# Cooperation in large-scale human societies – What, if anything, makes it unique, and how did it evolve?

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**Abstract**

There is much controversy about whether the cooperative behaviours underlying the functioning of human societies can be explained by individual self-interest. Confusion over this has frustrated the understanding of how large-scale societies could ever have evolved and be maintained. To clarify this situation, we here show that two questions need to be disentangled and resolved. First, how exactly do individual social interactions in small- and large-scale societies differ? We address this question by analysing whether the exchange and collective action dilemmas in large-scale societies differ qualitatively from those in small-scale societies, or whether the difference is only quantitative. Second, are the decision-making mechanisms used by individuals to choose their cooperative actions driven by self-interest? We address this question by extracting three types of individual decision-making mechanism (three type of "minds") that have been assumed in the literature, and compare the extent to which these decision-making mechanisms are sensitive to individual material payoff. After addressing the above questions, we ask: what was the key change from other primates that allowed for cooperative behaviours to be maintained as the scale of societies grew? We conclude that if individuals are not able to refine the social interaction mechanisms underpinning cooperation, i.e change the rules of exchange and collective action dilemmas, then new mechanisms of transmission of traits between individuals are necessary. Examples are conformity-biased or prestige-biased social learning, as stressed by the cultural group selection hypothesis. But if individuals can refine and adjust their social interaction mechanisms, then no new transmission mechanisms are necessary and cooperative acts can be sustained in large-scale societies entirely by way of self-interest, as stressed by the institutional path hypothesis. Overall, our analysis contributes to the theoretical foundation of the evolution of human social behaviour.

Keywords: human social evolution, large-scale societies, cooperation, evolutionary psychology, cultural group selection, institutions

# 1 Introduction

Understanding how large-scale human societies arose from small-scale ones and function is a central quest in science. It raises the question of how far this major evolutionary transition can be explained by the self-interested actor model common to the fields of (political) economics (Mas-Colell *et al.*, 1995; Pindyck & Rubinfeld, 2001; Ober, 2008; Fukuyama, 2011), archaeology (Stanish, 2017) and evolutionary biology (Alexander, 1987; Parker & Smith, 1990; Davies *et al.*, 2012; Alcock, 2013; Alexander, 2014). The answer to this question is crucial to improving our ability to engineer solutions to societal challenges, from climate change to genocides (Milinski *et al.*, 2008; Tavoni *et al.*, 2011; Alexander, 2014).

The behaviours that allow human societies to function and cohere are fundamentally cooperative in nature, as exemplified by exchange of resources between individuals and contribution to collective-action projects. Unlike any other species, humans today rely on exchange of resources with non-kin for nearly all of their vital needs, from food, to shelter, to medical care. Individuals exchanging resources are often unrelated and unfamiliar strangers, who know little if anything about each other and engage in massively large-scale and spatially-distributed collective-action projects. The contrast between modern human social behaviour and that of other social species is exemplified by the existence of the international space station – a pinnacle of human cooperation (Turchin, 2015). Constructing the space station required contributions of millions of taxpayers from multiple states, and required approximately three million person-years to build. It also involved massive division-of-labour and specialisation in the production of its component parts.

The human species has spent most of its existence living in small-scale hunter-gatherer societies (Boehm, 1999; Marlowe, 2005; Kelly, 2013). There are many cooperative behaviours in these societies, from food sharing, through to cooperative hunting and construction of dams (Kaplan *et al.*, 2009; Jaeggi & Gurven, 2013; Hooper *et al.*, 2015). But this cooperation occurs in small groups where individuals are either kin or personally know each other, directly or indirectly by reputation. Following the origin of agriculture around 10000 years ago, humans started to live in larger and larger groups, culminating in the modern states and space stations of today. These larger groups are only viable because of exchange and collective-action occurring between individuals.

But why would individuals cooperate in this new environment? Do the same evolutionary processes based on reproductive self-interest, which selected for cooperative behaviour in small-scale societies and other primates, provide a sufficient explanation for the ultimate reasons of such cooperation (Alexander, 1987; Cosmides & Tooby, 1992; West *et al.*, 2011; Pinker, 2015; Tooby & Cosmides, 2016) or is a different and novel evolutionary process needed (Richerson & Boyd, 2005; Turchin, 2015; Henrich, 2016)? In other words, can cooperation in large-scale societies be a (Nash) equilibrium behaviour among self-interested individuals (North, 1990; Greif, 2006; Powers *et al.*, 2016), or are individuals no longer be acting in their own self-interests (Richerson & Boyd, 2005; Bowles & Gintis, 2011; Turchin, 2015; Henrich, 2016)?

Despite much debate, there has been little movement towards a resolution of these questions, and hence little progress in understanding the evolutionary forces responsible for the transition from cooperation in small-scale societies to that in large-scale societies. To resolve this impasse, we here suggest that two mechanisms need to be disentangled theoretically and then analysed empirically. First, there is a need to determine how social interactions in large-scale societies are different from cooperation in small-scale societies. Are social *interaction mechanisms*–the constraint relationships between behaviour and outcomes–in large-scale societies qualitatively different from those in small-scale societies, or is the scaling up of interaction mechanism merely quantitative, and so does not involve any new fundamental kind of behaviour? Second, and regardless of the scale of society, there is a need to determine whether the *decision-making mechanisms*–the constraint relationships between cognitive state[1] and behaviour–used by individuals in interactions are driven by the incentives to individuals. To what extent is decision-making in social interactions dependent on individual rewards of cooperation? Because the decision-making mechanisms are likely to be complex cognitive traits with a genetic basis, they are unlikely to have changed significantly during the few thousand years since the origin of large-scale societies. This means that the same evolved decision-making mechanisms must be used by individuals in both small- and large-scale societies. However, different models of cooperation in large-scale societies have made very different assumptions about the decision-making mechanism that individuals use, and hence their sensitivity to incentives or self-interest.

This paper aims at contributing to the theoretical foundations of human evolution by

[1] The cognitive (internal) state of an individual itself depends on past (internal) state and the current environmental input, according to some state transition mapping that is part of the definition of the decision-making mechanism itself (Haykin, 1999; Enquist & Ghirlanda, 2005).

demonstrating the conceptual clarification that can be gained by disentangling interaction mechanisms from decision making mechanisms for understanding the transition to large-scale societies. We do so by addressing these mechanisms in a stylised way in three steps. (1) We start by providing an operational definition of social interaction mechanisms that allows us to delineate between different types of cooperative behaviours, and we synthesise what the empirical literature tells us about the similarities and differences between cooperation across human societal scales. (2) We then describe three broad decision-making mechanisms that have been widely used to describe human behaviour, and that make different assumptions about individual self-interest. We here synthesise what the empirical literature tells us about sensitivity to incentives, and use this to evaluate the fit of the different decision-making mechanisms to observed human behaviour. (3) Building on these concepts, we are led to ask what was the key mechanism explaining the evolution of large-scale societies: was it a change in the *transmission mechanism*, i.e. a change in the way traits are transmitted in a population so that cooperation more easily spreads, or was it a change in the interaction mechanism, i.e. did groups create new rules changing their social interaction mechanisms, such that cooperation would still be favoured by self-interested individuals? We discuss answers to this question in the light of the two main (evolutionary) hypotheses that have been proposed to explain the transition to large-scale societies; namely, the cultural group selection and the institutional path hypotheses.

# 2 Social interaction mechanisms in small-scale versus large-scale societies

For more than 2 million years nomadic hunter-gatherers lived in small-scale societies. Following sedentarisation and the subsequent Neolithic Demographic Transition around 10 000 years ago (Bocquet-Appel, 2011), large-scale societies arose. These societies are large in terms of number of individuals, and tend to have hierarchical organisation, i.e. chiefdoms and states (Johnson & Earle, 2000). To discuss the differences and similarities of cooperation in small- and large-scale societies, we start by introducing a model of social interaction that underpins our analysis and that is independent of societal scale and of decision-making or transmission mechanisms.

## 2.1 Games and material outcomes

We take our model of social interaction from game theory (Fudenberg & Tirole, 1991; Hurwicz, 1996), as this provides a common reference model across evolutionary biology and the social sciences (Gintis, 2007). We consider that a social interaction consists of the (measurable) behaviours (actions or stream of actions) of a group of interacting individuals and material outcome(s) of such behaviours. Material consequences of actions are usually multidimensional, e.g. calorie intake, size of shelter, or time of activity. But we assume that all material consequences of behaviours can be summarised by a single number, the material payoff to an individual, from which average group material payoff can also be evaluated. Material payoff is therefore a unifying currency, and this too has been used usefully to capture incentives in evolutionary biology and the social sciences. Hence, we take a social interaction as consisting of the behaviours and their material payoff consequences to interacting individual. The set of possible social interactions is formally called a *game form* in game theory (Hurwicz, 1996; Fudenberg & Tirole, 1991). This specifies all the behavioural options —-actions or stream of actions (e.g. cooperate or defect) —- available to each individual in a group and all their material outcomes. The game form thus defines the social interaction mechanism, and colloquially it can be thought of as the "rules of the game". This is often simply called a "game" in evolutionary biology, which is a language we follow here.[2]

We will focus on social interactions involving a social dilemma so that the interaction faced by individuals involve a tension between individual and group (material) payoff (Dawes, 1980; Kollock, 1998). We will call the action of an individual *cooperative* if (a) it increases the average payoff to interacting group neighbours and (b) it decreases the individual's own payoff relative to the average among group neighbours. Importantly, a cooperative act so defined does not say whether this act results in a net decrease or increase in the actor's payoff. It says, however, that if all group members cooperate, then average group payoff is larger that if individuals do not cooperate, and each individual has a larger payoff if others cooperate but itself. Hence the "dilemma", which is ubiquitous in human interactions, from the interpersonal to the international (Kollock, 1998).

[2]The definition of a game in game theory is the game form together with individual preferences (Hurwicz, 1996; Fudenberg & Tirole, 1991). It thus implicitly makes an assumption on the decision-making mechanisms, i.e. that individuals have preferences and that they will choose actions to try to satisfy those. This is unfortunate as the definition of a game therefore conflates social interaction mechanisms and decision-making mechanisms.

Another key observation of human social interactions is that individuals can change the rules of the game that they play, i.e. individuals can change the social interactions mechanism (North, 1990; Ostrom, 1990; Hurwicz, 1996; Greif, 2006; Kaplan *et al.*, 2005). An *institution* is defined as a family of games (game forms) that individuals can potentially choose between, given the current constraints of their physical environment and their technology (Hurwicz, 1996). The hallmark of an institution is the presence of two sets of social interactions (Powers *et al.*, 2016, p. 3): (i) active genesis of institutional rules through communication and/or bargaining by the individuals in a group – this is a political interaction (Hurwicz, 1996; Reiter, 1996); (ii) social interactions whose outcomes are material and which are affected by the institutional rules – this is the economic interaction. The key idea behind an institution is the formalisation of the point that humans, unlike other animals, can self-modify the material payoff structure of their social interactions, whereby they play both political and economic games. The former generates the institutionally devised rules (the "institutional rules") of social interactions defining the latter, and may possibly involve many informal and spontaneous communication events between subsets of the group of interacting individuals.

## 2.2 Two broad types of social dilemmas

Any cooperative act in the economic game can be placed on a scale representing the excludability of the economic good that it involves. At the one end of this scale is the voluntary exchange of private goods between individuals. These are goods that the actor controls or otherwise has property rights over, meaning that other individuals can readily be excluded from using them. Exchange of private goods allows individuals to obtain resources that they want but do not currently have. It also allows gains in efficiency from division of labour and specialisation (North, 1990; Greif, 2006). But it is not obvious that individuals will choose to engage in exchange, for two reasons. First, one individual must part with its goods before it receives anything in return. This means that an individual risks being cheated and receiving nothing in return (Greif, 2000). Second, the individual offering a good inherently knows more about its quality than the receiver, creating an information asymmetry that can be used to exploit the other party (North, 1990). Hence, exchange involves a social dilemma.

At the other end of the excludability scale are collective actions that involve the production and consumption of public goods such as village fortifications, or common-pool resources such as fish stocks, grazing land, or irrigation water (Hardin, 1968; Ostrom, 1990).

It is costly to monitor the behaviour of individuals producing and using this type of good, and hence to exclude those that do not contribute to it. This means that there is a social dilemma because of the temptation to enjoy the benefits without expressing the cooperative acts underpinning their production (Olson, 1965).

In the following discussion we categorise cooperative acts based upon whether they are closer to private ("exchange" games) or public goods/common-pool resources ("collective action" games) on the excludability scale.

## 2.3 The world until yesterday: cooperation in small-scale societies

### 2.3.1 Exchange

Hunter-gatherers engage in several types of exchange between individuals, and since such exchanges involve time and energy they necessarily involve cooperative behaviour. The most well studied is the exchange of meat between large-game hunters, i.e. food sharing. Male hunters donate food to other hunters in their group when they make a kill, and in turn receive food when the latter are successful. The exchange occurs repeatedly – essentially for an indefinite number of times – between members of the camp, which would number around 30 individuals (Marlowe, 2005; Kelly, 2013). The exchange of meat is also personal (North, 1990; Greif, 2006). People obtain first-hand information about the behaviour of others – they remember exactly who they have given food to in the past, and remind them of this when they are themselves hungry. This is supported by systems of institutional rules that regulate the conditions under which individuals should give food to others, and which apply to the whole group (Kaplan *et al.*, 2009). Group members enforce these rules upon each other through a variety of sanctions ranging from gossip and public ridicule through to hiding and ostracism (Boehm, 1999). Hunter-gatherers also exchange one type of commodity for another. A sexual division-of-labour is evident, particularly between males that specialise in hunting, and females that specialise in gathering plant materials (Marlowe, 2007). Among horticulturalists, we see the exchange of horticultural produce for meat, and the exchange of childcare for labour and sick care (Jaeggi *et al.*, 2016).

### 2.3.2 Collective action

Hunter-gatherers also engage in a variety of collective-actions related to subsistence, and here too this involves time and energy and thus necessarily cooperative behaviour. A prime case is cooperative hunting, where the actions of several individuals are necessary to prevent a prey from escaping (Kaplan *et al.*, 2009; Alvard & Nolin, 2002). Hunter-gatherers also engage in various collective construction projects, such as burning habitat, and building dams to trap fish (Kaplan *et al.*, 2009). Because the number of individuals taking part in the collective-action is relatively small, the payoff benefits are immediately and directly felt by the participants. In a small group of five hunters, if one individual does not pull its weight then it will directly feel the impact through a markedly reduced probability of catching prey. The benefits to an individual of cooperating are also returned with a small time delay, e.g. on the order of hours for cooperative hunting, or a few weeks for the construction of dams. The cost that an individual pays to receive this benefit is measured in terms of the opportunity cost of time and labour invested, or the direct contribution of material resources. Institutional rules regulate how exactly the benefits of collective action are distributed. For example, in the !Kung Bushmen, the owner of the first arrow that penetrates the animal controls distribution after a cooperative hunt (Testart, 1987).

## 2.4 The world today: cooperation in large-scale societies

### 2.4.1 Exchange

In larger-scale societies we see the specialisation and division-of-labour that already existed in hunter-gatherer societies become much more pronounced. Individuals now specialise in one occupation, and obtain essentially all of their vital resources through exchange with others. And this exchange is impersonal – it is often with unfamiliar strangers who may never meet again (North, 1990; Greif, 2006; Seabright, 2010). Consequently, individuals will not have first-hand information about how their exchange partners have behaved in the past. But crucially, the institutional rules of the (economic) exchange game have changed to account for this (Milgrom *et al.*, 1990; Greif *et al.*, 1994; Greif, 2006). For example, credit reference agencies supply information about the reputation of participants who will never physically meet. This is essentially an elaboration of the spreading of reputation by gossip seen in hunter-gatherers. Similarly, the state provides third-party enforcement of contracts through the sanctioning of individuals that do not act according to the agreed terms of an exchange. This acts as an elaboration of the enforcement of exchange norms seen in hunter-gatherer groups.

### 2.4.2 Collective action

Large-scale societies also engage in numerous collective actions, from building roads and fortifications through to the use of irrigation systems and fishing waters. These goods are produced and used by many more individuals, which means that the effect that any one individual feels as a result of its own effort will be negligible. The result of the collective-action can be delayed by a very long time, often on the order of years. As such, there would seem to be more temptation to not cooperate than in small-scale societies. But crucially, the institutional rules regulating collective actions have also changed. These now include third-party sanctioning by the state, which is facilitated by collecting contributions from taxes whose payment can be easily monitored. New institutional rules also incentivise individuals to monitor each other's use of common pool resources. An example is allowing monitors to keep a share of the fine levied on any individual that they find taking more than the agreed amount of resource (Ostrom, 1990; Guala, 2012).

## 2.5 Comparing cooperation across scales

As we move from small- to large-scale societies, a change in societal structure must occur to account for the change in size (Bonner, 2011). A much higher degree of specialisation and division-of-labour is observed in large scale societies, a feature predicted by the size-complexity rule: bigger entities have greater division of labour (Bonner, 2004; Bourke, 2011). At the same time, the exchange upon which this division of labour depends becomes more impersonal, with individuals less likely to have first-hand knowledge about the past behaviour of their exchange partners. In collective action, we see the number of participants become so large that the marginal effect of any one individual's contribution is negligible.

Qualitatively, though, both small- and large-scale societies face the same types of exchange and collective action problems. The organisational problems, however, become more difficult in large-scale societies, and as we increase scale we see more institutional rules that spread out into new domains such as long distance trade and large-scale construction projects. The increase in the number of rules with the scale of a society is striking. For example, the small-scale Kapauku Papuan society has around 120 rules regulating areas from property rights through to punishment for murder, whereas 40 000 new laws took effect in the United States in 2014 alone (Singh *et al.*, 2017). From this we can infer that as societies of any scale engage in new economic activities, the number of institutional rules that the society generates increases.

# 3 Decision-making mechanisms and the maintenance of cooperation in societies of any scale

## 3.1 Three broad decision-making mechanisms ("minds")

So far, we have focused on the (economic) games individuals play in small- and large-scale societies, and how these are at least in part humanly devised. But in itself this description does not specify how or why individuals take cooperative actions. We now present three main decision-making mechanisms (types of agent or "minds") that have been proposed in different fields of the literature to explain how individuals choose actions. For each hypothesised agent type, we indicate what assumptions it makes about how individuals take actions and the conditions that must hold for cooperative acts to be stable given this agent type.

(1) **The Rational Strategising Mind (hereafter RSM).** Individuals are assumed to try to maximise their personal payoff (Mas-Colell *et al.*, 1995; Ober, 2008; Fukuyama, 2011), which we take in this paper as being material payoff. For a cooperative action to be expressed it must be a (material) Nash equilibrium of the game at hand and hence incentive compatible (Kreps, 1988; Hurwicz, 1996; Fudenberg & Tirole, 1991). This is the standard model of human cognition assumed in economics, where it is used to make predictions about how individuals will behave in exchange and collective action situations. An RSM agent is a flexible, *payoff-sensitive* decision-making mechanism. There is a whole spectrum of RSMs, from myopic agents choosing actions that maximise short-term payoff, through to fully forward-looking agents that act to maximise long-term payoff, but all are self-interested.

For cooperative acts to be maintained in exchange and collective action games by

RSMs, the game must be repeated with known or unknown individuals. Both the conditioning of actions on past behaviour and endogeneous enforcement of property rights and contracts can create incentives for this agent to cooperate in large-scale societies (Milgrom *et al.*, 1990; Fudenberg & Tirole, 1991; Binmore, 2005b; Mailath & Samuelson, 2006; Binmore, 2006), and we emphasise that this really does hold regardless of societal scale (see Milgrom *et al.*, 1990 for a concrete example).

(2) **The Pleistocene Adapted Mind (hereafter PAM).** Individuals are assumed to have evolved behavioural rules that serve the actor's reproductive interest, that is, behaviour is self-interested, where "self" refers to genes only, genes giving rise to integrated individuals, or integrated groups of individuals, or combinations thereof (Alexander, 2014, p. 89). These behaviour rules have evolved in the Pleistocene social environment of small-scale societies and personal interactions (the Environment of Evolutionary Adaptedness, or EEA, e.g. Alexander, 1990; Barkow *et al.*, 1992; Cosmides & Tooby, 2013). Human psychology is thus supposed to solve the survival and reproductive puzzles posed by the EEA with individuals expected to treat interaction partners according to their degree of genetic relationship towards them (Alexander, 2014, p. 93). This is achieved by evolved domain-specific decision-making algorithms that were *payoff-sensitive* in the EEA. These are often called modules in evolutionary psychology, and are functionally specialised to solve particular adaptive problems, e.g. language acquisition, mate selection, or cooperative exchange (Lumsden & Wilson, 1981; Alexander, 1990, Barkow *et al.*, 1992, p. 24). Modules may do varying amounts of computation, ranging from a complex assessment down to the use of simple heuristic rules (e.g. Gigerenzer & Brighton 2009). This is the model of human cognition used in evolutionary psychology. It is used in thought experiments to make predictions about how individuals will behave based on the selective pressures of the EEA (Cosmides & Tooby, 1994).

The EEA would have selected for a psychology that initiates and monitors reciprocal exchanges, including specialised algorithms for detecting cheaters and calculating the probability that an exchange partner will reciprocate (Cosmides & Tooby, 1992). PAMs would now cooperate in large-scale societies whenever these algorithms were activated with inputs that resembled situations where it would have been incentive compatible to cooperate in the EEA.

(3) **The Social Learning Mind (SLM).**

Individuals are assumed to acquire their behaviour mostly from others through various forms of social learning. This is the standard model of human decision-making assumed in much of the literature on cultural evolution on cooperation (Henrich & McElreath, 2003; Richerson & Boyd, 2005; Richerson *et al.*, 2016). This type of agent may perform content-based social learning, where the choice of model to copy behaviour from depends upon the observed consequences of doing that behaviour. For example, behaviours that are observed to lead to higher payoffs would be more likely to be copied – this is a content-based transmission rule known as payoff-biased transmission. Alternatively, SLM agents may perform context-based social learning, in which who else performs the behaviour may matter more than the expected material payoff of doing that behaviour (Henrich & McElreath, 2003; Richerson & Boyd, 2005; Henrich & Boyd, 2016). Context-based social learning is cognitively less demanding than content-based learning, since it does not require the consequences of a behaviour to be observed and evaluated.

If SLM agents are dominated by context-based rather than by content-based learning, then they will be be insensitive to material payoff, and cooperation may be maintained as an equilibrium behaviour regardless of the (economic) game that they play, provided the agents have socially learned to cooperate. In that case how the type of exchange and collective-action games, and hence institutions, incentivise behaviour does not matter much because individuals are not self-interested. However, if individuals perform content-based social learning more frequently, they become more self-interested and sensitive to material payoff when choosing actions. Then, the type of game will matter more in explaining the sustainability of cooperative actions.

We wish to stress two points about these three agent types. First, the agent just described are *independent* of the scale of the society, and so apply to explaining behaviour in both small- and large-scale societies. Second, these agent types are necessarily abstract caricatures of human cognition, since they correspond to the general theoretical assumptions that researchers in different fields make about how human agents choose actions. While few, if any, researchers would argue that the human mind literally functions as any of the three agents and is likely to involve some mix of them, these caricatures are widely used to model how individuals take actions and to make predictions about how humans will behave. It is indeed useful to draw caricatures in order to delineate clearly different hypothesis. And to evaluate how well each model can explain human cooperative behaviour, we therefore need to look at the weight of evidence that pulls humans towards and away from each of the agent types. We discuss this here in relation to the payoff sensitivity of the different agent types and for the context of expressing cooperative behaviour. We therefore rank the decision-making mechanisms based on the extent to which choice of action is sensitive to expected payoff.

We start by noting that all three agent types assume that individual behaviour is plastic: none suggest that individuals have a hard-wired response to always cooperate or defect. Further, they all assume that individuals can express behaviour that they learn over their lifetime, although for PAM agents learning is domain specific and the content that is learnt is biased by the evolved algorithms (Cosmides & Tooby, 1992).

Next, we compare the agent types on the payoff-sensitivity scale, and can rank them from the more to the less payoff-sensitive as follows: RSM, then PAM, and finally SLM. Indeed, RSMs are expected to always try to increase their material payoff given the information available to them. PAMs, on the other hand, are expected to make incentive compatible decisions in situations that mirror the social environment of the EEA, e.g. where there is information about the past behaviour of potential partners or cues to recognise relatives. But they would be expected to undertake incentive-incompatible actions when environmental cues trigger the evolved algorithms in inappropriate circumstances (Johnson *et al.*, 2003; Burnham & Johnson, 2005; Hagen & Hammerstein, 2006; Raihani & Bshary, 2015). For example, individuals behave differently when "watched" by a pair of robotic eyes, which could mistakenly trigger algorithms that are sensitive to reputation (Burnham & Hare, 2007).

SLMs could undertake incentive-incompatible actions if their choice of model to learn from depends on context rather than content. For example, an SLM agent using a conformity-biased transmission rule would be likely to choose an incentive-incompatible action if the majority of other individuals in its group were also performing this action. Similarly, an SLM agent using a prestige-biased transmission rule could choose an incentive-incompatible action if a leader performed the action (Henrich *et al.*, 2015).

Experimental economics has long demonstrated in the laboratory that individuals are sensitive to material payoffs in exchange games that resemble the types of exchange problems identified above (Smith, 1962). Further, the levels of cooperation in a repeated Prisoner's Dilemma experiment are affected by whether the end point of the game is known, implying that individual decisions to cooperate are affected by the equilibria of the game (Roth & Murnighan, 1978). Individuals also adjust their behaviour in exchange situations in response to the reputation of their partners (Milinski, 2016). This all implies that humans act as if they were RSMs in these situations.

A different line of research involves experiments where cooperative acts are not incentive compatible, particularly public goods games without incentives to cooperate, but argues that individuals nevertheless still cooperate (Fehr & Gachter, 2002). This has been suggested as evidence pushing humans away from being self-interested (Fehr *et al.*, 2002; Boyd *et al.*, 2003). However, as in exchange games, when individuals play the public goods game for a longer period of time then they often start to behave in an incentive compatible manner (Binmore, 2005a; Sefton *et al.*, 2007). Further, analysis of multiple experiments and dissection of decision making reveals that such behaviour is likely to be consistent with responsiveness to payoff (Ledyard, 1995; Thomas *et al.*, 2016; Burton-Chellew & West, 2013; Burton-Chellew *et al.*, 2015, 2017). Finally, these games do not correspond to the types of exchange and collective action identified above. From these three points, we can conclude that the experiments where individuals do no behave as predicted by self-interest in all rounds of the game cannot be taken to imply that humans are not sensitive to material payoff in social interactions.

Some experiments have also reported quite substantial cross-cultural variation in behaviour in these games (Henrich *et al.*, 2006; Herrmann *et al.*, 2008; Gerkey, 2013). This can be interpreted as support for SLM, since it suggests that localised context-based social learning may be more important than maximising individual material payoff in determining behaviours in cooperation situations. However, these differences could also be explained by RSM or PAM agents acting in different economic environments (Baumard, 2013). Pertinent environmental differences include the value of long-term relationships given the institutional rules of the local market (North, 1990), and the fidelity with which reputational information is transmitted (Delton *et al.*, 2010; Greif, 2006). Variation in these features between cultures would cause RSM agents to correspondingly vary their levels of cooperation.

We can also ask whether humans routinely perform conformity-biased social learning. Conformity is very common in children (Haun *et al.*, 2014), although this is reduced if the actor being copied is not very successful at performing the task (Scofield *et al.*, 2013; Schillaci & Kelemen, 2014), or if conformity would conflict with the child's existing knowledge (Sobel & Kushnir, 2013). Moreover, several experiments with adults have demonstrated a lack of conformity, especially in situations where conforming would result in a reduction in material payoff (Lamba & Mace, 2011; Lamba, 2014; Burton-Chellew *et al.*, 2015, 2017) and that different individuals tend to use different social learning rules (van den Berg *et al.*, 2015; Molleman *et al.*, 2014).

Taken as a whole, the experimental literature demonstrates that incentive compatibility is a key driver of individual decision making in social interactions. Humans also seem to have mental modules for abstraction that allow them to create models of causality, and thus potentially conceive rules of interactions to regulate cooperative actions (Fukuyama, 2011), which pushes them away from SLMs on the payoff sensitivity scale. However, there is a pressing need for continued empirical work in both experimental and field studies to more precisely place our species on the payoff-sensitivity scale. A particular focus should be placed on the different time frames of net positive payoffs, i.e. whether the benefit is immediate or delayed, and whether it is conditioned on past behaviour towards the same partner (direct reciprocation) or based on reputation effects.

# 4 Transmission mechanisms vs social interaction mechanisms

As discussed in Section 2, large-scale societies both exist and are dependent on cooperative acts for their existence. Yet, evolutionary theory shows that, everything else being equal, the selection pressure on cooperative actions decreases drastically as group size increases and is unlikely to be favoured in large groups (Powers & Lehmann, 2017 for a review). So what was the key mechanism that allowed for cooperation to be sustained in the transition from small to large-scale societies? As emphasised in Section 3, there seem to be no real qualitative difference in the social dilemmas that individuals experience in small and large-scale societies. At the same time, the type of agent cannot have changed dramatically between small- and large-scale societies. Given this, two different hypotheses, the cultural group selection and the institutional path hypotheses, have been proposed to explain the maintenance of cooperative behaviour in the transition to large-scale societies. Both hypotheses turn out to implicitly assume a quantitative scaling up of the same kinds of exchange and collective action problems, but differ in what mechanism must have changed from other primates societies to allow cooperation to evolve in large groups.

## 4.1 New transmission mechanisms

The first hypothesis is the *cultural group selection hypothesis* (Richerson *et al.*, 2016), which posits that the main driver maintaining the expression of cooperative behaviour in the transition to large-scale societies is that humans exhibit novel mechanisms of transmission of behaviours between individuals. While the standard vertical transmission mechanism of population genetics or its analogue in cultural evolution, payoff-biased social learning (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985), are prevalent among other primates, humans are hypothesised to have a fondness for copying the majority behaviour in the group (conformist-biased transmission mechanism) or copying the behaviour of a leader (prestige-biased transmission mechanism). Hence, humans are assumed to be largely SLM agents using context-based social learning mechanisms because they have difficulty evaluating the costs and benefits of their actions, and so are not very sensitive to payoff. If different groups reach different patterns of behaviour, some with more cooperative acts, and some with less, then conformity-biased or prestige-biased transmission could maintain cooperative patterns of behaviour to be equilibria, because they decouple behaviour choice from payoff. Explicit formal models investigating these processes, and holding everything else constant in comparison to standard vertical transmission, have so far generally failed to show that conformist-biased transmission favours the spread of cooperative action (Lehmann & Feldman, 2008; Molleman *et al.*, 2013; Van Cleve, 2016; Powers & Lehmann, 2017), but prestige-biased transmission fares better (see Molleman *et al.*, 2013 for the most exhaustive analysis to date).

The process of cultural group selection may however be reinforced if competition between groups involves the physical displacement of less cooperative groups by their more cooperative neighbours, e.g. through warfare (Turchin *et al.*, 2013). Group competition by physical movement of individuals is also known as demic diffusion (Ammerman & Cavalli-Sforza, 1984). This is compatible with context-based, payoff insensitive, social learning mechanisms. However, competition between groups could also take the form of individuals either migrating to more successful groups, or imitating individuals in more successful groups (Richerson *et al.*, 2016). This is also known as cultural diffusion (Fort, 2015) and could be driven by context, with individuals migrating to larger groups or to groups with a prestigious leader. Cultural diffusion could also be driven directly by content, with individuals being sensitive to payoff when choosing which group to migrate. However, in this case there would need to be a mechanism of social interaction which ensures that cooperative behaviours give a higher payoff than non-cooperative actions *within* groups.

## 4.2 New social interaction mechanisms

The second hypothesis is the *institutional path hypothesis* (Powers *et al.*, 2016), which posits that the driver maintaining the expression of cooperative behaviour in the transition to large-scale societies is that humans have changed their social interaction mechanisms (changed the rules of the game), instead of changing the transmission mechanisms. Individuals are thus assumed to play political games affecting the economic game. The hypothesis is that as groups grew in size, individuals have refined and created new mechanisms supporting exchange by providing information about the past behaviour of a greater number of interaction partners, and/or to have changed systems of monitoring and sanctioning to handle larger numbers of individuals in collective action. These new mechanisms of social interaction would lead to cooperative actions increasing material payoff, and hence can be favoured even by self-interested individuals. This is compatible with RSM agents, and also with PAM agents to the extent that the institutional rules recreate the conditions for cooperation in the EEA. PAMs would be expected to favour the creation of institutional rules similar to those found in small-scale societies in circumstances that are ecologically similar to the EEA (Boyer & Petersen, 2012; Petersen *et al.*, 2012, 2013), e.g. to create rules of uniform sharing in periods of high resource variance (Cosmides & Tooby, 1994).

The types of economic games a group ends up with will be influenced by proximate factors such as asymmetries in power, influence, and information (Singh *et al.*, 2017), which determine the outcome of the political game. Furthermore, only a subset of the individuals affected by the institutional rules may take part in the political game, and the interests of those taking part may not be representative of the interests of the group as a whole. Consequently, the institutional rules need not be optimal for all group members, as exemplified by the rise of highly despotic states such as Ancient Egypt, where despotic leaders biased institutional rules in favour of themselves. As such, the institutional path hypothesis is compatible with the widespread existence of inefficient institutions (North, 1990; Acemoglu & Robinson, 2011). On the other hand, when the interests of group members are aligned, or bargaining strengths are equal, then efficient institutions are more likely to evolve (Ostrom, 1990; North, 1990; Greif, 2006).

The evolution of the ability to create and enforce rules by self-interested individuals, especially over food sharing and property rights, would have been necessary to support the hunter-gatherer lifestyle (Hill, 2009). If hunter-gatherers did not play political games, then the institutional path hypothesis cannot explain the origin of large-scale societies. But there is evidence that hunter-gatherers do indeed play political games, even though they lack the bureaucratic elements of large-scale societies. For example, when the extant Ache hunter-gatherer society transitioned from foraging to horticulture, they advocated and voted in local meetings to transfer fields from public to private ownership (Kaplan *et al.*, 2005). Further studies are needed to examine how other institutional rules in extant hunter-gatherers are formed.

## 4.3 Implications for cooperation in large-scale societies

Overall, the above analysis shows that a key question in determining the driving factors in the transition to large-scale societies is what decision-making mechanism determines the expression of cooperative action. If individuals are sensitive to payoff, then there *must* have been a change in the social interaction mechanisms, as proposed by the institutional path hypothesis. Without such a change, individuals should stop cooperating as group size increased because, when everything else is constant, the pressure on cooperation decreases rapidly with increasing group size. Conversely, if there was no change in the social interaction mechanisms then individuals *must* be less sensitive to payoff and hence a change in transmission mechanism used *must* do the work in explaining why cooperation is stable in large-scale societies.

Because humans undoubtedly do use social learning, the ingredients of the cultural group selection hypothesis may be partly complementary to those of the institutional path hypothesis (depending on the exact conceptualisation of "cultural group selection", see Pinker, 2015 for a discussion on this point). Indeed, competition between groups acts as an equilibrium selection device (Harsanyi & Selton, 1988; Boyd & Richerson, 1990; Binmore, 2005b), favouring equilibria that lead to a higher average payoff for group members. Cultural group selection traditionally stressed that these were equilibria because of particular mechanisms of transmission between individuals within groups (Richerson & Boyd, 2005; Boyd *et al.*, 2011; Henrich *et al.*, 2015). However, cooperative equilibria can also exist within groups under classic vertical or payoff-biased transmission, or under RSM agents that rationally choose their actions, if the right mechanisms of social interaction are in place. In this case, group competition can again act as an equilibrium selection device, spreading by cultural transmission mechanisms of interaction that lead to cooperation, without individuals acting against their self-interest (Harsanyi & Selton, 1988; Boyd & Richerson, 1990; Binmore, 2005b). This can act alongside the creation of mechanisms of interaction by bargaining and negotiation, helping to fill in where individuals are less than fully rational. On the other side, an explicit consideration of the political game for changing mechanisms of interaction can complement cultural group selection models, which typically leave unspecified how a group arrives at a particular equilibrium in the first place.

Despite the ingredients of the cultural group selection and institutional path hypotheses not being necessarily mutually exclusive, there is a need to understand whether the main driver of the evolution of cooperation in large-scale societies is a change in mechanism of transmission or of interaction. Without clarification, the perennial question of whether cooperation in large-scale societies is compatible with self-interested individuals will remain. Measuring the mechanisms of transmission that have led to the evolution of behaviours in the real world is challenging. However, determining whether observed cooperative behaviours are currently incentive compatible is less challenging. For example, we can more easily determine whether systems of monitoring and sanctioning are “altruistic”, or whether they are incentive compatible for the individuals doing the monitoring and sanctioning (Ostrom, 1990; Guala, 2012). If it is the former, then this suggests that novel mechanisms of transmission were key to determining their spread and maintenance. If it is the latter, then the creation of new mechanisms of interaction is likely to have been the key driver. Empirical work should thus pay more attention to the payoff sensitivity of monitoring and sanctioning behaviours.

# 5 Conclusion

Is the self-interested actor model of economics and evolutionary biology sufficient to explain the maintenance of the expression of cooperative behaviour during and after the transition to large-scale societies? To answer this question and narrow down the space of possible hypotheses explaining this evolutionary transition, we have emphasised that two mechanisms need to be disentangled. First, are social interaction mechanisms in large-scale societies qualitatively different from those in small-scale societies? Our review of the literature suggests that the answer is no. Both scales of society face fundamentally the same type of private exchange and public collective-action problems, but these problems became more difficult to solve on a quantitative scale in large-scale societies. Second, what is the decision-making mechanism by which individuals choose actions in exchange and collective-action scenarios? This must be the same in both small- and large-scale societies, as there would not have been not enough time in the past 10 000 years for genetic evolution to radically change the type of agent. The empirical evidence implies that humans are largely driven by material-payoff incentives in a way consistent with RSM and content-based SLM agents, but within constraints set by evolved preferences and predispositions as expected by PAM.

In light of these two assessments, we asked the question: what key mechanism allowed cooperative acts to be maintained as the size of private exchange and public collective-action problems increased? On one side the cultural group selection hypothesis focuses on the need of novel transmission mechanisms of behaviour. By stressing the role of context-based social learning mechanisms, it places far less importance on self-interest, and considers individuals to be SLM agents who are low on the payoff sensitivity scale when expressing cooperative actions. On the other side, the institutional path hypothesis focuses on the role of novel humanly-devised social interaction mechanisms. By stressing the role of changing the rules of the game, it assumes self-interested individuals and thus represents a null hypothesis compatible with standard economics and (genetic) evolutionary biology. Our analysis across societal scales suggests that it also provides a sufficient explanation for the maintenance of cooperation in the transition to large-scale societies. Having operationally delineated between three key mechanisms involved in this transition, we hope our paper contributes to resolving the impasses underlying the theoretical foundations of human evolution.

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