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Author for correspondence:
Benjamin C. Trumble
e-mail: ben.trumble@gmail.com

†Present address: Center for Evolution and Medicine, and School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA.
‡Present address: Department of Anthropology, Emory University, Atlanta, GA 30322, USA.

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Evolving the neuroendocrine physiology of human and primate cooperation and collective action

Benjamin C. Trumble†, Adrian V. Jaeggi‡ and Michael Gurven

Department of Anthropology, University of California Santa Barbara, Santa Barbara, CA 93106, USA

While many hormones play vital roles in facilitating or reinforcing cooperative behaviour, the neurohormones underlying competitive and cooperative behaviours are largely conserved across all mammals. This raises the question of how endocrine mechanisms have been shaped by selection to produce different levels of cooperation in different species. Multiple components of endocrine physiology—from baseline hormone concentrations, to binding proteins, to the receptor sensitivity and specificity—can evolve independently and be impacted by current socio-ecological conditions or individual status, thus potentially generating a wide range of variation within and between species. Here, we highlight several neurohormones and variation in hormone receptor genes associated with cooperation, focusing on the role of oxytocin and testosterone in contexts ranging from parenting and pair-bonding to reciprocity and territorial defence. While the studies reviewed herein describe the current state of the literature with regard to hormonal modulators of cooperation and collective action, there is still a paucity of research on hormonal mechanisms that help facilitate large-scale collective action. We end by discussing several potential areas for future research.

1. Introduction

Humans and to some extent other primates engage in various forms of cooperation and collective action ranging from parenting and pair-bonding to cooperative food production and sharing, territorial defence and warfare [1–3], with some of these behaviours going beyond the reaction norm of many mammals in terms of scale and coordination. Yet, the neurohormones underlying competitive and cooperative behaviours in vertebrates are largely conserved [4], raising the question of how endocrine mechanisms are shaped by selection to help modulate these extensive cooperative behaviours. Multiple components of endocrine physiology can evolve independently and be impacted by current socio-ecological conditions or individual status (figure 1), thus potentially generating a wide range of variation within and between species. This variation can inform ultimate function as individual or species differences in baseline hormone levels, acute reactivity or receptor distributions may reflect exaptations, different adaptive strategies, trade-offs or constraints [5,6], all of which could lead to individual differences in cooperation and collective action.

To illustrate how endocrine mechanisms evolved to facilitate human and primate cooperation, we focus on the contexts of cooperation typical of the 'human adaptive complex', i.e. the evolved human life history and social organization [7,8], and their primate analogues: parenting, pair-bonding, reciprocity and collective action. We focus our discussion on the role of two hormones in these contexts in depth, oxytocin (OT) and testosterone. We also highlight other neurohormones and variation in hormone receptor genes that have been associated with cooperation. In doing so, we aim to provide a roadmap for identifying shared and derived mechanisms underlying human and primate

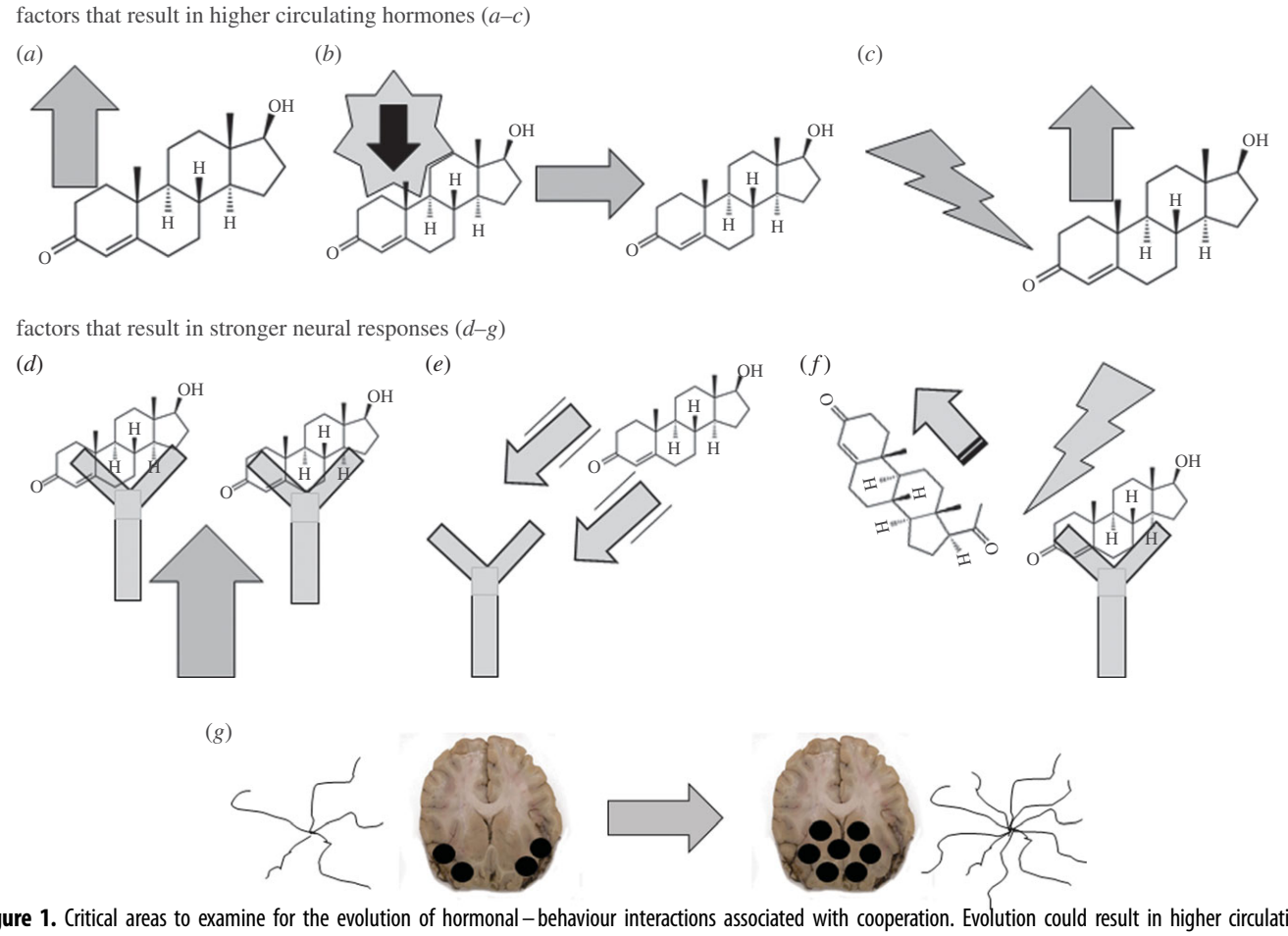

Figure 1. Critical areas to examine for the evolution of hormonal–behaviour interactions associated with cooperation. Evolution could result in higher circulating hormone levels to saturate receptors through: (*a*) higher baseline levels of hormones, (*b*) lower levels of binding proteins resulting in higher 'free' hormone levels and/or (*c*) larger acute increases in hormone levels. Neural responses to circulating hormones could be impacted by (*d*) greater hormone receptor density, (*e*) greater sensitivity of receptors to a hormone, (*f*) higher specificity of receptors for a specific hormone and (*g*) location and connectivity of the receptors to critical brain areas. (Online version in colour.)

cooperation that can give insights into the ecological and social selection pressures that produced them [6] (figure 1).

(a) Hormones and behaviour

In order for a hormone to directly impact behaviour, it must bind to receptors in critical regions in the brain (or other target tissues). Thus, while measuring circulating hormone levels is an excellent first step, it is crucial to also consider the hormonal receptors that turn chemical messages into electrical signals [4]. While most hormones are measured peripherally (outside of the brain), concentrations of hormones vary within the brain, and not all circulating hormones can enter brain tissue. The brain is protected by a selectively permeable set of capillary tissues called the blood–brain barrier, which protects cerebral tissue by only allowing certain substances in circulating blood to pass. Behaviour can only be directly influenced by hormones small enough to cross the blood–brain barrier (e.g. steroids), or that are produced locally in the brain (peptides like OT), or hormones that interact with others that can be active within the brain. Neurohormones like OT and testosterone are known to impact the reward (e.g. dopagenic neurons) and fear centres of the brain (e.g. amygdala), and thus have the ability to reinforce or discourage behaviour. Neuroimaging studies indeed find strong effects of OT and testosterone on behavioural and neural responses to social stimuli [9,10], thus highlighting their neuromodulatory effects.

Cooperative behaviour, whether food sharing or resource defence, is context and condition dependent; behaviours towards other individuals may differ based on their relatedness, social proximity or the actor's physical condition. This means that individuals need to adjust behaviours based on their social setting and local ecology. For example, group-living primates may tolerate relatives at the same feeding patch, while simultaneously protecting their patch against out-group members. Hormones and neurotransmitters can change rapidly in response to different social and environmental cues, enhancing tolerance of others in one social situation, intensifying the potential for aggression in another. Thus, hormones can exert the kind of flexible and rapid control needed to adjust behaviour to varying socio-ecological contexts.

(b) Studying hormonal mechanisms can inform ultimate function

Understanding the physiology and biology of hormone–behaviour interactions can provide insight into adaptations, exaptations, trade-offs and constraints in the evolution of these behaviours [5,6]. Selection may favour mutations for higher levels of a hormone that impacts physiology and social behaviour, resulting in higher baseline hormones. As baseline hormone levels affect many target tissues, such evolutionary changes may modulate many traits, some of which are not

Table 1. Examples of social contexts associated with OT and testosterone for humans and primates. Note that review articles were cited when possible; blank cells indicate that more research is needed, shaded cells are not applicable contexts.

hormone	social context	primates	human males	human females
OT	maternal care	all primates [13]		[14]
	paternal care	marmosets [15]	[16]	
	pair bond	marmosets [17]	[18,19]	
	friendships	chimpanzees [20,21], macaques [22], marmosets [23]	[9,13,24,25]	
	intergroup interactions		[26,27]	
testosterone	paternal care	marmosets [28], *not titi monkeys* [29]	[16]	
	pair bond		[16]	
	in-group		[30]	[31]
	out-group	chimpanzees [32]	[33]	*no effect* [34]
	intrasexual competition	chimpanzees [35], baboons [36], colobus monkeys [37], *not bonobos* [38]	[39,40]	[31]

the original target of the selective pressure; these by-products are commonly referred to as exaptations, and artificial selection experiments may quantify the linkage between traits, resulting in trade-offs and constraints on adaptation [6]. Changes in the acute reactivity of specific target tissues, such as mutations in receptor density or function, are more likely to be the original target of selection, and therefore reflect adaptations. A classic example often used to describe hormonal adaptations and exaptations is the female spotted hyaena; female hyaenas have relatively high levels of testosterone which probably evolved as an adaptation to facilitate female–female competition and aggression [6]. As a systemic by-product of high testosterone, female hyaenas are masculinized and develop penile-like clitorises which are used in greetings and rank-display between adult females [11]. In this case, the adaptation is higher baseline testosterone to facilitate competition, and the exaptation is the co-option of the pseudo-penis in social behaviour [6]. Generally speaking, evolutionary changes in acute reactivity and responsiveness of specific target tissue, e.g. through changes in hormone receptor genes, probably reflect selection for specific hormone–trait interactions and therefore represent adaptations, whereas evolutionary changes in baseline hormone levels are more likely to produce exaptations or trade-offs [9] (figure 1).

Phylogenetic analysis can be a useful way to examine when, and under what socio-ecological conditions a behavioural change occurred, and whether these behavioural changes were associated with any endocrine changes. However, in order to appreciate the adaptive importance of any evolutionary change in behaviour, the hormonal mechanisms must be understood (cf. figure 1); thus, evolutionary history, current utility and mechanism are critical for understanding the ultimate function of complex behaviours such as cooperation and collective action.

2. The role of oxytocin in the establishment and maintenance of cooperative relationships

Cooperation requires investment in a social relationship that generates direct or indirect fitness benefits, oftentimes by paying a short-term cost to reap a long-term gain. This creates several adaptive problems. First, ancestral mammalian asocial preferences need to be overcome to increase tolerance of others and shift behaviour in more prosocial directions. Second, suitable partners have to be identified, recruited and remembered, with the level of investment in each relationship adjusted to the expected fitness gains. Finally, benefits from cooperation generated within the relationship have to be protected from outside threats.

OT is fundamentally linked to each of these adaptive problems, in cooperative relationships of all levels [4,12,13] (table 1). OT achieves these functions by (i) decreasing social anxiety, (ii) enhancing social cognition and social memory, (iii) tracking the valence of social partners and regulating prosocial motivation and (iv) enhancing the social salience of outside threats. In the following sections, we discuss these functions in the various relational contexts that OT is involved in, ranging from the mother–infant bond to large-scale collective action. In each of these contexts, the function of OT is likely to be parochial, regulating cooperative investment within the relationship, but increasing xenophobia and protective aggression against out-groups [13].

(a) Origins of oxytocin in mother–infant bonds

For placental mammals, internal gestation and lactation are expensive for mothers both in terms of time and energy. Above and beyond the ancestral mammalian patterns of investment, extended human altriciality with multiple dependents escalates these costs [7]. Hormones that help facilitate bonding between mother and infant, particularly those that lead to higher levels of maternal investment by stimulating neural reward systems probably had a selective advantage by increasing offspring survival, and thus enhancing female reproductive success.

OT is strongly associated with smooth muscle contraction in the context of parturition (and OT analogues with egg-laying in non-mammals), as well as the milk let down response, which begins with infant stimulation (either suckling or crying) promoting a surge of OT that facilitates milk ejection [13,41]. The neuroendocrine physiology of OT was co-opted for numerous behaviours associated with maternal care including the regulation of the amount of care given by mothers and demanded

by infants [13,42] (table 1). While OT has similar impacts on lactation and behaviour across many mammals, human and great ape altriciality coupled with relatively high dependency loads may have placed additional selective pressures on proximate mechanisms that modulated maternal behaviour, in particular tolerance to a long period of offspring contact and (multiple) dependence. These selective pressures may have resulted in higher baseline levels of OT, larger acute increases in OT when exposed to offspring, greater densities or sensitivities of OT receptors in the brain, or greater neural connections between OT receptors and reward centres in the brain (figure 1), though little is currently known about the phylogeny of OT in primates. Similar changes probably resulted in the co-option of OT pathways for various other relational contexts as highlighted below.

It is important to reiterate that OT not only has socio-positive effects, it is also expected to affect protective aggression and to modulate trade-offs between current and future reproduction (in addition to being an important modulator of cognitive trade-offs [9]). Experimental evidence in mice demonstrates that maternal OT mediates defence of offspring against potential threats [43]. Studies in primates have yet to examine offspring defence but do find evidence that OT mediated in-group bias and defence at the level of larger social groups in marmosets and humans [23,26,27] (see also below). While OT is associated with increased maternal investment, there are conditions under which trade-offs between current and future offspring should lead to downregulation or even termination of investment. Studies have yet to test whether low-quality infants induce a smaller OT response in mothers or fathers, a hypothesis worth testing. Thus to summarize this section, OT evolved in placental mammals as a part of the milk let-down reflex, but then was later co-opted to help modulate maternal behaviour and mediate trade-offs between current and future reproduction.

(b) Oxytocin and male parental investment

Maternal care of offspring is universal among mammals, but less than 5% of male mammals (and no great apes) engage in any paternal care [44]. Many human fathers invest heavily in their offspring [16,44], making the paternal–infant bond a derived trait in humans. The human feeding niche requires extensive bi-parental care, as well as additional multi-generational support, all of which would benefit from extensive tolerance by human males of both their offspring and other family members [45]. The anxiolytic and bonding aspects of increased OT may be a critical proximate mechanism that keeps human males engaged in familial provisioning [46].

Human males may not provide milk for their children, but both baseline OT and acute increases in OT have been implicated with increased levels of paternal care [14,16,47]. Fathers who more intently play with their children show larger actuate increases in OT [48,49]. Additionally, fathers given exogenous OT engage in more physical contact, social reciprocity, eye gazing and object manipulation with their infants than males given a placebo [47]. Co-option of OT in paternal care is not limited to humans; in other primates with relatively high levels of paternal investment such as marmosets and tamarins, exogenous and endogenous changes in OT facilitate paternal care [15]. In sum, while males do not lactate, OT appears to have potentially beneficial impacts on male parental investment in the few primate species that do engage in paternal care.

(c) Oxytocin and pair-bonds

From a female perspective, OT modulation of pair-bonding behaviour can be seen as an extension of the female's reproductive context [13], but there is growing evidence that OT also facilitates pair-bonding in male primates including humans. OT levels were highly correlated among marmoset pairs, and pairs with higher OT levels were more affiliative, though females showed increases in OT when engaged in grooming, while males only showed increases in OT when engaging in sexual activity [50]. OT administration in marmosets led to more huddling with reproductive partners, while OT antagonists resulted in reduced proximity [17]. OT administration in marmosets also decreased socio-sexual contact with strangers, thus increasing fidelity within the pair bond [51]. In humans, males display acute increases in OT when shown pictures of their girlfriends, but not when shown pictures of other women [52], suggesting the importance of context and connection, and not just sexual behaviour [18]. Indeed, men and women who rate their relationships as stronger have higher basal levels of OT [19]. However, as a mediator of investment in pair-bonding, OT is subject to trade-offs in relationship investment based on relationship quality. For example, in aggressive individuals, OT administration increases jealousy [53], as well as the propensity for intimate partner violence, a potential tactic to limit a mate's access to members of the opposite sex [54]. In sum, OT is associated with the regulation and maintenance of pair-bonds, above and beyond sexual behaviour, with studies indicating both positive and negative impacts of OT on relationships depending on the social context.

(d) Oxytocin and friendships

Beyond parental care and pair-bonding, humans and some primates engage in cooperative relationships among both related and unrelated individuals, i.e. friendships [55–57]. Friendships involve the reciprocal exchange of various social behaviours such as grooming, food sharing and coalitionary support [2,58–60], and appear to be regulated by OT. For example, a greater number and intensity in female friendships in macaques is associated with higher levels of baseline OT, though the same effect was not found among male macaques [22]. In chimpanzees, acute increases in OT occur following food sharing, leading to an intensification of reciprocal investment in the relationship [21]. Grooming also results in acute increases in OT, with greater increases after grooming by kin or friends [20]; short-term endogenous changes in OT thus track the valence of social relationships, which is crucial for adjusting cooperative behaviour to partner value. As such, OT provides a mechanism for regulating investment in reciprocal relationships.

The extensive reciprocal cooperation with changing partners required by the human foraging niche and fission–fusion sociality [8] was probably facilitated by a further co-option of OT to increase prosocial disposition and motivate the establishment and regulation of cooperative relationships with new partners. Indeed, prosociality increases following OT administration in a variety of economic games mimicking resource-sharing contexts [24,61]. Additionally, experimental evidence suggests that both endogenous release of OT [62] and exogenously administered OT make individuals more willing to trust their partners in economic games [25]. In this context, the fact that the appropriate level of investment in the relationship, exemplified by trust (i.e. the belief that a social

Table 2. Examples of other potential hormonal mechanisms associated with human and non-human primate cooperative behaviour. Review papers cited where possible, blank cells indicate that more research is needed.

hormone	context	primates	human males	human female
serotonin	in-group	macaques [72]	[73–75]	
prolactin	paternal behaviour/pair-bonding	marmosets [76], tamarins [77]	[16]	
oestrogen	in-group			no effect [34]
cortisol	in-group	marmosets [78], baboons [79], bonobos [38], macaques [53]	[80–82]	

partner will cooperate), can be increased by endogenous OT or artificial OT administration (and reduced by testosterone; see below) highlights OT's role in adjusting cooperation to expected fitness gains. To conclude, OT has been co-opted beyond just parental care and pair-bonding to influence many aspects of prosocial behaviour, and species differences in reciprocal cooperation should be reflected in evolutionary changes in OT physiology (figure 1).

(e) Oxytocin and intergroup interactions

As mentioned before, the formation of an in-group at every relational level (parent–infant, pair-bonds, friendships) also creates an out-group which could threaten the benefits generated by cooperation and result in a parochial psychology probably mediated by OT. In some species, interactions with out-groups can be a context of large-scale collective action; males in several non-human primate species from capuchins to chimpanzees engage in coalitional aggression against out-groups [63,64]. Little is currently known about hormonal mechanisms underlying such coalitional aggression in other primates, though testosterone is involved in border patrols among chimpanzees (see below) [32]. In humans, OT administration increases in-group conformity [65], increases ethnocentrism and decreases trust of out-group members [66], as well as increasing willingness to lie to out-group members [67]. Thus, while OT mediates aspects of bonding with in-group members, it also fosters an out-group psychology.

Internal and external warfare among small-scale hunter–gatherer groups arguably resembles coalitionary aggression in chimpanzees [1] and to the extent that this indicates an ancestral adaptive problem, the OT mediated in-group/out-group psychology described above [68] might reflect shared adaptations for coalitional aggression among humans and chimpanzees. However, in the past 8000 years shifts to more defensible resources such as livestock or agricultural land have led to increases in the frequency, scale and intensity of warfare [8]. In this context, culturally evolving mechanisms for co-opting the parochial effects of OT could have been crucial for success in warfare [69–71]; for instance, the creation of stable cooperative units with fictive kinship categories ('brothers in arms') could perhaps amplify in-group loyalty and xenophobia, while the rigid hierarchies and systems of reward and punishment typical of successful armies might be partly based on hormonal mechanisms for dominance and subordination shared with other hierarchical primates. In summary, there is good evidence that OT modulates parochial psychology in humans, though little research has examined its effects in real intergroup interactions in any species. It is an open question whether the large-scale collective action seen in human warfare is mediated by derived mechanisms or ones shared with other primates.

3. Testosterone, competition and paternal investment

While we have thus far focused on OT, there are a number of other endocrine mechanisms associated with social behaviour (tables 1 and 2); when it comes to conflict and competition, either in human or animal models, most hormonal research has focused on testosterone. Testosterone is related to many male reproductive trade-offs; higher levels of testosterone have anabolic effects on muscle tissue which, while beneficial for male–male physical confrontations, can force energetic trade-offs between costly muscle mass and immune function [83]. The evolution of testosterone in vertebrates probably began with male–male competition over access to mates. Muscle tissue is calorically costly to maintain, as muscle mass uses approximately 20% of daily basal metabolic rate in adult human males [84], and testosterone is also lipolytic, burning off fat reserves that could be vital during lean times [85]. Males in better condition can afford higher levels of testosterone and the associated physiological costs; thus there is a wide range of testosterone levels within and between individuals [86,87].

Males in poor condition cannot maintain high levels of testosterone; illness and injury lead to rapid decreases in testosterone [88–90], as does short and longer term fasting [91,92], and extensive energetic expenditure [93]. While some human and chimpanzee populations show no seasonal variation in testosterone [94,95], large studies of subsistence human and wild baboon populations report decreases in testosterone during leaner times [96,97]. Despite population variation in baseline testosterone, even populations with low baseline testosterone express acute increases in testosterone of the same relative magnitude as those reported in energetically replete populations [98]. Because maintaining consistently high levels of testosterone can be energetically expensive (among other costs to parenting and potential immunosuppression), many seasonally breeding species avoid these costs by only producing high levels of testosterone during the mating season [87].

(a) Testosterone, parenting and pair-bonding

While OT tends to increase during parenting, many species, including humans, show decreases in testosterone [16,99]. Higher levels of testosterone are correlated with mating effort in seasonally breeding [100,101] and non-seasonally

breeding primates [16,35]. Engaging in mate competition, mate guarding and courtship takes a significant amount of time and energy. For primates that engage in paternal behaviour, the energetic costs of investing in new reproductive opportunities trades off against investment in paternal care of current offspring. Thus, it is not surprising that males in species with paternal care tend to have lower levels of testosterone while engaging in paternal behaviour [102]. For monogamous species, reproductive effort not only trades off against parenting, but also with investment in a single mate versus other mates [16,29,103]. Thus, high testosterone levels are associated with short-term mating strategies, and low testosterone levels with long-term mating strategies.

(b) Testosterone and dyadic competition

Acute increases in testosterone during male–male competition permit short-term benefits such as increased sugar uptake by muscle cells during physical confrontations while avoiding the energetic costs of a continually high testosterone phenotype [104,105]. The dynamics of acute and longer term (e.g. seasonal) testosterone change have been well studied using a life-history theory framework with a theoretical model called the challenge hypothesis (CH) [99]. The CH has been applied to dyadic encounters in many vertebrates from fish [106] to birds [99], and mammals including primates [35,107,108]. The acute male–male competition portion of the CH, which has since been expanded upon by Wingfield and co-workers [109], has also been applied to human male sports competitions among unrelated men, resulting in increased testosterone during and following competition [39]. It should be noted that while in humans this research is usually conducted among young, college-age males who are in the peak age range for testosterone, acute increases in testosterone occur across a wide range of ages [98], and even among women [31].

While engaging in physical competition often results in acute increases in testosterone in both competitors, the winners of male–male competition appear to have larger increases in testosterone across many taxa [107], including many, though not all, studies in humans [39]; this phenomenon is often called the 'Winner Effect' or 'Winner-Challenge Effect'. In humans and animal models, repeated acute increases in testosterone during physical activity have the potential to benefit muscle physiology [104,105,110] (though see [111,112], and the rebuttal [113]). In animal models, repeated winning during conflict can result in more aggressive strategies and the increased probability of winning future fights [107,114]. The mechanism responsible for acute increases in testosterone during competition or even physical activity has yet to be elucidated, and indeed some types of non-competitive physical activity result in greater increases in testosterone than direct male–male competition [115]. It is therefore difficult to test whether acute increases in testosterone during physical activity are an adaptation, or exaptation. That said, it is important to note that acute increases in testosterone also occur during competition in the absence of physical activity (e.g. chess, dominoes and video games) [30,116,117]. Acute increases in testosterone during even non-physical interactions help prepare the competitor, by activating receptors in the amygdala that increase the salience of violent threat [10], and also via acute benefits to muscle physiology in the event that the confrontation escalates to violence [105]. Additionally, there appears to be an anticipatory rise in testosterone prior to sports competition, even before any physical activity has taken place, perhaps preparing the body both physically and mentally [118]. Thus it seems likely that acute increases in testosterone during competitive non-physical activity, or in preparation for physical competition, are indeed adaptations to prepare the competitor both mentally and physically, while avoiding the costs (e.g. energetic, potentially immunosuppressive, parenting) of consistently elevated testosterone.

(c) Testosterone and intergroup competition

While many mammalian competitions are dyadic with a single winner and a single loser, human and other primate competitions often involve large groups of related or unrelated individuals. Consistent with the parochial psychology described above (e.g. [65,66]), men and women engaging in competition against another team show larger increases in testosterone than when they are scrimmaging with their own teammates [30,31]. Interactions between testosterone and OT may reinforce each other to produce these parochial effects (see below). Additional evidence with more salient in-groups come from Dominica, where men playing dominoes against competitors from neighbouring villages tended to have larger increases in testosterone than individuals playing against competitors from their home community [117]. A recent study found that acute increases in testosterone can increase cooperation within an in-group via increased parochial altruism when facing a potential out-group [119]. Interestingly, research conducted among Tsimané, where community membership is fluid and community-based competitions often pit men against their kin, show no evidence of a team-based winner effect [98].

Competition between sports teams often allow individuals to show their prowess regardless of their team's success; indeed, studies find that males who outperform their teammates show larger increases in testosterone, regardless of whether their team won or lost [98]. In chimpanzees, certain 'impact' males increase the likelihood of a border patrol [120,121], and some of these impact patrollers also went on to become alpha male and achieve high reproductive success. It is not known whether these impact patrollers show acute spikes in testosterone beyond that of other chimpanzees on the same patrol, but such a study would be an interesting comparison given that high impact human soccer players have larger acute increases in testosterone than others on the same team [98]. Thus, individual differences in performance or motivation are probably related to differences in endocrine physiology, with substantial effects for collective action.

4. Synthesis and future directions

While the above studies describe some of the current state of the literature in regards to two potential hormonal modulators of cooperation at various relational levels, there is still a paucity of research on hormonal mechanisms that help facilitate large-scale collective action. Three potential areas for future research are discussed below; (a) interactions between hormonal systems, (b) genetics and sensitivity of hormone receptors and (c) phylogenetic analyses.

(a) Interactions between hormonal systems

Most studies of hormone–behaviour interactions focus on a single behaviour and a single hormone, but not interactions between endocrine systems. Interactions are important because considerations of adaptive value or exaptation for a particular hormone requires knowledge of the average effects of that hormone across all conditions, even when those conditions may vary across levels of other hormones. A few papers have addressed the possibility of interactions between a limited number of hormones. For example, the 'Dual Hormone Hypothesis' examines interactions between cortisol and testosterone with respect to dominance [122]; in particular, when male social status is under threat, high testosterone men become aggressive, though only when cortisol is low [123]. Another line of evidence examines the 'Steroid/Peptide Theory of Social Bonds' focusing on the inter-related roles of testosterone, OT, vasopressin and social bonding [103]. Other studies have examined the impact of cortisol on testosterone following fatherhood [124]. These are excellent first steps, as individual hormones do not exist in isolation. There are many examples of hormonal systems that overlap in their response to a stimulus; during mammalian stress response, rapid increases in catecholamines (epinephrine and norepinephrine) have acute impacts on heart rate and blood pressure, and release glucose stored in the liver to increase energy necessary to fight or flee from the stressor. Catecholamines also release enzymes that speed up the ability of the body to release cortisol. Thus, there are networks of synergistic and antagonistic hormones that reinforce and feedback into other hormonal systems. With the advent of new imaging techniques like multiplex technology, it is now possible to measure multiple hormones simultaneously, and to explore interactions not only between baseline hormone levels, but also among levels during acute changes in these hormones, in relation to different treatment conditions.

How do OT and testosterone interact to produce cooperation at the various relational levels discussed here? While testosterone and OT are usually considered diametrically opposed forces, with testosterone promoting aggression and OT promoting bonding (e.g. [13,103]), there is evidence in mouse models that higher levels of testosterone can promote OT binding [125] and receptor transcription [126]. OT can also augment Leydig cell testosterone production [127,128]. Studies in humans show that both testosterone and OT increase simultaneously in a range of activities from sexual activity [18], to hunting [46], to in-group/out-group competition [26,33], and that exogenous OT administration increased salivary testosterone levels and enjoyment from parenting in fathers [47] (though note that not all OT administration studies find concurrent increases in testosterone [129]). Taken at face value, this evidence may suggest the potential for OT and testosterone to work in concert to promote cooperative or coalitional behaviours. For example, high levels of OT could increase tolerance within an in-group and simultaneously facilitate negative interactions with out-group members [26,67,68], while a concurrent rise in testosterone could prepare both body [105] and mind [10] for potential violent interactions. Thus, testosterone and OT could be working in a coordinated fashion to facilitate investment in cooperative relationships (mostly low testosterone, high OT), but also protective aggression against out-group threats at any relational level (high testosterone, high OT). Beyond parenting and mating contexts [103], studies examining interactions between testosterone and OT in terms of baseline levels and acute changes in relation to cooperative behaviour have yet to be conducted [47].

(b) Beyond hormone concentrations: genetics and sensitivity of hormone receptors

Most studies examining hormone–behaviour interactions have focused on measuring baseline and/or acute changes in circulating hormones, or the behavioural changes induced by an exogenous administration of a hormone; yet circulating hormone levels comprise only one component of a broader biological communication network that facilitates different behavioural responses (figure 1). A classic example of the role of hormone receptors, above and beyond circulating hormone levels, comes from monogamous prairie voles and polygynous montane voles, both of which have the same circulating levels of OT but differ in receptor distribution in the brain [130]. As the effects of these changes are highly localized (as opposed to the systemic effects of changes in baseline levels), they probably represent adaptations resulting from selection on specific behaviours, in this case pair-bonding and parenting [7].

For a hormone to have an impact on behaviour then, it must activate receptors in critical brain regions. Most hormone receptors are laid down during sensitive organizational periods, such as perinatally and during puberty [131–133]. Most experimental work on receptors is with murine models, where exposure to androgens is critical for the development of androgen receptors and the organization of brain physiology. Male mice gonadectomized prior to puberty never develop the level of androgen receptors required for activation of male behaviours, even when exposed to high levels of testosterone during adulthood [131]. This may explain some sex differences in male and female response to exogenous testosterone (table 1); studies in humans find that males given testosterone supplementation show changes in behaviour on economic games [33], while women show no behavioural change [34]. Interestingly, female hyaenas are one of relatively few species where testosterone regulates female aggression, and females have relatively high levels of circulating androgens *in utero* and during the peri-pubertal period; female hyaenas thus develop androgen receptors and behaviour typically associated with male mammals [6,11].

It is difficult to measure receptor densities in living animals. Most studies that directly measure receptor densities sacrifice the animal, and then stain brain tissue. Another, less invasive method to examine individual or species differences in receptors is through variation in the genetics of hormone receptors (table 3). With regards to androgens, the number of CAG codon repeats on the androgen receptor modulates the impact of circulating androgens; fewer CAG repeats result in greater androgen receptor protein expression and transcriptional activity, which result in greater impact per unit of circulating androgen [150]. In non-human primates, macaques and marmosets have no variation in CAG repeats (monomorphic), while baboons and chimpanzees show polymorphic variation [151]. Several studies have reported that human males with fewer CAG repeats have higher levels of upper body strength, self-reported competitiveness and greater testosterone response to potential mate exposure [150,152], though not all studies find associations between strength and CAG repeat length [153,154].

Table 3. Examples of receptor genetics associated with cooperative behaviours for humans and primates. Review articles cited when possible, blank cells indicate more research is needed.

receptor genetics	context	primates	human males	human females
androgen receptor	short CAG repeats → less prosocial		in Chinese, *but not Israeli men* [134]	*no effect* [134]
oestrogen receptor (ER-b)	shorter allele (suggesting more oestrogenic activity) linked to lower minimal acceptable offer			[134]
serotonin transporter (5-HTT)	longer allele more prosocial, shorter allele more anxious	macaques [135–137]	[138]	
dopamine receptor (DRD4)	DRD4 allele increase in fairness	*no effect in macaques* [135]	[139]	
vasopressin receptor	vasopressin receptor AVPR1A-RS3 carriers less fair in dictator games		[140,141]	
	double deletion of DupB region (which includes RS3) decreases social cognition, competence	chimpanzees [142] no deletion in bonobos [143]		
	vasopressin receptor AVPR1A-RS3 more likely to divorce		[144]	
OT receptor	OXTR SNPs (rs53576 and rs2254298) increase prosociality	no variation in chimpanzees and bonobos [143]	mixed results [145,146], *but some meta-analyses show no significant effect* [147]	
	OXTR and pair-bonding	*receptor differences in primates do not map onto mating system* [148]		
prolactin receptor	pair-bonding	*receptor differences do not map onto paternal care* [149]		

Though the genetics of androgen receptors may be a promising avenue, the evidence for impacts of several candidate single nucleotide polymorphisms (SNPs) associated with the OT receptor gene *OXTR* appears less conclusive, as indicated by a recent meta-analysis finding no significant overall effects of *OXTR* variation on social behaviour [147] (though another meta-analysis vindicated an association with autism [145]). Furthermore, bonobos and chimpanzees do not exhibit these candidate SNPs despite differences in social behaviour [143], and variation in *OXTR* as well as prolactin and vasopressin receptor genes across primates more broadly do not easily map onto social and mating systems [148,149,155]. Finally, suggestive results have been found for various other receptor genes, as summarized in table 3. For example, chimpanzees with a deleted DupB region of the vasopressin receptor have impaired social cognition and fewer allies [142]; in human males, deletion of a portion of the same region (RS3) is associated with higher divorce rates [144]. In summary, there is a limited, but growing body of evidence that variation in the genetics of hormone receptors may impact social behaviour above and beyond circulating hormone levels (e.g. figure 1), thus providing more direct evidence for adaptation [9].

In sum, hormonal reinforcement of behaviour need not just result from increased hormone levels, but also increased receptor sensitivity or density, or even increased neural transport of hormonal signals to critical brain regions. When considering the evolution of mechanisms that could reinforce behaviour, it is therefore essential to focus not just on hormones, but also their binding proteins (which modulate the bioavailability of circulating hormones), receptor sensitivity and specificity, and the location of those receptors in critical brain regions (figure 1). For example, most circulating testosterone in humans is bound to carrier proteins (sex hormone-binding globulin (SHBG) and albumin), with only about 2% of circulating testosterone unbound or 'free'. Testosterone bound to SHBG is unavailable for use in target tissues, so species level variation in SHBG could influence the bioavailability of testosterone even for two species with the same total levels of testosterone. Advances in endocrinology, receptor genetics and neuroimaging will make it possible to examine how changes in hormones impact brain physiology in ways that impact changes in behaviour [10,156].

(c) Phylogenetic approaches to hormonal mechanisms

Examining the evolutionary history of the mechanisms that mediate hormonal physiology is a vital step for disentangling adaptations from exaptations, trade-offs or constraints [6]. Phylogenetic analyses of more than 100 avian species suggest that environmental constraints shape reproductive behaviour and mediate both baseline and peak levels of androgens [157]. However, phylogenetic analyses examining differences in

hormone–behaviour interactions, particularly those related to cooperation, competition and collective action in primates, have yet to be conducted. One of the few studies looking at closely related primate species with different social ecologies found substantial differences in chimpanzee and bonobo hormonal responses to competition [38]. An integrated phylogenetic approach, examining both baseline and acute changes in neurohormones and receptor densities, binding proteins and other potential hormonal mechanisms across primate species, is needed to advance our understanding of evolved human behavioural endocrinology.

5. Conclusion

While most of the hormone–behaviour interactions discussed here were species typical (e.g. the role of OT in marmoset paternal care), individuals within many species vary in their degree and willingness to cooperate, reflecting different adaptive strategies. The rich literature on animal and human personality, or 'behavioural syndromes', is similarly focused on the adaptive logic of relatively stable, individual differences [158]. Hormones may play a proximate role in modulating certain aspects of personality variation. For example, testosterone has been linked to behaviours conceptually related to dispositional dominance [159]. Basal levels of hormones like testosterone may serve as biomarkers of individual difference, given its relative temporal stability. A recent study among high fertility Senegalese men showed that higher testosterone was associated with greater extraversion [160], lower parenting effort and greater tendency to be married polygynously [161], whereas in a US sample high testosterone men also had larger testes, engaged in less parenting and showed weaker neuronal activation in response to pictures of their babies [102]. Thus, one potential underlying proximate cause for individual differences is that both baseline and acute changes in neurohormones like testosterone or OT vary within and between individuals. As mentioned above, it is likely that such hormonally mediated personality differences play a substantial role in shaping cooperation and collective action [121].

Despite sharing the same conserved components of the endocrine architecture with other primates and mammals, humans cooperate in more contexts and at larger scales [1–3]. A critical question for future research is whether high levels of cooperation in humans differ mechanistically from other species, and in particular whether they are driven by changes in circulating hormone levels that impact various behaviours, e.g. through selection for reduced dominance (testosterone) and increased tolerance (OT), or whether selection for specific behaviours has changed endocrine physiology in more targeted ways (e.g. differences in receptor density or selectivity, binding proteins, etc.; cf. figure 1) [7]. Answering these questions has potential implications for various theories of human and primate cooperation such as the cooperative breeding hypothesis [3] (which posits a general increase in social tolerance and cognition, e.g. through higher OT levels) or the self-domestication hypothesis [162] (general decrease in aggression, e.g. through lower testosterone). It is likely that with a better understanding of interactions between hormones, a stronger focus on hormone receptors and better tools to examine neuronal function, we will have a better understanding of the hormonal modulation that facilitated the evolution of large-scale human and primate coalitional behaviour.

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