver is aware of the total sum in play, and can accept or reject the offer. If the receiver rejects the offer, both players lose all of the money. The most egalitarian allocation is a 50:50 split of this endowment. However, it is in the receiver's economic best interest to accept *any* sum offered greater than zero monetary units, as any sum renders the receiver better off than they were previously. However, a behavioural hallmark of interactions in ultimatum games is that receivers will frequently reject offers that they perceive to be unfair – that is, being offered much smaller than a 50:50 split of the initial endowment can trigger rejection of these offers, a punishment-like behaviour that is detrimental to both parties. A post-test saliva sample was obtained after the ultimatum game was completed. Consistent with high testosterone and low cortisol predicting a financially adaptive response, participants who showed an increase in testosterone and a decrease in cortisol were more likely to accept typically "unfair" offers, thus acting in their economic best interest. On the other hand, if both cortisol and testosterone increased, participants were more likely to reject the offer, thus compromising their economic interests likely in the service of social motives (e.g., the motive to punish the other player in the face of perceived social provocation).

Furthermore, both studies found that the dual-hormone interaction statistically mediated the associations between psychological traits and bargaining behaviour. For example, in the ultimatum game study, higher scores on a personality measure of trait aggression were related to increased rejection of unfair offers, and this trait aggression-behaviour association was mediated by the dual-hormone interaction. Specifically, high trait aggression predicted increased testosterone and cortisol levels, which in turn predicted rejection of unfair offers. However, low trait aggression predicted increased testosterone and decreased cortisol levels, which in turn predicted acceptance of unfair offers.

Variation in the Pattern of the Dual-hormone Interaction

A few investigations have also observed important variations in the effects of dual-hormone interactions in regulating antisocial behaviour, such that it is the individuals with high basal testosterone and *high*, rather than low, basal cortisol who show such tendencies. For example, research on trait psychopathy in a large sample of males and females (n = 237) found a positive relationship between testosterone and self-reported psychopathy in males who also had high levels of cortisol. The association was not observed in males with lower levels of cortisol, and was also not observed in females (n = 123). In another study of reactive aggression in females, participants (n = 53) were insulted by an accomplice in a pre-recorded video (Denson et al., 2013a). Participants believed that this accomplice was another participant, and that the interaction was live. In particular, the participant first made a brief speech about her life goals. The insult comprised derogatory remarks about the quality of the speech and the participant's level achievement and her life goals. Following this, participants were given an opportunity to retaliate by subjecting the insulter to bursts of white noise during what was presented as a competitive reaction time task against the participant who had insulted them. Testosterone was positively associated with the extent of retaliation in participants with high cortisol, but not those with moderate or low cortisol. These findings are

also conceptually similar to the results of the second study in Mehta et al. (2015) described earlier, wherein participants who increased in testosterone and increased cortisol levels showed a greater tendency to reject unfair offers in an ultimatum game, which may be interpreted as a form of reactive aggression.

Aside from psychopathy and reactive aggression, recent work has also examined joint hormonal regulation of unethical behaviour. In particular, Lee et al. (2015) investigated cheating tendencies in two studies. In the first study, with male and female participants (n = 82), cheating was measured by the extent to which participants overstated the number of correctly solved logic puzzles (solving a greater number of puzzles led to a higher monetary gain for participants). Individuals with higher baseline testosterone were more likely to engage in cheating behaviour only if their cortisol levels were high. The second study in this sequence, also conducted on male and female participants (n = 117) found an especially striking result. In addition to replicating the original testosterone × cortisol interaction on cheating found in the first study, hormone assays on post-test saliva samples revealed that the participants who had cheated showed *lower* levels of cortisol and negative affect. Furthermore, there was evidence of a dose-response relationship – the greater the extent of cheating, the greater the decrease in post-test cortisol concentrations relative to pre-test cortisol concentrations. This finding led the authors to propose a cheating-as-stress-reduction hypothesis, which suggests that intrinsically high levels of endogenous cortisol (accompanied by a generally aversive psychophysiological state) may predispose individuals to act unethically as a way to reduce stress levels that are otherwise too high.

Together, these studies suggest that high testosterone and high cortisol may also predict antisocial tendencies. However, it is unclear when these tendencies will follow from this particular combination (high testosterone, high cortisol) and when they will follow the standard predictions of the dual-hormone hypothesis (high testosterone, low cortisol), as has

been the case in previous work that has examined aggressive or antisocial behaviour (Dabbs et al., 1991; Pfattheicher et al., 2014; Popma et al., 2007). We suspect that in populations and situations where aggression and violence may be harmful for status, high testosterone and low cortisol should be associated with lower levels of aggression and violence (e.g. among groups of women in which gender socialization would suggest that aggression would have a negative effect on status). Establishing the boundary conditions for the effects of each of these hormone profiles will be an important step in understanding dual endocrine contributions to behaviour.

Moderators of the Testosterone × Cortisol Interaction

Personality: Some studies are revealing that personality traits may also interact with the hormone profiles to regulate behaviour. For instance, a recent study provides suggestive evidence that dual-hormone effects may be particularly pronounced in individuals with a high level of trait dominance (Pfattheicher, 2017). Male participants (n = 153) had the opportunity to make monetary gains by depriving money from another individual (selecting this option was considered to be a dominant behaviour – alternatively, participants could also choose not to take money from the other individual, which was the non-dominant option). In support of the dual hormone hypothesis, there was a statistically significant testosterone × cortisol interaction; testosterone was positively related to dominant behaviour only among individuals with low cortisol. This study also found that testosterone and cortisol further interacted with self-reported trait dominance to predict dominant behaviour (this three-way interaction was marginally significant). Specifically, the dual-hormone interaction effect was driven by individuals high in trait dominance, and was not statistically significant in individuals low in trait dominance. While the author acknowledges that the evidence is merely suggestive and potentially underpowered, the finding does open important avenues for interactions between hormones and self-reported personality traits in explaining dominant behaviours (for some

related research on exogenous testosterone × self-reported trait dominance interactions predicting competitive and aggressive behaviour, see Mehta et al., 2015; Carré et al. 2017).

Other research has focussed on problematic adolescent behaviour. One study (Tackett et al., 2014) that examined externalising behaviour in male and female adolescents (n = 104) found that high testosterone predicted higher rates of antisocial tendencies when cortisol was low, but only in individuals with higher levels of traits associated with personality disorders – disagreeableness and emotional instability. Furthermore, this moderation by disagreeableness and emotional instability was recapitulated in another mixed-sex adolescent sample (n = 104) using a different hormone, estradiol, which, like testosterone, is released by the HPG-axis (Tackett et al., 2015). This finding also extends the dual-hormone hypothesis to include HPG-hormones beyond testosterone, an important step for research in this area. The existence of the personality × cortisol × testosterone (or estradiol) interactions on antisocial behaviour may have clinical relevance in terms of diagnosis, treatment, or rehabilitation.

Social Context: Endocrine contributions to behaviour are also dependent on social context. For instance, the dual-hormone effect on the decision to compete again *after* a competition depends on whether one had won or lost the first competition (study 2; Mehta & Josephs, 2010). Male participants (n = 57) were randomly assigned to win or lose in a competitive scenario (a supposed intelligence test based on speed), and were then asked whether they wished to participate in the competition again. Basal testosterone predicted an increased likelihood of choosing to compete again only when basal cortisol was low *and* when an individual had lost, suggesting that this endocrine profile may predispose individuals to attempt to reclaim status when it is lost or compromised, as when losing a competition. Another study using female participants (n = 120) found a very similar effect (Henry et al., 2017). Participants performed a computerised competitive task in pairs, with individuals randomly allocated to win or lose the task, with entailed visual motor responses. Testosterone

was positively correlated with task performance in participants with low, but not high levels of cortisol. Most importantly, this interaction was further influenced by the status of having won or lost the competition. In particular, the testosterone × cortisol interaction on competition performance was observed in the participants assigned to lose. As with Mehta and Josephs (2010), these results suggest that the status undermining effects of losing competition may interact baseline hormone profiles to predict performance.

Another important social context is inclusion or exclusion from a group. Social exclusion is easily induced in laboratory settings using the Cyberball task, in which a participant can be excluded from digital social interactions that others are having (Williams & Jarvis, 2006). One study on male participants (n = 74) found a marginally significant interaction between testosterone, cortisol, and social context in predicting a laboratory measure of aggression. Among participants in the inclusion condition, there was a positive association between basal testosterone and a laboratory measure of aggression only when basal cortisol was low (Geniole et al., 2011). But among participants who were excluded, the opposite dual-hormone interaction pattern emerged: the pattern suggested that testosterone was positively related to aggressive behaviour only among high-cortisol individuals. While this was a tentative association, it does add inductive support to the notion that social context can exert an effect on dual-hormone contributions to behaviour, and may help clarify the contexts in which different dual-hormone interaction effects occur.

Future Directions

Adaptive Value of Dual-Hormone Profiles: An important unresolved question is the general adaptiveness of behaviours that appear to arise from high testosterone and low cortisol concentrations. An important example in this regard is risk-taking behaviour. A certain level of risk-seeking enables an individual to seize opportunities and rewards that may be fleeting and may therefore be quickly lost. This combination of hormones may also enable

individuals to engage more effectively with high-uncertainty situations in order to gain rewards. However, risk-taking can also result in significant costs at both individual and societal levels. Excessive risk-taking is likely to compromise the health and safety of an individual and those around him or her (e.g., driving at very high speeds, unprotected sexual intercourse, drug use). Depending on the social influence of the risk-taker, excessive risk may also have enormous and wide-ranging consequences, such as destabilizing markets and declaring wars. Another example is antisocial behaviour such as aggression. It may be in certain populations and contexts (e.g., male adolescents in a delinquency program), aggressive actions such as physical violence may be more adaptive for status attainment whereas in other populations (e.g., university students, work organisations) such aggressive actions would likely impair status attainment. A better understanding of the adaptive nature of aggression may potentially help explain some of the inconsistent results. Understanding the biological bases of behaviours such as risk-taking and aggression, and the conditions in which these endocrine profiles may be adaptive or maladaptive is therefore an important goal for continued research.

Investigations of Neural Mechanisms: The neural processes underlying dual-hormone effects remain poorly understood. Mechanistic elucidations will enhance our knowledge of how these effects are occurring. For instance, glucocorticoids downregulate the androgen receptors to which testosterone binds (Burnstein et al., 1995; Chen et al., 1997). Thus, even when testosterone levels are high, if cortisol is causing androgen receptor downregulation, testosterone molecules may be unable to bind to the relevant receptors, diminishing further psychophysiological effects.

Network- and region-level neural processes are also likely to be associated with these dual-hormone effects. One possibility derives from the brain's fundamental capacity to detect and react to reward signals. At the endocrine level, increased testosterone and decreased

cortisol have independently been associated with enhanced reward-processing and reward-seeking (Hermans et al., 2010; Mehta et al., 2015b; Montoya et al., 2014; van Honk et al., 2004). For example, testosterone increases activity in mesolimbic reward centres, including the nucleus accumbens within the ventral striatum and the ventral tegmental area (Hermans et al., 2010; Op de Macks et al., 2011; Welker et al., 2015). On the other hand, some studies have shown that cortisol concentrations are positively correlated with widespread reductions in activity in reward-related networks, such as the striatum and basolateral amygdala (Montoya et al., 2014). Of course, it would also be incorrect to characterise the effects of cortisol to be generally "anti-rewarding", as there is some evidence that cortisol may stimulate the dopamine release in the nucleus accumbens (Oswald et al., 2005; Pruessner et al., 2004). However, overall, cortisol does appear to be implicated in the brain's reward circuitry.

Reward processing is theorized to underlie some of the behaviours discussed in this chapter (e.g., risk-taking, social status). Although there are separate neural studies of testosterone and reward processing and cortisol and reward processing, there is no direct test of the dual-hormone hypothesis in relation to neural reward systems. According to the dual-hormone hypothesis, testosterone would have a positive association with reward processing (e.g., ventral striatum activity) only under low, but not high, cortisol concentrations. This reward processing may in turn mediate the effects of these hormones on behaviours such as risk-taking.

Although there is no direct evidence for the dual-hormone interaction predicting neural reward processing, there is some new indirect evidence with respect to a psychological marker of reward processing. Specifically, a recent study of male and female undergraduate participants (n = 98) found a particularly interesting effect: In an economic game, basal testosterone concentrations were positively correlated with self-reported enjoyment and

satisfaction with the game in participants with low, but not high, cortisol concentrations (Mehta et al., 2017). This study provides initial evidence for the idea that motivation for reward, as expressed by factors such as task-enjoyment and related neural systems linked to reward, may underpin the influence of the testosterone×cortisol interaction on behaviour.

In addition to reward, another mechanism likely at play is threat, which the brain is also extremely sensitive to. Both cortisol and testosterone enhance the neural processing of threat and negative affect (Denson et al., 2013b; Goetz et al., 2014; Hermans et al., 2008; Mehta & Beer, 2010). However, whereas cortisol triggers neurophysiological systems that may be more oriented toward social avoidance, testosterone triggers approach-oriented behaviours, likely to engage with the threat rather than avoid it. Covariation in endogenous cortisol and testosterone will lead to differential modulation of the relevant brain networks, which would manifest in different behavioural repertoires. For example, in a small study of healthy males (n = 19), participants with higher concentrations of testosterone and lower concentrations of cortisol showed greater activation in brain regions associated with cognitive control (the dorsolateral prefrontal cortex) in an anger-control task (Denson et al., 2013b). In comparison, participants with high concentrations of both testosterone and cortisol did not show this pattern of activation, suggesting that prefrontal activity may mediate the effect of hormone interactions on psychological processes.

Psychopharmacological Experiments to Understand Causality: Pharmacological approaches the benefit of enhancing our understanding of causation. All of the effects discussed in this chapter arise from endogenous variation in steroid concentrations. That is to say, the causal theory underlying the dual-hormone hypothesis is that cortisol inhibits the action of testosterone. However, the testosterone × cortisol interaction is not truly able to offer evidence for this causal statement. Although it may also be the case that testosterone inhibits the action of cortisol, existing research does provide some clues that support our

interpretation of the testosterone × cortisol interaction - that it is cortisol inhibiting the effects of testosterone.

By experimentally varying the concentrations of cortisol and testosterone, pharmacological manipulations will be able to generate important insights about the effects of different combinations of these hormones on behaviour. Of the four relevant pharmacological manipulations of testosterone and cortisol, three are readily and easily implemented with no health concerns. These are: 1) increasing cortisol concentrations with drugs such as hydrocortisone, 2) supressing cortisol activity with drugs such as dexamethasone, and 3) increasing testosterone concentrations with drugs such as nasal sprays, topical gels and creams, or via ingestion. Researchers frequently use these approaches, especially for increasing cortisol and testosterone. The fourth possibility, pharmacologically supressing testosterone activity, may pose some ethical and logistical issues. Antiandrogen drugs such as inhibitors of gonadotropic releasing hormone (which stimulates testosterone release), are also used for chemical castration. Though an important recent investigation has administered testosterone antagonists (cetrorelix acetate) to healthy volunteers (Goetz et al., 2014), we anticipate that there may be significant hurdles in conducting such studies, both in terms of obtaining the relevant research ethics approval, and also in recruiting male participants who may be willing to volunteer for such an experiment. This is not to say that experiments aiming to reduce testosterone concentrations are impossible, only that they are not nearly as expedient as those increasing testosterone, or increasing and decreasing cortisol. Fortunately, the combinations of the greatest interest (at present) are high levels of testosterone with low levels of cortisol, or high levels of both testosterone and cortisol. These can be mimicked pharmacologically by administering a testosterone enhancer alongside hydrocortisone (to increase cortisol levels) or dexamethasone (to suppress cortisol levels).

Experimental Manipulations of Stress to Understand Causality: A recent pilot study (Prasad et al., 2017) offers some evidence of a potential non-pharmacological route to understanding causality. The researchers manipulated participant stress by either engaging them in a social stress task (increasing cortisol) or in a relaxation task (decreasing cortisol). Participants (n = 39) were randomly assigned to either the stress or relaxation conditions. Consistent with the dual-hormone hypothesis, testosterone interacted with this acute stress manipulation to predict subsequent behaviour (retaliations in an ultimatum game). Basal testosterone was positively related to retaliatory behaviour (greater rate of rejecting offers) only in the low stress (low cortisol) condition, but this association was not seen in the high-stress (high cortisol) condition. Although this is only a pilot study that requires replication and extension, it does open up avenues for new work using acute stress and relaxation tasks as cortisol manipulators. These types of study designs will be especially useful in providing non-pharmacological experimental tests of the dual hormone hypothesis.

Other Statistical Models Analysing Two Hormones: This chapter has reviewed evidence for the interaction between testosterone and cortisol concentrations as a predictor of behaviour, but other approaches also attempt to incorporate both testosterone and cortisol in describing human social behaviour. It will be important to carry out studies that test and compare different approaches directly to one another. For example, one line of research examines the coupling between testosterone and cortisol, which is captured in the magnitude of the positive correlation between the two hormones (Shirtcliff et al., 2015; Dismukes et al., 2015; Johnson et al., 2014). The notion of coupling follows on the observation that in several cases, cortisol and testosterone may share a strong positive association with one another, whereas in other cases that two hormones may show weaker or no coupling. This coupling has been used to describe antisocial aggression in adolescence. Hormone coupling is the topic of Chapter 38 of this volume, and is therefore not discussed further here.

Sex Differences: The dual-hormone hypothesis appears to hold for both sexes, at least as far as several of the studies described here are concerned (Mehta & Josephs, 2010; Mehta et al., 2015a; Mehta et al., 2015b, study 2; Tackett et al., 2014, 2015; Grotzinger et al., 2018). However, there are also a few differences. For instance, there are cases where an effect was noted in males but not females (Welker et al., 2014; Zilioli et al., 2014; Ronay et al., 2018). In other cases, all the participants were of only one sex, which would complicate drawing inferences for the other sex (e.g., Edward & Casto, 2013; study 2, Mehta et al., 2015). Because studies with male-only samples outnumber those with mixed-sex or female-only samples, it is presently unclear how the dual-hormone hypothesis explains the hormone-dominance relationship in several status-seeking behaviours in females, including antisocial punishment (Pfattheicher et al., 2014), overbidding (van den Bos et al., 2013), or number of subordinates (Sherman et al., 2016).

At a more general level, the dual-hormone hypothesis on interactions between cortisol and testosterone is a specification of broader interactions between the HPA-axis and the HPG-axes. As the results describing estradiol × cortisol interactions suggest, the HPG-axis secretes hormones other than testosterone that may contribute to dominance and status-seeking behaviour (Tackett et al., 2015). Because only one study reports this effect, and because the result is restricted to externalizing behaviours such as aggression, it is important to expand the scope of studies to other types of dominance-oriented behaviour. To this extent, stereotypically "female" sex hormones such as estradiol and progesterone should be more widely incorporated into future research on dual-hormone contributions to social behaviour in both males and females.

Potential Bias Introduced by Measurement Techniques: A little-considered but an important issue is the technique of quantifying hormones. Typically, participants provide saliva samples from which hormone concentrations are quantified using one of several

analytical approaches. Most researchers use immunoassays to measure steroid hormone concentrations, but growing evidence indicates that this technique is susceptible to measurement error (Welker et al., 2016). A devil's advocate argument against the dual-hormone hypothesis is that the testosterone × cortisol interaction does not reflect a true physiological interplay that drives behaviour, but merely indicates varying levels of glucocorticoid (or other steroid) interference of the testosterone assay, a concern that extends across immunoassay methods. Therefore, it is particularly important to consider the results from quantifications that are not reliant on immunoassays. A much more precise technique for estimating testosterone in both hair and saliva is liquid chromatography tandem mass spectrometry (Welker et al., 2016). The two hair-based studies described in this chapter that support the dual-hormone hypothesis have used this technique (Grotzinger et al., 2018; Ronay et al., 2018). Because the testosterone × cortisol interaction was detectable with liquid chromatography tandem mass spectrometry, these findings provide preliminary evidence that it is not merely an artefact arising from the use of immunoassays.

Statistical Power and Replication: While the testosterone × cortisol interaction has been observed in different contexts and with different response variables (hence the motivation for this chapter), it is important to acknowledge the low statistical power characterising many of the dual-hormone findings, as well as failures to replicate the key effect. As with other subdisciplines in experimental psychology, social endocrinology research is often characterised by low statistical power to detect small to medium sized effects. There are several components to statistical power, but the most commonly cited cause of low power is sample size. Although some of the studies described here have a large number of participants (e.g., 400), others have very few (under 30). Furthermore, there have also been notable failures to detect the testosterone × cortisol interaction in a few studies with large samples. For instance, in a study of competitive behaviour, aggression, and motivation

(n = 326), Oxford et al. (2017) found that aggression was associated with low cortisol levels but not with high testosterone (i.e., a main effect of cortisol, rather than a testosterone × cortisol interaction). Another study (Mazur & Booth, 2014) examined the link between testosterone, cortisol, and antisocial deviance in a large data set from American army veterans (n = 4,462). While testosterone was, in general, positively correlated with antisocial behaviour, the relation was not moderated by cortisol.

We recommend that if researchers have data of sufficient quality for both cortisol and testosterone and a theoretically relevant psychological variable, they should perform exploratory tests for the dual-hormone hypothesis, even if it is not the hypothesis of central significance to the research. For any psychological study that analyses both testosterone and cortisol, it becomes trivially straightforward to conduct an additional analysis to test the dual-hormone hypothesis. The publication of these analyses, though exploratory, will provide at least an impression of how readily the effect replicates. In particular, if the dual-hormone hypothesis is biologically plausible, then evidence for it should appear in studies that are testing other research questions as well.

Overall, this line of research would also certainly benefit from several large, direct replications of key findings (e.g., Mehta & Josephs, 2010). These efforts should be sufficiently powered to detect even small effects, and should perhaps be pre-registered so as to guard against false discovery or undisclosed exploitation of researchers degrees of freedom during data analysis. At present, we are aware of one pre-registered study of the dual-hormone hypothesis (Ronay et al., 2018). Further efforts in these directions would add significantly to the empirical foundation of the dual-hormone hypothesis, providing researchers with more accurate estimates of the underlying effect sizes.

Conclusions

Hormones have long been known to influence human social behaviour, and the dual-hormone hypothesis provides a framework with which to both design and interpret research on these influences. It should be noted that the dual-hormone hypothesis is very much in its infancy. While the accumulation of support across a range of response variables relating to dominance and status-seeking is certainly encouraging, large knowledge gaps remain. We have described some of these gaps in the present chapter. Researchers should prioritize these important unknowns so as to shed light on how the interactions between endocrine systems influence human social behaviour.

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