

MEETING REVIEW**Genetics and developmental biology of cooperation**

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Abstract

Despite essential progress towards understanding the evolution of cooperative behaviour, we still lack detailed knowledge about its underlying molecular mechanisms, genetic basis, evolutionary dynamics and ontogeny. An international workshop "Genetics and Development of Cooperation," organized by the University of Bern (Switzerland), aimed at discussing the current progress in this research field and suggesting avenues for future research. This review uses the major themes of the meeting as a springboard to synthesize the concepts of genetic and nongenetic inheritance of cooperation, and to review a quantitative genetic framework that allows for the inclusion of indirect genetic effects. Furthermore, we argue that including nongenetic inheritance, such as transgenerational epigenetic effects, parental effects, ecological and cultural inheritance, provides a more nuanced view of the evolution of cooperation. We summarize those genes and molecular pathways in a range of species that seem promising candidates for mechanisms underlying cooperative behaviours. Concerning the neurobiological substrate of cooperation, we suggest three cognitive skills necessary for the ability to cooperate: (i) event memory, (ii) synchrony with others and (iii) responsiveness to others. Taking a closer look at the developmental trajectories that lead to the expression of cooperative behaviours, we discuss the dichotomy between early morphological specialization in social insects and more flexible behavioural specialization in cooperatively breeding vertebrates. Finally, we provide recommendations for which biological systems and species may be particularly suitable, which specific traits and parameters should be measured, what type of approaches should be followed, and which methods should be employed in studies of cooperation to better understand how cooperation evolves and manifests in nature.

KEYWORDS

altruism, behaviour, indirect genetic effects, social behaviour, social effects

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1 | INTRODUCTION

The question of how cooperation evolves has been a major conceptual puzzle for biologists for centuries. Despite significant inroads in our understanding of the evolution of cooperation over the past 60 years, it remains one of the major challenges in biology to date. While most research into cooperation has been devoted to the functional significance of cooperation, an increasing number of scientists argue that a more holistic approach incorporating functional and mechanistic aspects of phenotypic traits is necessary to provide a complete picture (Bshary & Oliveira, 2015; Soares et al., 2010; Taborsky & Taborsky, 2015; Weitekamp & Hofmann, 2014). First, by only focussing on the functional significance, one implicitly assumes that cooperation is not constrained by the underlying physiological, neural, molecular and developmental mechanisms. However, behaviours such as cooperation can only evolve by changes in those underlying mechanisms (Fawcett, Hamblin, & Giraldeau, 2013). Second, an integrative approach allows us to address questions of convergent molecular evolution (Aubin-Horth, 2015) which is of particular importance for cooperation as it is thought to have evolved multiple times independently (Maynard-Smith & Szathmari, 1997). Finally, theoretical and empirical research can be mutually informative. Detailed knowledge of the mechanisms underlying cooperation and evolutionary constraints on cooperative traits could lead to the development of models that better reflect the actual environmental complexity (McNamara & Houston, 2009; Soares et al., 2010).

Our goal in the workshop “Genetics and Development of Cooperation” organized by the University of Bern, held in Bern, Switzerland, in February of 2016, was to explore new horizons in the fields of genetics and developmental mechanisms of cooperation. A list of the guest speakers and the titles of talks, as well as the names of the workshop participants, is provided in the Supporting Information. In the workshop, we focused on cooperative strategies such as reciprocity, mutualism, and coercion between family groups and non-kin for feeding, protection and raising young. We also discussed cooperative parental care, parent–offspring and sibling conflict, and communal nesting. Plenary talks were used as a launching pad for discussion sessions and poster sessions showcased individual participants’ research. In the following sections, we relate the content and questions raised by the workshop sessions. Moreover, we provide an outlook and further avenues for research in an effort to synthesize the various key points raised by the workshop.

2 | MODES OF INHERITANCE OF COOPERATION

Defining cooperation is notoriously difficult because of the complex interplay of fitness costs and benefits that accrue over different time periods and the varieties of situations under which it occurs (Sachs, Mueller, Wilcox, & Bull, 2004). For the purpose of the workshop, we followed the definition given in Taborsky and Taborsky (2015)

stating that “cooperation refers to the simultaneous or consecutive acting together of two or more individuals by same or different behaviours.” Cooperative acts are typically costly for the individuals involved, but their net result is a fitness benefit. Cooperation can evolve if it yields immediate or delayed fitness benefits for all partners. Alternatively, if one partner can coerce the other into cooperation, only the receiver gains fitness benefits. Cooperative acts that yield direct fitness benefits for all partners are, for instance, improved prey capture when hunting in small groups in wolves (MacNulty, Smith, Mech, Vucetich, & Packer, 2012), lowered predation risk through flocking behaviour in birds (Beauchamp, 2003), reduced heat loss in huddling penguins (Ancel, Visser, Handrich, Masman, & Le Maho, 1997) and increased energetic benefit during V-formation flight in migrating birds (Voelkl & Fritz, 2017; Voelkl et al., 2015). Altruistic behaviours, however, impose costs on actors without yielding direct benefits and result in a net decrease in the actor’s direct fitness while increasing the recipient’s fitness (Lehmann & Keller, 2006). Examples of altruism include sterile castes of social insects that raise a queen’s offspring (reviewed in Ratnieks and Wenseleers (2008)), but also the willingness to share food, engage in collective warfare, or to bear costs to punish noncooperators in encounters with unrelated and even unknown individuals in humans (Fehr & Fischbacher, 2003).

An explanation of how such costly altruistic behaviours may evolve is predicated in the theoretical work by Hamilton who suggested that altruistic genes evolve under the scenario of inclusive fitness (Hamilton, 1964a, 1964b). In his seminal paper (Hamilton, 1964b), he stipulates under which conditions altruism should evolve by deriving the famous Hamilton’s rule, $rB > C$. Under this scenario, costs to the focal individual (C) are outweighed by the benefits to the receiver (B), weighted by the genetic relatedness (r) between the two individuals. If the costs and benefits are similar, cooperation should arise based on genetic relatedness, which is also known as kin selection. Despite this illuminating theoretical foundation, definite evidence for specific drivers for the evolution of cooperation remains difficult to identify for many species that display cooperative behaviours. For example, the evidence for kin selection as a driver of cooperation is mixed (Riehl, 2013; Taborsky, Frommen, & Riehl, 2016) and costs and benefits can be difficult to assess and compare objectively within and between species (Hatchwell & Komdeur, 2000; Sachs et al., 2004). Knowledge of the genetic, molecular and physiological mechanisms that underlie cooperative behaviours can greatly improve our understanding of the evolution of cooperation. For instance, genetic variation in cooperative behaviours reflects their evolutionary potential, that is, how those traits can respond to natural selection. Evolutionary theory predicts that cooperative behaviour, like other phenotypic traits, should have a heritable basis if they are the product of adaptive evolution (Hofmann et al., 2014; Komdeur, 2006; Tinbergen, 1963). In fact, there is some empirical support for heritable differences in cooperative behaviours (e.g., in western bluebirds *Sialia mexicana* (Charmantier, Keyser, & Promislow, 2007), and in humans (Cesarini et al., 2008). However, an individual’s cooperative tendency is likely to be influenced additionally by social

and nonsocial environmental conditions to allow for plasticity during development or to fine-tune pay-offs in its current situation (Fischer 2014; Kasper, Kölliker, Postma, & Taborsky, 2017; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992; Stiver, Dierkes, Taborsky, & Balshine, 2004; Sanderson et al., 2015b). Moreover, nongenetic inheritance of cooperation through social interactions and cultural transmission may add additional layers to the complexity of the evolution of cooperation (Uller & Helanterä, 2017; Avital & Jablonka, 2000; Danchin et al., 2011), but this field is thus far underdeveloped for cooperation.

2.1 | Genetic inheritance and indirect genetic effects

For a cooperative—or any other—trait to be subject to selection, it needs to vary among individuals. This variation should result in differential fitness and should be heritable (Lewontin, 1970). Quantitative genetic models allow researchers to explore the extent to which genetic variation influences phenotypic variation by estimating the proportional contributions of heritable genetic variation and environmental variation to the total phenotypic variation. By combining these estimates with estimates of the fitness consequences of this variation, we can predict how a trait will respond to selection (Lande & Arnold, 1983).

Accounting for the social environment of individuals adds a further dimension to cooperative behaviour because it involves interactions with other individuals, making the behaviour of an individual contingent upon the behaviour and genotype of its social partners. Therefore, the cooperative phenotypes should be considered as being partly influenced by interactions with social partners and the genes they carry, that is, their “interacting phenotype” (Moore, Brodie, & Wolf, 1997). This influence of the social environment sets those traits apart from traits that are solely influenced by heritable genetic and nonsocial environmental components, and therefore requires additional theoretical considerations (Bleakley, Wolf, & Moore, 2010). Especially for cooperative traits, we can expect that the genotypes of interaction partners affect the fitness of an individual in a similar way as the individual's own genes (McGlothlin, Wolf, Brodie, & Moore, 2014). For instance, in species that provide biparental care, parents can negotiate the amount of care each provides which equally affects both parents' fitness in terms of offspring survival (McNamara & Houston, 2005). Another example where social environment may play a key role is cooperative breeding, where helpers might adjust their helping effort based on the contributions of other group members (Adams, Robinson, Mannarelli, & Hatchwell, 2015). Parents can reduce their level of care when helpers are present (Johnstone, 2011; Taborsky, Skubic, & Bruintjes, 2007), or where subordinates are coerced into helping (Clutton-Brock & Parker, 1995; Fischer, Zöttl, Groenewoud, & Taborsky, 2014).

In his talk, “A social effects perspective on kin selection,” Jason Wolf outlined the quantitative genetic version of Hamilton's rule that takes into account the impact of the focal individual's own phenotype on its fitness (“nonsocial selection gradient,” β_N), but also the

phenotype of the individual with whom it interacts (“social selection gradient,” β_S , Figure 1 (McGlothlin et al., 2014). This model demonstrates that selection will favour altruism when the benefits (β_S), weighted by the phenotypic similarity of the partners, are greater than the costs ($-\beta_N$). In cases where phenotypic similarity solely arises due to genetic relatedness, it is equivalent to Hamilton's relatedness term (McGlothlin et al., 2014; Queller, 1992). However, genetically unrelated individuals can be phenotypically similar. Covariances between the partners can arise due to the influence of genes expressed in another individual, providing an “alternative pathway from genotype to fitness” via indirect genetic effects (IGEs, McGlothlin et al., 2014). Unlike a direct genetic effect (DGE) where an individual's genotype directly affects its phenotype, IGEs are the expression of one individual's genotype influencing the expression of another individual's phenotype. Thus, IGEs need to be scaled by a parameter that reflects the genetic influence of an interaction on the trait expressed in the focal individual. Here, the interaction effect coefficient (ψ) illustrates this relationship and ranges from -1 to 1 (Figure 1). In the absence of genetic relatedness, cooperation should only evolve if benefits scaled by the interaction effect coefficient ($\psi\beta_S$) outweigh costs ($-\beta_N$). This framework provides an extension of the quantitative genetics approach to Hamilton's rule to interactions between unrelated individuals. Mutually beneficial behaviours can evolve even in the absence of relatedness between the interaction partners, because both partners gain direct net fitness benefits immediately or with some delay, and hence, no conflict of interest occurs (Lehmann & Keller, 2006). Many examples of cooperation in birds (Riehl, 2013), fish (Wong & Balshine, 2011), vampire bats (Wilkinson, Carter, Bohn, & Adams, 2016), humans (Jaeggi & Gurven, 2013) and insects (Field & Leadbeater, 2016; Gadagkar, 2016) demonstrate that interaction partners are indeed often unrelated. Therefore, kin selection may not be the primary evolutionary force driving cooperation in these systems (Taborsky et al., 2016), and alternative hypotheses focusing on the IGEs should be considered.

2.2 | Nongenetic inheritance

Heritability is not limited to the transference of genetic information from parent to offspring. Nongenetic information can potentially contribute to the evolution of a cooperative trait if it is transmitted from one generation to the next (Uller & Helanterä, 2017). Distinguishing between different forms of heritability is crucial, because the form of transmission determines who inherits from whom and also how reliable the transmitted information is. In his talk “Nongenetic inheritance, maternal effects, epigenetics, and cultural transmission: where are we now?,” Etienne Danchin discussed the concept of inclusive inheritance, which allows not only for the transference of information via genes, but also through mechanisms of nongenetic inheritance (Danchin, Wajnberg, & Wagner, 2014). Nongenetic inheritance is defined as the transmission of factors other than the DNA sequence from ancestors to offspring that affect the offspring's phenotype (Bonduriansky & Day, 2009). Some of these mechanisms include heritable epigenetic effects, parental effects,

ecological (or habitat) inheritance and cultural (or social) inheritance (Danchin et al., 2011).

Narrow-sense epigenetic inheritance occurs when phenotypic variation arises from heritable changes in gene expression, rather than differences in the DNA sequence itself. This variation can occur as a result of structural changes to the genome. For example, the modification of histone proteins or the methylation of cytosine bases in DNA can upregulate, downregulate or silence gene expression (Jenuwein & Allis, 2001; Lee, Smith, & Shilatifard, 2010; Suzuki & Bird, 2008). These epigenetic modifications can be inherited from one generation to the next (Danchin et al., 2011; Jablonka & Raz, 2009). For example, mice that are conditioned to fear an odour for its associated negative stimulus pass on the fear of this odour to their descendants. Hypomethylation of an odour receptor gene (*Olfir151*) is transferred via the gametes, resulting in naïve mice having an innate fear of the odour (Dias & Ressler, 2014). If and how epigenetic inheritance influences cooperative traits and learned social behaviours warrants further investigation.

Parental effects—effects that parents have on the phenotype of their offspring, but not via the inherited genome—can also act as mechanisms for nongenetic inheritance (Mousseau & Fox, 1998). The relevance of parental effects is now widely accepted and considered an additional source of heritability that contributes to parent-offspring resemblance with important evolutionary implications. Parental effects can be genetic, when parental genetic variation is the cause of the environmental component affecting offspring development (Danchin et al., 2011). However, parental effects can also be nongenetic (Danchin et al., 2011). For instance, helping tendencies in cooperative breeders have been shown to be influenced by maternal identity (Kasper et al., 2017). To date, the exact mechanism of transmission is unclear, but candidate mechanisms are maternal allocation of resources towards egg size or composition (Robinson, Fernald, & Clayton, 2008; Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007; Taborsky et al., 2007), or parental care quality (Fischer, 2014; Goodson, Saldanha, Hahn, & Soma, 2005), which may have subsequent bearing on offspring phenotypes. Parental effects can be accounted for in quantitative genetics models by including them as IGEs (see “Genetic inheritance of cooperation”).

Individuals may modify their environments through a process known as “niche construction” that might alter the selective forces they experience (Laland, Matthews, & Feldman, 2016). These modified environments can be passed down to offspring through ecological inheritance, which contributes to inclusive heritability (Danchin et al., 2011). For example, termite mounds are cooperative efforts to modify temperature and humidity and are inherited both within and across generations (Odling-Smee, Laland, & Feldman, 2003). Within the quantitative genetic framework we developed earlier, this means that phenotypes of others (i.e. the “partners” in Figure 1) modify the environment, which changes the selection gradients affecting the fitness of the focal individual (β_N and possibly β_S in Figure 1) and these environments can be inherited.

Finally, cooperative behaviours can also be transmitted via cultural inheritance (Avital & Jablonka, 2000; Danchin et al., 2011). For

cultural information to be conveyed, a trait must be (i) socially learned, (ii) transmitted across generations or from older to younger individuals, (iii) expressed sufficiently to be picked up by younger individuals and (iv) individuals must be able to generalize the social information to use it in new contexts (Danchin & Wagner, 2010). For example, in cooperatively breeding long-tailed tits, *Aegithalos caudatus*, individuals preferentially help at the nests of related birds. Kin recognition and inclination to help are determined through the similarity of vocalizations, which are learned in early development (Hatchwell, Ross, Fowlie, & McGowan, 2001; Sharp, McGowan, Wood, & Hatchwell, 2005). If kin recognition operates only via those vocalizations and individuals are able to recognize kin they have never encountered before based on their dialect, kin recognition depends on culturally inherited differences in song.

An important consideration for all nongenetic inheritance mechanisms is their significance relative to genetic inheritance mechanisms. The contributions of nongenetic inheritance are likely to be highly variable depending on the trait and species in question, and their effect on the pace and direction of evolution and maintenance of traits can be highly significant (Kirkpatrick & Lande, 1989). For instance, nongenetic inheritance could explain the missing heritability—a lack of genetic markers explaining parent-offspring resemblance—in certain traits. Nongenetic inheritance could also play a role in the spread of novel alleles, maladaptive behaviours and major organizational transitions (Danchin et al., 2011). An interesting way to investigate the relative importance of nongenetic inheritance is by incorporating it in quantitative genetic models through the introduction of a double pedigree: one for genetic and one for nongenetic correlations (Day & Bonduriansky, 2011; Helanterä & Uller, 2010).

Prior to any empirical efforts, it is vital to consider under which conditions nongenetic inheritance is expected to be adaptive. In a group discussion on “Nongenetic inheritance and the evolution of social/cooperative traits” led by Reinder Radersma, we explored such conditions for adaptive nongenetic inheritance. First, the transference of information across generations is beneficial in cases where the environment varies in a repeatable and predictable way over time. Generation time should be shorter than the period of environmental change, leading to a correlation between the parental phenotype and the environment the offspring will encounter. Second, changes in the environment should happen at a rate faster than the genome is able to accommodate (English, Pen, Shea, & Uller, 2015b; Leimar & McNamara, 2015; Figure 2). Third, within-generation phenotypic plasticity should not be too costly, or individuals are physically, developmentally or behaviourally constrained to adequately respond to the changing environment (Uller, 2008). Finally, the benefits of nongenetic inheritance of a trait must outweigh the costs of the inheritance mechanism (Uller, 2008). The reliability and quality of the information offspring or parents are able to gather about the environment is a critical component of the costs and greatly affects the adaptiveness of different inheritance mechanisms (Leimar & McNamara, 2015). Further theoretical development, in tandem with empirical studies, should help to elucidate and quantify

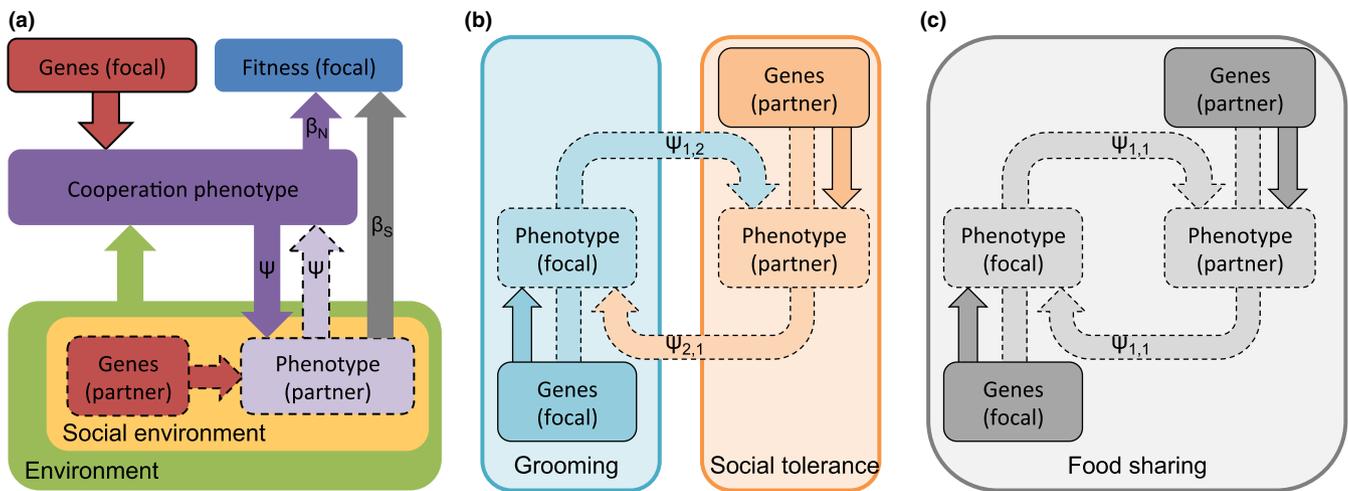


FIGURE 1 Indirect genetic effects on cooperation. An individual's own genes and its environment jointly influence its cooperation phenotype (direct genetic effect, solid black outline), which influences the focal's fitness ("nonsocial selection gradient," β_N). Cooperative behaviours are expressed in a social setting that constitutes a component of the environment. (a) Nonreciprocal indirect genetic effect: A cooperation partner's genes influence the focal's phenotype indirectly via the partner's phenotype (indirect genetic effect, dashed black outline). The strength of the influence of the genes in the social environment on the focal's phenotype is reflected by the interaction effect coefficient, ψ , and thus, the focal's fitness is affected by genes expressed in other individuals ("social selection gradient," β_S). (b) Two different traits expressed in two individuals influence each other reciprocally. For instance, the focal individual grooms its partner, which leads to an increased tolerance towards the focal ($\psi_{1,2}$), which, in turn, results in more grooming by the focal ($\psi_{2,1}$). (c) The same trait expressed in two different individuals influences itself reciprocally. For instance, the focal's propensity to share food with its partner could increase the partner's propensity to share food and vice versa ($\psi_{1,1}$). Assuming a ψ of 0.75, the feedback loops depicted in (b) and (c) lead to a five- and ninefold increase in the evolutionary rate compared to models without IGEs (Moore et al., 1997)

nongenetic inheritance of cooperative traits and behaviours in the future.

2.3 | Relevance of IGEs and nongenetic inheritance to understanding the evolution of cooperation

The IGE framework has the potential to improve our understanding of the evolution of cooperation by modelling how social interactions with conspecifics shape the fitness of cooperating individuals. Specifically, IGEs can be thought of as epistatic interactions between the focal trait and genes expressed in conspecifics and are thus part of the genetic architecture of a trait (Meffert, Hicks, & Regan, 2002). By providing the possibility of more realistic models of the nonadditive selective pressures posed by the social environment on cooperative traits, different conclusions about the rate and even the direction of evolution might be drawn than from frameworks that do not explicitly model IGEs. For instance, for social interactions that involve feedback loops between the same or different traits expressed in interacting individuals, the rate of evolution is expected to be 5–9 times faster than in the absence of IGEs, given that ψ is rather high (Figure 1b,c, Moore et al., 1997). Furthermore, by changing the resemblance of relatives, the presence of IGEs could mask or exaggerate heritable genetic variance (Bijma & Wade, 2008).

The inclusive inheritance framework provides a more nuanced view of the evolution of cooperation by treating inheritance as a multidimensional phenomenon. For instance, failing to incorporate cultural inheritance into models of evolution of human behaviour is

demonstrated to lead to substantive discrepancies between predicted and observed evolutionary outcomes (Richerson & Boyd, 1978). Moreover, the phenotype with maximum fitness can differ depending on the mode of inheritance—for example between genetic and cultural inheritance—and thus conflict between these systems can arise. This means that maladaptive behaviours like costly acts of altruism towards unrelated individuals could spread in a population in cases where variance in cultural transmission is higher than variance in genetic transmission. Consequently, positive cultural selection could override negative selection in the genetic domain (Aguilar & Akçay, 2017).

3 | GENETIC AND MOLECULAR PATHWAYS UNDERLYING COOPERATION

A cursory review of genetic mechanisms in various systems demonstrates that there are numerous molecular pathways leading to the evolution of cooperative traits (Table S1). Although a variety of molecular mechanisms have been identified, the overwhelming majority of studies indicate that hormonal regulatory pathways seem to hold the key to the evolution of cooperation in many of the examples found in social insects and vertebrates (Table S1).

The changes in how reproductive hormonal signalling systems work can have significant consequences for the emergence of helping behaviour which is often associated with suppressed reproduction. The interplay between insulin-signalling pathway, juvenile

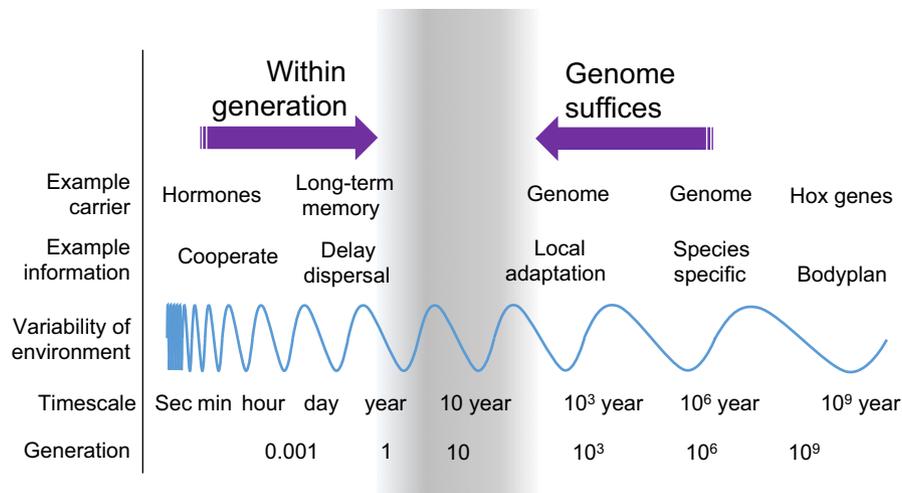


FIGURE 2 Nongenetic inheritance indicated on the information retention axis (in grey). The information retention axis symbolizes the timescale at which information needs to be retained in a biological system to be adaptive. This adaptiveness depends on the variability of the selective environment. There is scope for nongenetic inheritance when information needs to be transferred over generations (arrow pointing to the right), and the environment is too variable for genes to adapt (arrow to the left). The number of generations, the timescale and the variability of the environment are conceptual examples—roughly at scale—and are study system specific. The types of information and the information carriers are hypothetical examples

hormone (JH) and vitellogenin (Vg) is a fundamental component involved in the evolution of cooperation in insects. Here, both JH and Vg are related to reproduction with JH being a gonadotropin and Vg being a yolk protein (Corona et al., 2007). In many insect species, JH and Vg are synergistically regulated (Comas, Piulachs, & Bellés, 1999; Handler & Postlethwait, 1978; Sheng, Xu, Bai, Zhu, & Palli, 2011). In contrast, the regulation of JH and Vg in eusocial honeybees, *Apis mellifera*, is antagonistic (Corona et al., 2007) and regulates caste differentiation and division of labour in honeybees. The same regulatory pattern in the interplay between JH and Vg was recently discovered in two subsocial species, the European earwig *Forficula auricularia* and the burying beetle *Nicrophorus vespilloides* (Engel et al., 2016; M. Wu, J.-C. Walsler, L. Sun, M. Kölliker, unpublished). These findings suggest that this pathway may be co-opted in posthatching parental care behaviours and in social evolution (Corona et al., 2007).

In vertebrates, oxytocin (OXT), vasopressin (AVP), their nonmammalian homologs mesotocin, isotocin (IT) and vasotocin, and dopamine and serotonin are key endocrine players in cooperative behaviour (Anacker & Beery, 2013; Ebstein, Israel, Chew, Zhong, & Knafo, 2010; Madden & Clutton-Brock, 2011; Soares et al., 2010). These hormones affect social affiliation (Reddon et al., 2015), social recognition and approach (Thompson & Walton, 2004), reward estimates (Messias, Paula, Grutter, Bshary, & Soares, 2016a), social learning (Messias, Santos, Pinto, & Soares, 2016b; Soares, Paula, & Bshary, 2016) and pair bonding (Insel & Shapiro, 1992). For example, in humans, OXT is suggested to favour trust and parochial cooperation (De Dreu, 2012), whereas AVP increased cooperative tendencies in reciprocal interactions (Rilling et al., 2012). Cooperation can also be enhanced or decreased by social stress and its underlying hormones (glucocorticoids, GCs). For example, in many social species,

reproductive suppression of subordinate individuals is regulated by behaviours of dominant individuals that elicit higher levels of GCs in subordinates (Creel, Creel, & Monfort, 1996; Sanderson et al., 2015a).

The neuroendocrine pathways regulated by hormones appear critical for the evolution of cooperative behaviours in vertebrates (Donaldson & Young, 2008; Goodson, 2005, 2013; O'Connell & Hofmann, 2011a, 2011b; Soares et al., 2010), but the strength and direction of their regulatory effects depends upon the species, social context and sex. A recent comparison of brain gene expression of IT and AVT and their receptors between different social and nonsocial species pairs of cichlids revealed contrasting patterns (O'Connor, Marsh-Rollo, Ghio, Balshine, & Aubin-Horth, 2015). Furthermore, experimentally increased OXT (or its homolog IT) increased helping behaviours and decreased aggression in cooperatively breeding meerkats, *Suricata suricatta* (Madden & Clutton-Brock, 2011), and the sensitivity to social information in *N. pulcher* (Reddon, O'Connor, Marsh-Rollo, & Balshine, 2012), but it decreased sociability in this species (Reddon, Voisin, O'Connor, & Balshine, 2014). However, the direction of the effect of IT treatment depended on the pretreatment sociability in goldfish (Thompson & Walton, 2004), and OXT had no effect in house mice, *Mus musculus domesticus* (Harrison, Lopes, & König, 2016). In humans, experimentally administered OXT increased cooperation within groups, but also enhanced competition between groups (De Dreu, 2012). Interestingly, these effects of OXT on social behaviour in humans have been demonstrated to differ between women and men (Gao et al., 2016).

The evolution of sociality from solitary ancestry and the evolution of cooperative from noncooperative behaviours requires the emergence of novel social traits (Taborsky & Taborsky, 2015). Genes present in solitary species could be co-opted towards social

evolution. For example, *Vg* encodes the precursor of yolk protein (Corona et al., 2007). In subsocial European earwigs and burying beetles, *Vg* expression is associated with parental care (Roy-Zokan, Cunningham, Hebb, McKinney, & Moore, 2015; M. Wu, J.-C. Walser, L. Sun, M. Kölliker, unpublished), but in eusocial honey bee, it regulates division of labour and caste differentiation (Amdam, Norberg, Fondrk, & Page, 2004; Amdam, Norberg, Hagen, & Omholt, 2003). Another example is the *PebIII* gene which had a direct genetic effect on the metamorphosis of the solitary insect *Drosophila melanogaster* (Sabatier et al., 2003). In the subsocial European earwigs, this gene is coregulated and co-adapted between parent and offspring. RNAi knockdown of this gene showed an indirect genetic effect on offspring development and a direct genetic effect on maternal future reproduction in the earwigs (M. Wu, J.-C. Walser, L. Sun, M. Kölliker, unpublished). Potential neofunctionalization or subfunctionalization of this gene was found in the eusocial termite *Reticulitermes flavipes*, with differential expression of two transcripts of *PebIII* between reproductive castes (Steller, Kambhampati, & Caragea, 2010).

4 | NEUROBIOLOGICAL MECHANISMS OF COOPERATION

Group-living animals often cooperate, as well as compete, with the same individuals multiple times over their lifespan. To assess the costs and benefits of social interactions, individuals need to continuously process social stimuli and keep track of past interactions. Responding to the multitude of daily social challenges encountered by social species requires behavioural flexibility and social competence (sensu Taborsky & Oliveira, 2012; Bshary & Oliveira, 2015). These complex social decisions require highly developed neuronal networks, which integrate many brain areas and populations of neurons (Platt, Seyfarth, & Cheney, 2016). For example, group size and the corresponding availability of social partners predict structural changes of the thickness of grey matter in multiple brain regions (Sallet et al., 2011). Group size also leads to functional change in terms of different co-activation of two brain regions, the superior temporal sulcus and the rostral prefrontal cortex (Sallet et al., 2011). To understand how individuals make flexible social decisions while engaged in cooperative or competitive interactions, researchers often focused on species with more complex cognitive abilities such as humans or primates. However, recent work has highlighted that many physiological and neurological mechanisms are conserved across taxonomic groups (O'Connell & Hofmann, 2011b). Further, seemingly cognitively demanding abilities, such as individual recognition or keeping track of past interactions, might be the result of learning processes involving operant-conditioning rather than sophisticated cognitive mechanisms (Bshary, Zuberbühler, & van Schaik, 2016). Hormones and ontogeny can also affect the cognitive skills necessary for the ability to cooperate. We suggest these consist of three aspects: (i) event memory, (ii) synchrony with others and (iii) responsiveness to others. For example, zebra finches failed to sustain cooperation in a prisoner's dilemma task when their stress hormone

levels were experimentally raised. These hormones reduce memory capacity required for reciprocity and remove the incentive for cooperation (Larose & Dubois, 2011). In addition, humans and many animals cooperate better when they are more receptive to social stimuli through synchronization in terms of personality, experience or hormonal physiology. For example, shared excitement synchronizes brain activity in humans to enable better cooperation in times of need (Nummenmaa et al., 2012).

It is now well established that two evolutionarily conserved neural circuits are fundamental in regulating social decision-making in vertebrates and are commonly referred to as the social decision-making network (SDMN) (O'Connell & Hofmann, 2011b). The SDMN is comprised of two neural circuits: the mesolimbic reward system, which evaluates the salience of external stimuli to generate an adaptive response, and the social behaviour network, which evaluates external stimuli (Goodson, 2005). Only the interconnected activity of both systems enables animals to regulate and implement adaptive behavioural outputs in response to environmental challenges and opportunities. Many hormones that influence key aspects of cooperative behaviour, such as OXT, AVP, dopamine or serotonin, are part of the SDMN. However, even though the SDMN is doubtlessly an important player in social behaviour, it remains an open question whether cooperative behaviour itself is regulated by the SDMN.

5 | DEVELOPMENTAL REGULATION OF SOCIALITY/COOPERATIVE BEHAVIOUR

Modes of development can have a huge impact on the evolution of early phenotypic specialization vs. extended phenotypic plasticity (English, Browning, & Raihani, 2015a). Invertebrates, and in particular eusocial insects, are more prone to early developmental specialization because they have to commit to the development of a certain phenotype before metamorphosis (Wilson, 1971). Most social insects show a strict behavioural and morphological caste differentiation determined by different developmental trajectories, which leads to a division of labour in insect colonies (Wilson, 1971). Arguably, the most famous example is the development of queens in honeybees induced by the ingestion of royal jelly (Kaftanoglu, Linksvayer, & Page, 2011). Early caste determination is a common phenomenon in most eusocial insects where nutrition and inhibitory pheromones play an important role (Schwander, Lo, Beekman, Oldroyd, & Keller, 2010). There are, however, a number of social insect species that are cooperative breeders without morphological specializations, which can switch between the role of subordinates and dominants within a lifetime (Field & Leadbeater, 2016; Gadagkar, 2016).

In contrast to many social insects, most social vertebrates remain morphologically and behaviourally flexible throughout their life. For example, dominant breeders and subordinate group members in cooperatively breeding vertebrates maintain their full reproductive capacity (Bell, Nichols, Gilchrist, Cant, & Hodge, 2012; Brintjes, Bonfils, Heg, & Taborsky, 2011), but can adapt their social roles and behaviours contingent on the social context and environmental

conditions (Bruitjes & Taborsky, 2011). Therefore, most social vertebrates do not develop morphological specializations based on their social rank or role (Carter, English, & Clutton-Brock, 2014; Huchard et al., 2014; Sanderson et al., 2015b; Taborsky et al., 2015; Zöttl et al., 2016; but see Jarvis, 1981; Fischer, Bessert-Nettelbeck, Kotrschal, & Taborsky, 2015). Nevertheless, early behavioural specialization might be beneficial, for instance, when deciding if and when to disperse (Fischer, 2014; Zöttl, Chapuis, Freiburghaus, & Taborsky, 2013), if and when to challenge the dominant individual in the home territory (Sharp & Clutton-Brock, 2011), and whether to rear offspring communally or solitarily (Manning, Dewsbury, Wakefield, & Potts, 1995). All of these decisions require specific behavioural repertoires. Bolder, more risk-prone phenotypes are more successful dispersers (Chapman et al., 2011) while larger individuals with superior fighting abilities are better able to challenge dominants for territory takeovers (Huchard, English, Bell, Thavarajah, & Clutton-Brock, 2016). A communal nest requires individuals to express prosocial behaviours towards breeding partners and foreign young (Dugdale, Ellwood, & Macdonald, 2010; Weidt, Hofmann, & König, 2008; Weidt, Lindholm, & König, 2014). Social behaviour can be costly (Cram, Blount, & Young, 2015; Grantner & Taborsky, 1998), and misdirected behaviours may have high fitness costs and can lead to evictions from the group (Bell et al., 2012), infanticide (Schmidt et al., 2015) and even to fatal conflicts (Enquist & Leimar, 1990). Thus, environmentally induced developmental programming of behavioural strategies, for example, via parental effects or own early experience, might be also important in cooperatively breeding vertebrates.

The cues responsible for early phenotypic specialization are diverse and can induce phenotypic specializations between and within social groups. For example, intragroup caste specialization is dependent on group size (Ferguson-Gow, Sumner, Bourke, & Jones, 2014) or the level of competition between nests (Passera, Roncin, Kaufmann, & Keller, 1996) in ant species. In cooperatively breeding vertebrates, group size can influence maternal investment in eggs. Smaller eggs are produced when more helpers are available to compensate for the reduced maternal investment in individual eggs (Russell et al., 2007; Taborsky et al., 2007). In turn, offspring developing in larger groups may express different behavioural phenotypes than offspring from small groups as a result of developmental plasticity (Fischer et al., 2015). Within-group factors such as the provision of more or better food to particular group members can lead to divergent behavioural phenotypes such as the development of different caste phenotypes in social insect societies (Schwander et al., 2010) or different degrees of competitiveness in some vertebrates (Buston, 2003; Heg, Bender, & Hamilton, 2004; Huchard et al., 2016).

A second important role of developmental plasticity in social organization is the regulation of conflict within groups. The level of conflict in cooperative societies is particularly high when subordinates are fertile and therefore have a vested interest their own breeding opportunities. Subordinates queuing for a dominant position may compete with other subordinate group members about the position in the social hierarchy (Huchard et al., 2016). If access to

reproductive opportunities is strongly skewed towards a few dominant individuals, conflicts over reproduction can also arise between dominant breeders and maturing subordinates (Heg et al. 2004). As social rank is often size-dependent, developmental plasticity of growth strategies may play a key role in either reducing or enhancing conflict. In response to social cues obtained from other group members, growth may be strategically enhanced to outcompete rivals or reduced to lower potential conflict with dominant group members. In her talk "Measuring cooperation and associated phenotypes in the field: developmental trajectories and genetic basis," Elise Huchard showed that in cooperatively breeding meerkats, growth rates remain flexible throughout the entire ontogeny (Huchard et al., 2014). In this species, rank position depends on size and age, and subordinate females queue for the position of the dominant female, which is usually the oldest and heaviest female of the group. When Huchard and colleagues (Huchard et al., 2016) experimentally increased the growth rate of a subordinate by supplemental feeding, same-sex rivals responded by accelerating their own growth and food uptake. Conversely, subordinates of the cooperatively breeding cichlid fish, *N. pulcher*, inhibit their growth if their size difference to the same-sex dominant breeder becomes too small, as subordinates reaching body sizes too close to that of dominants risk expulsion from the group (Heg et al. 2004).

Finally, developmental processes may mediate conflict between dominant breeders and their offspring and future helpers or workers. In cooperative societies, not only are offspring dependent on care, but become carers themselves later in ontogeny. The optimal contribution to alloparental care required by dominant breeders vs. the optimal contribution subordinate helpers are willing to give may diverge and depend on the options for dispersal and independent breeding by subordinates (Russell & Lummaa, 2009). For instance, in his talk "Hormonal signals, epigenetic regulation, maternal effects, and their consequences for cooperation and conflict," Nikolaus von Engelhardt suggested that breeding females endow eggs with hormones or RNA transcripts, which might influence growth and behavioural propensities of offspring in a way that optimizes maternal fitness. These maternal effects may then influence the offspring's future willingness to contribute to alloparental care of younger broods. At the prenatal stage, offspring depend on parental cues to adjust their development, as they do not directly experience their environment. However, offspring may use cues obtained postnatally to "disagree" with the maternal programme and reverse their behavioural tendencies (Fischer et al., 2015).

Because of the important role of developmental plasticity in the regulation of cooperative behaviours, it is conceivable that in the course of the evolution of cooperation, environmentally induced phenotypic plasticity precedes, or even facilitates, genetic adaptation (known as the "plasticity-first hypothesis" West-Eberhard, 2003; see Levis & Pfennig, 2016 for a review). In a first step, plasticity enables a rapid adaptive response to changing environments through phenotypic accommodation. In a second step, genetic accommodation allows for the relatively slow refinement of genotypes by accumulating beneficial genetic mutations. This, together with the co-option of genes as

discussed in previous sections, could provide an answer to the long-standing question of how novel cooperative traits emerge when cooperative species evolve from noncooperative ancestors. As the underlying genetic architecture of cooperative behaviour is arguably complex and polygenic, genetic adaptation alone is unlikely to account for these relatively fast transitions. Thus, phenotypic plasticity that precedes genetic adaptation as described above might offer another explanation for the fast emergence of cooperative traits.

6 | OUTLOOK

In previous sections, we discussed ways in which cooperative behaviour can be transmitted from one generation to the next, either genetically, through heritable epigenetic changes, or through social learning and culture. We also outlined reasons why the evolutionary dynamics of cooperative traits might be less straightforward than generally assumed. Following Anna Lindholm's talk and the ensuing discussion, we now focus on practical considerations and we provide promising avenues for future research in the genetics and development of cooperation.

6.1 | Which systems are suitable?

The suitability of a system will ultimately depend on the exact question under investigation. In general, information on individuals is required for quantitative genetic approaches and desirable for molecular genetic approaches. Some taxa show a naturally occurring array of closely related species with a range of cooperative social behaviours. For example, Hymenoptera display a wide cooperative continuum from solitary to subsocial to eusocial species (Wilson, 1971), and species of the teleost family Cichlidae represent a wide range of social systems from nonsocial to highly social (Heg & Bachar, 2006; Taborsky, 1994). The parasitoid bethylid wasps presented by Ian Hardy at the workshop provides an excellent example of a tractable social study system. In one of these species, *Sclerodermus harmandi*, multiple unrelated foundresses cooperatively rear each other's offspring on a single host resource (Kapranas, Hardy, Tang, Gardner, & Li, 2016). There is a broad scope for experimental manipulation of resource size, relatedness, foundress number, and offspring survival in bethylid wasps (e.g., Sreenivas & Hardy, 2016). The quasisocial nature of this species makes it a particularly suitable candidate for the study of cooperative behaviours in insects at the threshold of the evolution of complex sociality.

Comparisons between the genomes and transcriptomes of species along the continuum of sociality can indicate likely genes and pathways for further investigation (Kapheim, 2016; Rehan & Toth, 2015; Robinson, Grozinger, & Whitfield, 2005; Toth & Rehan, 2017; Trapp, McAfee, & Foster, 2016). Comparisons within species are also useful to examine possible molecular causes of phenotypic variance. Systems in which individuals differ in their tendency to cooperate or cheat in social situations (Santorelli et al. 2008), or in the amount of alloparental care to provide (Fischer, 2014; Kasper et al., 2017), are

particularly well suited to studies of the underlying genetic architecture or gene expression patterns on the basis of cooperative phenotypes. Furthermore, the evolution of cooperative behaviours might not only depend on interactions within, but also between species (West, Griffin, & Gardner, 2007) or between different organizational levels of sociality (West & Gardner, 2013). We provide an example for multilevel cooperation, namely between microbiota and their host, in the Supporting Information.

6.2 | Which specific traits and parameters should be measured?

It is of paramount importance to understand the biology of a system well enough in order to be able to accurately quantify fitness, and to decide which traits to measure. It is especially important to carefully consider if the phenotype measured is indeed a target of selection. In some instances, it might be better to measure the underlying mechanism, for instance an individual's physiology or cognitive ability, instead of the behavioural phenotype (behavioural gambit, Fawcett et al., 2013). Moreover, the interaction coefficient ψ could itself be considered a trait that varies genetically between individuals and is thus subject to selection (Bleakley & Brodie, 2009) and of particular importance for the evolution of cooperative traits. For instance, ψ can be estimated empirically as the partial regression coefficient of a phenotype on its partner's phenotype while keeping the direct genetic influence constant. However, this requires isogenic lines or large-scale breeding designs with repeated measures of the same genotype with different social partners. Measuring individual-level phenotypic proxies could provide a more feasible approach for vertebrates, assuming a close phenotype-genotype resemblance (Edenbrow et al., 2017). Those proxies could be estimates of the extent to which traits covary between interaction partners, for example, spatial proximity.

6.3 | What type of approach should be followed?

Ideally, questions about the genetic basis of cooperative traits should combine both field observations and controlled laboratory studies. Moreover, insights gained from theoretical modelling of mechanisms underlying cooperation (see Supporting Information) and quantitative genetic modelling, for instance indirect genetic effects, should be considered. While the study of wild populations provides a more realistic picture of selective pressures in nature, a laboratory setting allows for easier control of confounding nongenetic effects (e.g., parental or other transgenerational effects) that potentially distort estimates of heritability (Kasper et al., 2017). Ideally, field studies should use cross-fostering techniques to account for and estimate those effects (Hadfield, Heap, Bayer, Mittell, & Crouch, 2013). Likewise, laboratory experiments should use offspring of wild-caught individuals to preserve natural patterns and breadth of genetic variation within the population and avoid artefacts due to genetic drift or laboratory-specific selection. Furthermore, studying individuals in highly artificial test settings that do not properly reflect the actual biology of a species could lead to ecologically or evolutionarily meaningless

results. This caveat is corroborated by recent studies that found an effect of laboratory rearing on gene expression, physiology, behaviour and social dynamics in paper wasps *Polistes fuscatus* (Jandt, Thomson, Geffre, & Toth, 2015) and an effect of the laboratory environment on prosocial behaviour of chimpanzees (Tennie, Jensen, & Call, 2016).

6.4 | Which methods should be employed?

As with selection of study species, approach, trait and setting, the most appropriate experimental method depends on the questions being asked. Quantitative genetic methods provide insight on the relative proportions of heritable and several types of environmental variance of cooperative traits and their covariance with other traits, and thus on the inheritance and genetic architecture of a cooperative trait. Combined with selection experiments, they can be used to predict how traits respond to selection. This could be followed up by quantitative trait locus or genomewide association study approaches to search for candidate genetic polymorphisms that are responsible for phenotypic differences in cooperative tendency. Recent association studies in humans have shown that particular genotypes for the oxytocin receptor (OXTR) gene were highly associated with Asperger syndrome, a type of autism (Di Napoli et al. 2014). Particular genotypes may also be associated with OXTR and social empathy as measured through cooperative games (Thompson et al. 2013). Several new technologies are available for the manipulation of gene expression at the transcriptomic level (e.g., RNA interference, Castel & Martienssen, 2013), or by altering genes at the DNA level (e.g., gene editing via CRISPR-Cas, Hsu, Lander, & Zhang, 2014). These approaches could be employed to verify and validate candidate genes once identified by the above approaches. Future studies should incorporate new technologies for detecting genetic and epigenetic signatures of cooperation. For example, comparing genomes between closely related species exhibiting a continuum from solitary lifestyle to advanced sociality may provide insights into the genomic structure underlying cooperation and the evolution of sociality along phylogenetic trees (Fischman, Woodard, & Robinson, 2011; Kapheim et al., 2015). Furthermore, exploring correlations of epigenetic marks with phenotypic variation in cooperativeness may provide insight into how gene expression is regulated in response to environmental factors (Jensen, 2015; Li-Byarlay, 2016). Investigating the stability of those epigenetic marks over time can shed light on the molecular pathways connecting previous social experience to future cooperative behaviour (Cardoso, Teles, & Oliveira, 2015; Shpigler et al., 2017). In conclusion, we advocate a holistic approach that integrates complementary methods to unravel the proximate and ultimate causation of cooperation and social evolution, including comparative phenotypic and genomic approaches to tackle questions of adaptation and convergent evolution, the study of norms of reaction and shifts in gene regulatory networks to appreciate the role of phenotypic plasticity, and the study of interactions between individuals and their social and physical environment to unravel the role of natural selection.

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AUTHOR CONTRIBUTION

C.K. and M.V. organized the workshop and led the writing of the manuscript. All authors contributed original ideas and helped draft the manuscript

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