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Evolution of genetic and physiological mechanisms of cooperative behaviour

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Emergence of cooperative behaviour requires the evolution of proximate mechanisms to overcome the conflict of fitness interests inherent in social interactions. Reciprocal trading and enforcement of help are means by which cooperation can ensue between social partners subject to conflicting fitness interests. We discuss potential routes to the evolution of mechanisms of cooperative behaviour, with a special focus on vertebrates. We emphasize that a stable social organization, the exertion of social control and the experience-based propensity to act cooperatively are fundamental building blocks of cooperation. Genetic, neural and endocrine mechanisms involved in the regulation of cooperative behaviour are apparently deeply conserved in the phylogenies of different taxonomic groups. At the same time, the functions of regulatory systems diverge enormously between taxa, revealing functional independence and modular evolution of key components at both genetic and physiological levels.

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The evolution of proximate mechanisms of behaviour

Evolution-oriented behavioural biology is currently experiencing a paradigm shift from a rather narrow focus on the functions and adaptive nature of traits to a more comprehensive approach incorporating psychological, physiological, genetic, ontogenetic and epigenetic mechanisms [1,2]. This reflects a recollection of the initial aims of ethology, which have been aptly summarized in Niko Tinbergen's seminal paper on that theme [3]. The recent urge for a more comprehensive understanding of behaviour, after a period in which 'behavioural ecology' with its tight slant on adaptive value has dominated the field, coincides with methodological developments now allowing researchers to ask questions about regulatory mechanisms at physiological and genetic levels, that is unprecedented [4,5,6••]. This broader approach to studying behaviour enables us, for the first time in the history of the biological study of behaviour, to address the pertinent question about the *evolution of proximate mechanisms* underlying behaviour [2,7••].

An integrative approach to the study of social behaviour

Animals regularly interact with conspecifics, which can be both each other's strongest allies and fiercest competitors for resources. The resulting conflict and cooperation characterizing many intraspecific interactions selects for adequate responses to the behaviour of social partners [8••]. Like any other behavioural trait, these interactions are the products of genetic and physiological mechanisms that affect Darwinian fitness and evolve via natural selection [6••]. Comparative analyses suggest that in both social insects and vertebrates, regulatory elements of social behaviour at genetic and (neuro)physiological levels are remarkably conserved [7••,9,10••]. Hence it seems obvious to ask whether and to which extent the evolution of cooperative behaviour, arguably *the* conundrum of Darwinian rationale, is influenced by the functionality and constraints of underlying genetic, epigenetic, endocrine, and neural mechanisms.

Where do we find cooperation, and how can it evolve?

Cooperation refers to the simultaneous or consecutive acting together of two or more individuals by same or different behaviours. It can evolve when all partners of a cooperative action obtain a fitness benefit from their behaviour, that is when the fitness benefits of the action outweigh its costs in the short or long term to each participant either by mutualism, reciprocity or correlated pay-offs (e.g., involving relatedness). Alternatively, the behaviour may be beneficial only to the receiver of a cooperative act, who can coerce another individual to behave cooperatively. In mutualistic interactions, there is typically no conflict of fitness interest between social partners, because the behaviour straightforwardly raises the direct fitness of the actor [11]. A familiar example of mutualistic interactions is group hunting, where individuals share forces to obtain prey, which typically provides a net benefit to all participants [12]. In case of mutualistic interactions the mechanisms of the involved behaviours can evolve by the same principles as any non-cooperative behaviour, because the potential fitness consequences to a social partner hardly matter. By the same token, if individuals act cooperatively towards others because their fitness pay-offs are correlated due to relatedness between them, that is because the behaviour is selected by indirect fitness benefits to the cooperator, there is usually little conflict of fitness interests. This applies for instance to many cooperatively breeding birds (e.g. [13]). More interesting for the question how the mechanisms controlling cooperative behaviour can evolve is the case where there is a distinct conflict of fitness interests between the involved parties. In that case, behavioural mechanisms will be selected that maximize the benefits of one party at the expense of another [14]. We shall further focus on this possibility.

If there is a conflict of fitness interests between social partners, cooperation can evolve by reciprocity or coercion. Individuals may receive fitness returns by cooperation if their interaction partners pay back received help, either concurrently or in the future. Reciprocal cooperation or 'trading' of that kind usually involves negotiation between social partners [15], which involves rules that are subject to selection [16,17]. Reciprocity and trading require a number of cognitive abilities, including individual (or 'class') recognition, the ability to relate the behaviour of others to own pay-offs, and a certain degree of social memory. The requirement for social memory depends on whether actions and reactions occur concurrently ('coaction') or with some time lag ('reciprocity' [18•]). Reciprocity and trading has been demonstrated in a wide range of vertebrates, from fish to mammals [19–22]. Social bonds can favour such exchanges of cooperative behaviours [23]. Both the neuroendocrine 'social behaviour network' involving steroid and neuropeptide hormones, and the mesolimbic reward system involving dopaminergic signalling pathways constitute important regulatory mechanisms responsible for the concerned behaviours [4,7••].

A much simpler form of reciprocal cooperation can ensue if individuals 'return' received help to others, that is not to the individual from which they received help. Such 'generalized reciprocity' has been shown to afford evolutionarily stable levels of cooperation under a wide range of conditions (e.g. [24,25]). This cooperation mechanism is particularly intriguing because it does not require specific cognitive abilities, except the recognition of received help [26,27]. Hitherto it has been experimentally demonstrated in rats, monkeys and humans, but because of its mechanistic simplicity, it is expected to be much more widespread [26,28,29]. In vertebrates, neuroendocrine regulation of generalized reciprocity may be mediated primarily by the nonapeptide system, particularly oxytocin or its orthologs [30–32].

One social partner forcing another one to cooperate constitutes the second possibility to generate cooperative behaviour among social partners subject to a conflict of fitness interests. Enforced cooperation can be evolutionarily stable if the costs to avoid such manipulation are higher for an individual than to accept being exploited. The generation of cooperation by this means requires some sort of dominance asymmetry between social partners, the ability of the receiver of enforcement to respond appropriately to the dominant's demand, and the ability of the dominant to accept the resulting cooperation as consummatory response. Enforced cooperation occurs in a wide range of taxa and contexts [33–38]. Steroid hormones are important regulatory components of social interactions based on dominance asymmetries, which can affect the cooperation propensity of subordinates [39–41].

Hitherto, cooperation between social partners with a conflict of fitness interests has been studied mainly regarding its mode of action and its potential adaptive value, without considering underlying psychological, physiological and genetic mechanisms. If we wish to fully understand the evolution of cooperation, however, we need to unravel the required components, the involved decision rules, the ecological functionality, potential synergistic effects and eco-evolutionary feedbacks, trait evolvability and mechanistic constraints [6••,42,43,44•,45–49,50•,51]. In particular, we need to understand the emergence of novel traits that are prerequisites for such seemingly demanding interaction, and the mechanistic building blocks of cooperative behaviour, taking into account the effect of potential conflict of fitness interests on the evolution of involved proximate mechanisms.

Routes to the evolution of mechanisms of cooperative behaviour

Obviously, the evolution of sociality from solitary ancestry and the evolution of cooperative from non-cooperative behaviours require the emergence of novel social traits, such as individual or 'class' recognition and social memory. High degrees of pleiotropy would naturally limit the emergence of novel traits, but recent analyses quantifying the degree of pleiotropy across different organisms revealed that it is much more restricted than previously thought, and that genotype-phenotype maps are highly modular [52].

Two main evolutionary routes to novelty in social traits have been evaluated in cooperative animal societies, hitherto best exemplified in social insects. (1) Evolving new social behaviours from ancestral gene networks that gain increased regulatory flexibility and are co-opted for a new function; (2) emergence of genetic novelty, which is particularly required for the evolution of the most advanced forms of eusociality [53–55]. The first route builds on the existence of distinct, ancestral molecular modules regulating the physiology and behaviour of solitary species, which have undergone modification during the transition to (eu)sociality. These distinct modules are combined to produce social pathways orchestrating all steps of an appropriate behavioural expression from perception of a stimulus to the final motor action. Regulatory processes are connected strongly within, but only weakly between modules, allowing largely independent module evolution and functional flexibility [54]. An example for co-opting of conserved elements in this context is the gene network around the juvenile hormone (JH) and vitellogenin (*Vg*). In solitary insects and reproductive queens, JH upregulates Vg and stimulates oocyte maturation, while in workers of eusocial bees, ants and termites, the two genes inhibit each other [56].

Evolution of novel genes, the second major route to evolutionary novelty, is assumed to be associated with later stages in the transition from solitary to (eu)social life style [10••]. It can be identified with help of 'taxonomically restricted genes' (TGRs). In the honey bee genome, 700 such TGRs were detected, which exist *solely* either in the honey bee, in hymenoptera, or in insects [55]. These genes were found to underlie disproportionately often novel phenotypes involving worker traits, and to undergo rapid changes of coding sequence [57]. Remarkably, independent evolutionary transitions from solitary to (eu)social life styles differ in their particular genomic changes, but the different transitions have similar *general* features [58].

Here we aim to evaluate whether the same two general routes to evolve cooperative behaviours, namely co-opting of conserved elements and de novo evolution, may likewise apply in vertebrates. While molecular mechanisms generating genetic novelty are not yet well explored in vertebrates, several conserved signalling systems are known to be involved in the behavioural and physiological building blocks of vertebrate cooperation. Here we identify three building blocks and discuss their underlying regulatory mechanisms, and the insights thus far achieved regarding their evolution.

Proximate building blocks of cooperation

The first building block of cooperation is a stable social organization that remains functional even if conflicts of interest occur among individuals. Unnecessary friction or repeated negotiations of dominance relationships and task commitment can be avoided if individuals express appropriate social behaviours dependent on their (relative) social state and the particular context [8••]. Developmental processes and current social stimuli underlie the expression of appropriate social behaviour. A key developmental mechanism in this context is the early acquisition of social competence, that is the ability of individuals to flexibly use social information in order to optimize their social performance [8••]. The early programming of the vertebrate stress axis [hypothalamic-pituitary-adrenal (HPA) or -interrenal (HPI) axis] seems central for determining social performance later in life: in fish, mice and rats, social enrichment results in both (i) a lower stress responsiveness, as revealed by the expression of stress axis genes in the brain and by behavioural test results, and (ii) a better performance during social challenges [59,60,61•]. In the cooperatively breeding cichlid *Neolamprologus pulcher*, for instance, these behavioural effects enhance the functionality of social groups by increasing the tolerance of subordinates and reducing the duration of contests [62,63]. Furthermore, in rodents the development of social competence is accompanied by higher concentrations of the neural plasticity marker BDNF in the brain [64].

Immediate social experience may also trigger the physiological state of an animal in order to prepare it to perform appropriate social behaviour. For example, watching a fight between conspecifics changes the physiological state of a bystander in the cichlid *Oreochromis mossambicus* [65]: the bystander experiences a surge of androgens, probably thereby getting prepared for an aggressive encounter in the near future. Hormonal systems are known to generally affect sociability, which is a precondition for group life. The oxytocin-like peptides including oxytocin (mammals), mesotocin (birds, reptiles and amphibians) and isotocin (fish), and their receptors, which form the vertebrate nonapeptide signalling system together with arginine vasotocin/vasopressin, have often been highlighted as *the* promotor of social behaviour. However, due to the modular nature of the nonapeptide system and its species-specific evolution [66•], general predictions of the direction of effects can often not be made, even within a vertebrates class. For instance, while in humans, non-human mammals and goldfish oxytocin/isotocin favours social approach [66•], in the cooperatively breeding cichlid *N. pulcher* it has exactly the opposite effect [67], while no effect was observed on approach behaviour in zebra finches [66•]. In general, long-term social relationships such as pair or family bonds may help to reduce conflict. However, the physiological regulation of pair bonding involving the vasopressin or the oxytocin system seems to strongly diverge between different vertebrate taxa [66•], revealing that taxon matters when studying mechanisms of social behaviour [68]. In fact, to date there is no clear evidence that nonapeptides are at all *causally* involved in the process of bonding.

The second building block of cooperation between individuals that are subject to a conflict of fitness interests is the exertion of social control to prevent cheating, and to manifest the division of tasks between dominants and subordinates. Here, differences in social rank play an important role, which are often associated with differential sex steroid profiles, in particular variation in androgen and progesterone levels (cichlids: [39,69] mole rats: [70]).

High rank often needs to be persistently reinforced, which typically occurs by dominants' aggression. Also here, the functionality of the underlying hormonal regulation may diverge between species. For instance, activation of the AVT system has been assumed to favour aggressive tendencies in dominants of mouthbrooding cichlids [71], but in the cooperatively breeding cichlid *N. pulcher* no association between aggression and AVT could be identified [72]. Furthermore, comparative evidence suggests that an induction of increased stress levels in subordinates by repeated aggression of dominants is unlikely to act as general control mechanism in cooperative breeders, as dominants often have higher corticoid levels than subordinates [73]. However, during specific critical circumstances, such as during a dominant female's pregnancy (meercats [74]), or because of particularly harsh environmental conditions (superb starlings [75]), dominant aggression can effectively restrain subordinate reproduction through an activation of the HPA axis, with downstream effects on gonadotropin-releasing hormone in the hypothalamus and resultant blocking of ovulation. A similar pathway was proposed to be involved in species in which dominants can achieve complete reproductive suppression of subordinates, such as in eusocial naked mole rats and Damaraland mole rats [76].

Alternatively to active control by dominant aggression, subordinates can pre-emptively provide honest signals of submission or of their helping propensity [77], or of low reproductive intent [39]. For example, the circulating levels of androgens are lower in male helpers of *N. pulcher* showing high levels of submission towards breeder males, thereby conveying an honest signal of their low reproductive potential [39]. Subordinates can exhibit self-imposed reproductive suppression in systems where dominants would inevitably kill subordinates' offspring. In common marmosets, the pituitary gonadotropin levels dropped rapidly and ovulation stopped when individuals were introduced into groups where they had to obtain a subordinate role [78].

Mechanisms of the third building block of cooperation, the actual propensity to behave cooperatively, have been predominantly studied in vertebrates in the context of reciprocity or when commodities are exchanged, with a focus on the role of the nonapeptide system. Like for the effect of nonapeptides on social approach, general trends appear to be absent. Activation of the oxytocin (humans: [79]) and the AVT/AVP system (humans: [80]) were found to enhance cooperative tendencies as often as they were reported to inhibit cooperation (OT: humans [81]; AVT: cleaner wrasse [82]) or to exert effects strongly contingent on social context (OT: humans [80,83]). Experimental work on Norway rats suggests that the effects of oxytocin on reciprocal cooperation may be mediated mainly by its role in modulating social anxiety rather than a specific effect on the generation of trust (M Dietz, M Taborsky, unpublished data). A general anxiolytic effect of oxytocin seems to affect cooperation propensity also in capuchin monkeys [84].

Notably, the physiological mechanisms mediating helping behaviour in cooperative breeders are hitherto not well understood. Thus far the role of two hormones has been studied more closely in meerkats, cortisol and prolactin. Their effects seem to depend on the particular care behaviour considered. Cortisol but not prolactin was positively associated with alloparental pup-feeding [85]. In contrast higher prolactin but lower cortisol levels immediately advanced babysitting in male helpers of this species [86].

Conclusions

When compiling existing information about the mechanisms underlying cooperative behaviour in vertebrates and its essential building blocks embedded in social interactions, at first glance the picture seems blurred. It becomes quickly clear, however, that the same regulatory systems often have divergent functions and effects in different taxa. Despite the obvious conservation of neural and neuroendocrine components among very divergent vertebrate lineages [7••,66•], the functions of the involved regulatory systems seem to vary substantially, suggesting independence by modular evolution. Two candidates stand out as being involved apparently in all three building blocks of cooperation, the vertebrate stress axis and the nonapeptide system. They act in very different ways, though, often showing directly opposing effects in different species. To some extent this resembles the regulatory shifts in 'old' genes to new functions in the social insects [10••]. The enormous variety of cooperative behaviours shown in vertebrates and the flexibility of their context-dependent expression are unlikely to be governed merely by two hormonal systems, however. We are only just beginning to understand the regulatory and signalling networks responsible for the expression of vertebrate cooperation.

Conflict of interest statement

Nothing declared.

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