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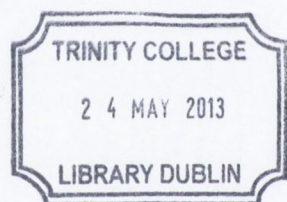
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The Social Evolution of Intellect

Luke McNally

Thesis submitted to University of Dublin
for the degree of Doctor of Philosophy

2013



Thesis 9931

Declaration

I declare that I am the sole author of this thesis and that the work presented here, unless otherwise referenced, is entirely my own. I also declare that the work has not been submitted, in whole or in part, to any other university as an exercise for a degree or other qualification. Lastly, I agree that the Library may lend or copy this thesis upon request.

Luke McNally

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Summary

The high levels of intelligence seen in humans, other primates, certain cetaceans and birds remain a major puzzle for evolutionary biologists, anthropologists and psychologists. In recent times two main explanatory frameworks have emerged: the 'social intelligence' and 'cultural intelligence' hypotheses. Both theories emphasise different advantages of intelligence: the ability to negotiate a complex social environment for the social intelligence hypothesis; and the ability to easily acquire novel behaviours from others for the cultural intelligence hypothesis.

While much comparative work has found some support for these hypotheses, the field generally lacks any rigorous foundation in fundamental evolutionary theory. In this thesis, I begin to redress this deficiency by applying a combination of models from social evolution theory and comparative methods to the primate cognitive evolution. Specifically: (1) I develop an artificial neural network model to probe the theoretical foundations of the social intelligence hypothesis. The model pits the neural networks against each other in social dilemmas, while the networks themselves evolve in size and structure using a genetic algorithm. My results show that transitions to more cooperative groups can create selection for intelligence owing to the cognitive demands of reciprocity, and that Machiavellian arms races may arise with intelligent strategies creating further selection for intelligence. (2) I use theoretical models and a comparative analysis to assess the roles of cognitive capacity and lifespan in the evolution of cooperation. I analytically show that phenotypic assortment owing to five important forms of conditional cooperation - partner choice, direct reciprocity, indirect reciprocity, punishment and kin discrimination - is expected to be monotonically increasing with both cognitive capacity and lifespan, suggesting that both should favour cooperation. I support these model predictions by using Bayesian phylogenetic mixed models to show that non-human primate with bigger

brains and longer lives are more likely to engage in two important forms of cooperation - coalition formation and food sharing. (3) I examine the role of cooperation in creating selection pressures favouring tactical deception, a trait often used to infer the cognitive abilities of non-human animals. I use a simple game theoretic model to show that conditional cooperation creates selection for deception so as to avoid being detected as a cheater, and use a phylogenetic comparative analysis to show that non-human primates that engage in more forms of cooperation also engage in more deception. (4) I use simple direct fitness models and Bayesian phylogenetic mixed models to illustrate the role of phenotypic assortment in favouring the evolution of culture. The results suggest that similar factors are important for the evolution of cooperation and culture and suggest a fundamental connection between the social and cultural intelligence hypotheses. Overall, my results suggest that the human mind is fundamentally social and evolved as a facilitator of cooperation and culture.

Acknowledgements

While carrying out the work for this thesis I benefitted from the comments, discussion and/or collaboration of many individuals including: Adam Kane, Andrew Jackson, Ashleigh Griffin, Colby Tanner, Dan Cornforth, Deirdre McClean, Ewan Harney, Franjo Weissing, Graeme Ruxton, Ian Donohue, James Marshall, Joe Colgan, Ken Irvine, Kevin Healy, Luke Holman, Mafalds Viana, Natalie Cooper, Nicola Marples, Owen Petchey, Rolf Kmmmerli, Roman Popat, Sam Brown, Steven Lydon, Stuart West and Sylvie Estrella.

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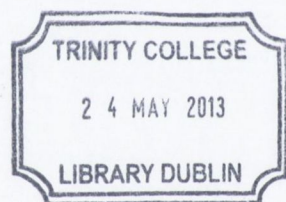
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Chapter 1

General introduction

1.1. Cognitive evolution

The human brain and the cognitive abilities it endows us with are arguably the most complex set of traits ever produced by natural selection. Indeed one major cause of the divergence in views between Wallace and Darwin regarding the evolution of humans by natural selection stemmed from Wallace's denial that human intelligence could have arisen via natural selection (Wallace 1870; Pinker 2010). Few biologists today would deny that human intelligence arose via natural selection. However, real insights into the forces underlying brain expansion during human evolution have only begun to emerge in recent decades, largely spurred by comparative work on non-human primates.

1.2. The 'social brain'

The title of this thesis alludes to an essay by English psychologist Nicholas Humphrey entitled 'The social function of intellect', which revolutionised theories of human cognitive evolution (Humphrey 1976; Emery *et al.* 2007). Prior to Humphrey's essay, most theories of primate brain evolution fit into the "man the toolmaker" paradigm, holding that it was the ability to master our physical and ecological environments that had selected for advanced human cognitive capacities (Oakley 1949). Humphrey's suggestion was that rather than the demands of the physical or ecological environments, it was the demands of negotiating a complex and ever-changing social environment that had selected for brain expansion within the primate lineage. A new paradigm emerged from Humphrey's seminal thesis: the "social intelligence" or "Machiavellian intelligence" hypothesis (Byrne & Whiten 1988; Dunbar 1998). As this field matured, greater focus began to fall on the roles of behaviours such as cooperation and deception in selecting for large brains and associated advanced psychological capabilities such as theory of mind and shared intentionality. The central claim of this hypothesis is that large brains confer a fitness

benefit by facilitating the appropriate responses in social interactions. In recent decades much evidence, mainly from comparative analyses of primates and other vertebrates, has accumulated supporting the social intelligence hypothesis (Dunbar 1998; Dunbar & Schultz 2007). However, while the social intelligence hypothesis has enjoyed much empirical success it has become clear that it is not the whole story of human cognitive evolution, as it fails to explain much phylogenetic variation in brain size, particularly grade-shifts (systematic differences among clades) within the primates (van Schaik *et al.* 2012).

1.3. The cultural brain

A new theory of cognitive evolution has recently risen from within the social intelligence hypothesis: the "cultural intelligence hypothesis". This theory has developed mainly from the pioneering study of Reader & Laland (2002), which showed that rates of innovation (individual learning of novel behaviours) and social learning (the learning of behaviours from others) show strong correlations with brain size across the primates. This theory holds that increased brain size evolves as a mechanism to increase general learning capabilities, which lead to the acquisition of new, fitness enhancing behaviours through innovation and social learning (van Schaik & Burkhardt 2011; van Schaik *et al.* 2012). The cultural intelligence hypothesis places particular focus on the benefits of social learning, which can allow for the acquisition of suites of behaviours that would otherwise be unattainable by a single individual. It has also been stressed that, at least for primates, the cultural and social intelligence hypotheses should not be seen as alternatives but rather complementary hypotheses for explaining brain evolution (van Schaik *et al.* 2012). Therefore the cultural intelligence hypothesis helps to reconcile the "man the toolmaker" view of cognitive evolution with the social intelligence hypothesis by elucidating the key role of sociality in the acquisition of novel adaptations to the physical environment. This view is supported by recent analyses showing that both social skills and learning abilities

appear to compose an axis of "general intelligence" in primates (Reader *et al.* 2011).

1.4. Social evolution theory

Both the social and cultural intelligence hypotheses clearly have large social components: the social intelligence hypothesis focusing on the role of cognition in cooperation and conflict between individuals and the cultural intelligence hypothesis focusing on the acquisition of novel behaviours from others. Despite this however, there has been little integration of social evolution theory into the study of brain evolution.

Social evolution theory is a theoretical framework for the study of the fitness effects of interactions between individuals. The main focus of this framework is on the importance of correlations among the phenotypes of different individuals (Frank 1998). The importance of these correlations for the evolution of social behaviours was first proposed by Hamilton in his development of inclusive fitness theory (Hamilton 1963, 1964, 1970). Hamilton's central insight was that correlations between the genotypes of interacting individuals can have a profound effect on the direction of selection on social traits. In the case of altruistic behaviours for example, a positive correlation among the genotypes of interacting individuals can lead to the behaviour being favoured by natural selection if this correlation exceeds the cost to benefit ratio of the behaviour, as an altruist will be surrounded by a sufficient number of other altruistic individuals to outweigh the costs of their behaviour. When this correlation is restated as genetic relatedness (r) Hamilton's rule follows: $r > b/c$, which is the condition for the behaviour to be favoured by selection. This correlation between the genotypes of interacting individuals is often owing to kinship, leading to this process often being termed kin selection (Maynard Smith 1963).

While genetic correlation has been shown to be responsible for many striking examples of social behaviours (West *et al.* 2007), it is not the only possible source

of phenotypic correlation (or phenotypic assortment) among individuals; conditional behaviour is another possible route to phenotypic correlation (Frank 1998; Queller 2011). The most well known example of conditional social behaviour is that of direct reciprocity (Trivers 1971). The essence of direct reciprocity is that a social partner's investment in some social behaviour is correlated with your past actions towards them. While reciprocity has been the most influential form of conditional social behaviour in evolutionary biology, there are many other examples including indirect reciprocity (basing my behaviours on what you have done to others; Alexander 1987; Nowak & Sigmund 1998), generalised reciprocity (basing my behaviours on what others have done to me; Pfeiffer *et al.* 1005; Barta *et al.* 2011), partner choice (choosing partners based on how cooperative they are; Roberts 1998; Sheratt & Roberts 1998; McNamara *et al.* 2008), punishment (harming those who don't cooperate; Boyd & Richerson 1992; Gardner & West 2004), and reward (giving some benefit to those who cooperate; Oliver 1980; Rand *et al.* 2009).

1.5. Intelligence and phenotypic correlation

Much of the substance of the social intelligence hypothesis regards phenotypic correlation via conditional behaviour. The central tennet of this hypothesis is that increased cognitive capacity allows individuals to keep track of social relationships and adjust their behaviour accordingly. In essence the suggestion here is that intelligence can function as a mechanism to alter phenotypic correlations among individuals to an individual's benefit. For example, the presence of advanced cognition may allow an individual to keep track of another individuals level of cooperation accurately and respond accordingly. This could allow individuals to create a positive correlation between their level of cooperation and that of their partners, thus allowing them to establish mutually cooperative relationships and gain a fitness benefit. Additionally, advanced cognition may

allow an individual to deceive others by concealing social behaviours that may otherwise be punished (e.g. cheating), thus reducing the magnitude of phenotypic correlations and allowing them to yield benefits without the associated costs.

While less immediately obvious than in the case of the social intelligence hypothesis, phenotypic correlation may also be key in the evolution of increased brain size via the cultural intelligence hypothesis. Social learning allows individuals to gain novel behaviours that others have produced by innovation (van Schaik *et al.* 2012). Therefore the discovery of novel behaviours via innovation may be viewed as investment in a public good which is transferred to others via social learning. As with any public good, phenotypic correlation between individuals, either via kin selection or conditional behaviour, is likely to increase selection for investment in that good.

1.6. Research outline

The central aim of this thesis is to integrate social evolution theory into the study of primate brain evolution with a particular focus on the importance of phenotypic correlation. Specifically:

Chapter 2: While correlative evidence from comparative analyses provide much support for the social intelligence hypothesis, there is still little theory showing its logical consistency. I use an artificial neural network model to show that the evolution of cooperation via direct reciprocity creates selection pressures favouring increased investment in cognition. Furthermore, I show that the evolution of intelligent strategies creates further selection for intelligence, leading to a Machiavellian arms race.

Chapter 3: I turn to a more general analysis of the role of cognition and lifespan in creating the phenotypic correlations necessary for the evolution of cooperation via conditional behaviour. First, I show that the potential for this assortment to arise

is expected to be monotonically increasing with both cognition and lifespan for five important mechanisms of conditional cooperation: partner choice, direct reciprocity, indirect reciprocity, cooperation in response to punishment and kin discrimination based on phenotypic or environmental cues. I then present a comparative analysis in support of these theoretical models, showing that two forms of cooperation coalition formation and food sharing are more likely to occur in primate species with bigger brains and longer lives.

Chapter 4: I examine the role of conditional cooperation in creating selection for tactical deception, a behaviour considered indicative of advanced psychological abilities such as theory of mind. I use a simple game theoretic model to show that conditional cooperation can create selection for tactical deception, as deception allows individuals to yield the benefit of cooperation without paying the associated costs, and provide support for this model by using a comparative analysis to show that tactical deception is more common in more cooperative primate species.

Chapter 5: I present a general theoretical model for the coevolution of innovation and social learning. The model highlights the importance of phenotypic correlation in selection for investment in culture, in the form of increased brain size, via a coevolutionary feedback between innovation and social learning. I also present a comparative analysis of the frequencies of innovation and social learning in primates which supports the importance of both phenotypic correlation/assortment among social partners and coevolutionary feedback in the evolution of culture.

Chapter 2

Cooperation and the evolution of intelligence

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Authors' contributions: LM and AJ conceived the idea; LM developed and analysed the model; LM, SB and AJ interpreted results; LM wrote the manuscript with input from SB and AJ

2.1. Introduction

Natural selection never favors excess; if a lower cost solution is present it is selected for. Intelligence is a hugely costly trait. The human brain is responsible for 25% of total glucose use, 20% of oxygen use and 15% of our total cardiac output; despite only making up 2% of our total body weight (Clarke & Sokoloff 1999). Explaining the evolution of such a costly trait has been a long-standing goal in evolutionary biology, leading to a rich array of explanatory hypotheses, ranging from evasion of predators to intelligence acting as an adaptation for the evolution of culture (Deaner *et al.* 2000; Barton 2006; Reader *et al.* 2011). Among the proposed explanations arguably the most influential has been the social intelligence hypothesis, which posits that it is the varied demands of social interactions that have led to advanced intelligence (Reader *et al.* 2011; Humphrey 1976; Jerison 1973; Byrne & Whiten 1988; Whiten & Byrne 1997; Dunbar 1998; Kaplan *et al.* 2000; Adolps 2003; Emery *et al.* 2007).

In recent years, the cognitive demands of reciprocity (basing my behaviours on what you have previously done to me), one of the mechanisms posited as important in the maintenance of cooperation in humans and other intelligent taxa, has been suggested to be a causal factor in the evolution of advanced intelligence and human language. This has been particularly apparent in the evolutionary game theory literature, where conjecture regarding this relationship is frequent (e.g. Nowak & Sigmund 1998; Nowak & Sigmund 2005; Nowak 2006; Nowak 2008). Indeed there is a rich history of work relating intelligence and reciprocity in the game theory literature, though most of this work has focused on the cognitive abilities required for the evolution of cooperation, rather than the possible role that the negotiation of these interactions has in the evolution of intelligence, e.g. (Rubinstein 1986; Abreu & Rubenstein 1988; Gilboa & Samet 1989; Fogel 1993; Ho 1996; Miller 1996; Harald & Fogel 1996; Chellapilla & Fogel 1999). As

well as the cognitive abilities required for the coordination of partners during cooperative acts, both direct (decisions based on what you do to me) and indirect (decisions based on what you do to others) reciprocity have additional demands in terms of the ability to remember previous interactions and to integrate across these interactions to make decisions in cooperative dilemmas (Stevens *et al.* 2005; Brosnan *et al.* 2010; Brosnan & de Waal 2002; Stevens & Hauser 2004; Barrett & Henzi 2005; Hauser *et al.* 2009; Melis & Semmann 2010). These cognitive demands, combined with the occurrence of cooperative behaviour between unrelated individuals in intelligent taxa, suggest that selection for these mechanisms of cooperation could, at least in part, be responsible for advanced cognitive abilities (Brosnan *et al.* 2010).

The many subfields within the social intelligence hypothesis, have shown a rich elaboration of verbal arguments, and data from comparative studies support many of their predictions (e.g. Pawlowkil *et al.* 1998; Dunbar 2003; Byrne & Corp 2004). However, verbal reasoning and comparative analysis alone are not sufficient to assess the relative merit of competing hypotheses (Gavrillets & Vose 2006); mechanistic models are needed to assess the plausibility of these different explanations for advanced cognition.

Here I use an artificial neural network model to focus on the potential for direct reciprocity, a behaviour that is widespread in humans, to select for advanced cognitive abilities. Rather than manufacturing some form of functional relationship between intelligence and fitness I allow this relationship to emerge based on the demands of decision-making in two social dilemmas, and analyse the consequences for the evolution of intelligence.

2.2. Methods

2.2.1. The social dilemmas

In order to consider the dynamics of cooperative social interactions I use the framework of two classic social dilemmas, the iterated prisoner's dilemma (IPD) and the iterated snowdrift game (ISD). In both games two players must choose between cooperation and defection during repeated rounds. In the event of mutual cooperation or mutual defection, both players receive payoffs R or P respectively, while a defector exploiting a cooperator gets T and the cooperator gets S . In the prisoner's dilemma the benefit of an individual's cooperative behaviour goes to their opponent, while they pay all of the costs (e.g. food sharing, reciprocal coalitionary behaviour). This results in a payoff order of $T > R > P > S$. Here the worst possible outcome for an individual is to cooperate while their opponent defects, while the best outcome is to defect while the opponent cooperates. In the snowdrift game the benefits of cooperative behaviours are shared between opponents, and the costs are shared if both individuals cooperate (e.g. cooperative hunting, coalitionary behaviour with shared benefits). This results in a payoff order of $T > R > S > P$. Again the best outcome for an individual is to defect while their opponent cooperates, though the worst possible outcome for an individual is for neither them nor their opponent to cooperate. In both games the overall payoff (sum of both individual's payoffs) is greatest for mutual cooperation and lowest for mutual defection.

All of this means that the equilibrium frequency of cooperation for a single interaction (single-interaction Nash equilibrium) will be zero in the prisoner's dilemma but will be non-zero for a single interaction snowdrift game (Hauert & Doebeli 2004). These single interaction Nash equilibria provide a useful benchmark against which to assess the effects of contingent behaviours (i.e. those that depend on the behaviour of others) in repeated interactions.

2.2.2. The neural network model

Any attempt to define a metric of intelligence will always be a contentious matter. However, comparative studies across taxa have usually focused on two main classes of brain properties as proxies of intelligence; metrics based on relative or absolute size of the brain or certain brain regions, and metrics based on more specific properties such as numbers of cortical neurons (Roth & Dicke 2005). It is with this tradition in mind that I develop an artificial neural network model, with evolving network structure, using the number of neurons, i , as a proxy for intelligence. Each individual can display varying levels of intelligence, from simply being characterized by a binary response of "always cooperate" or "always defect" to large neural networks that possess complex neuronal structure, allowing for computations to inform decisions based on payoffs and the integration of longer term memory into their current decision-making processes.

Each individual in my simulated populations possesses a neural network, which determines their behaviour in social dilemmas (illustrated in Fig. 2.1). The networks each have two input nodes, which receive the payoffs of the individual and their opponent in the previous round as inputs, and one output node, giving the probability that they cooperate during their next interaction. The hidden layer of each individual's network has an evolving structure, possessing different numbers of cognitive and context nodes (Elman 1991) (Fig. 2.1). Cognitive nodes allow for computation based on the values of network inputs and context nodes, which in turn allow for the build-up of memory based on previous states of their associated cognitive nodes. Individuals could possess between 0 and 10 cognitive nodes, and each cognitive node had the potential to have a context node with a recurrent connection.

Computation in the network is implemented via synchronous updating of nodes. The value of each input node is passed to each of the network's cognitive nodes, multiplied by the weight linking the two nodes. Each cognitive node is also passed the current

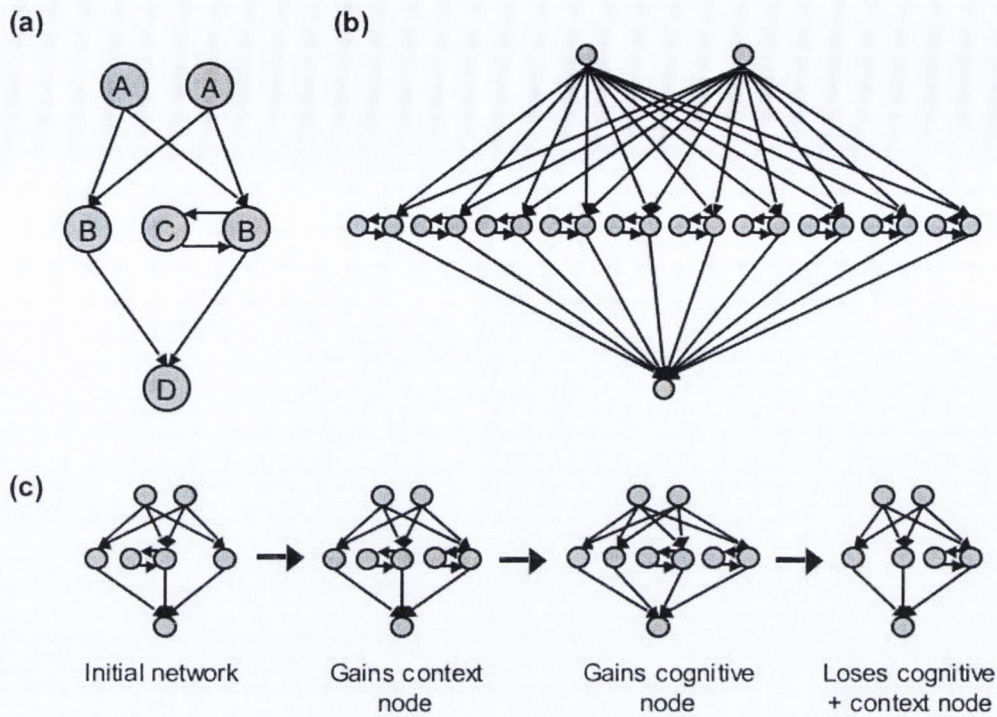


Figure 2.1: The artificial neural network model. A schematic to aid in the understanding of the network structures is shown in (a). Input nodes, which receive the payoffs of both players in the previous round are labeled A. Cognitive nodes, which can receive input from both input and context nodes are labeled B. Context nodes, which store the previous state of their cognitive node and return this state (times a weight) as input in the next round are labeled C. The output node which receives inputs from the cognitive nodes and gives the individual's decision to cooperate or defect is labeled D. The most complex artificial neural network allowed in the simulations is shown in (b), possessing 10 cognitive nodes and 10 context nodes. A sample of a possible sequence of mutations to network structure is shown in (c). Individuals gain and lose cognitive and context nodes by random mutation. If a cognitive node with a connection to a context node is lost by mutation the context node is also lost.

value of their associated context node (if they possess one) multiplied by the weight linking the two nodes. These weights simply control the strength of interaction between two nodes in the network, i.e. how much they activate or inactivate each other. The cognitive nodes sum across all of the weighted values that they receive and pass this value through a sigmoidal squashing function, $f(x) = 1/(1 + \exp(-x - t))$, where x is the input to the node and t is the node's threshold. This results in a value between 0 and

1, analogous to a probability of activation. All context nodes are then passed the value of their associated cognitive nodes. This allows the context nodes to build up memory of previous interactions without having to store the actual sequence of events that have occurred. The internal states of these context nodes could be considered analogous to emotional states, building up memory over multiple interactions. Finally the values at all cognitive nodes are then passed to the output node (multiplied by their weights), summed, and again passed through a sigmoidal squashing function. This output gives the probability that the individual will cooperate in the current round. As the sigmoidal function asymptotes to 0 at $-\infty$ and 1 at ∞ there will always be inherent noise in the network's probabilistic decision. This property of the function also means that it is easy to minimise noise in the networks behaviour if that behaviour shows a lack of contingency (as the node can always be near one of the asymptotes), while contingent behaviour will show greater noise (as switching is more difficult to achieve near the asymptotes). This formulation has intuitive appeal over simply adding extraneous noise to individual decisions, as in nature we would expect individuals to make few mistakes when their behaviour is non-contingent, while more complex decisions would be expected to be more error-prone. As the network cannot make decisions without an input each individual has an additional trait encoding whether they cooperate or defect in the first round.

I allowed networks to evolve according to natural selection using a genetic algorithm where fitness is the mean payoff per round from the iterated games minus a penalty for the individual's intelligence, i . When individuals reproduce, mutations allow for the gain and loss of nodes from the hidden layer of their network with a fixed probability. Context nodes could only be gained if there was already a cognitive node present without an associated context node. The loss of a cognitive node with an associated node resulted also in the loss of the associated context node.

The addition of extra cognitive nodes gives networks the potential to perform complex

computation based on payoffs by increasing the dimensions of internal representation of the network. The addition of context nodes gives the potential for the integration of longer-term memory of previous interactions in these computations. If an individual possessed no hidden layer nodes in its network, its behaviour in all rounds was decided by its first round move, i.e. they either always cooperated or always defected. The weights of each node in the network (arrowed lines in Fig. 2.1) and the threshold of each node were encoded as continuous genetic traits, again subject to mutation during reproduction. This means that, while the number of nodes in the network constrains the possible behavioural repertoire, it is the way that the constituent parts of the network interact that actually decides the individual's behaviour. In this way my metric of intelligence assesses the potential for complex behaviour that the individual possesses, rather than the appropriateness or wisdom of their behaviour, similarly to the measures of intelligence used in comparative studies.

2.2.3. Model implementation

In order to elucidate when selection favored intelligence I ran 10 replicates of the model for both the IPD and ISD, with each replicate lasting 50,000 generations. The payoff values used for all simulations were $R = 6$, $P = 2$, $T = 7$ and $S = 1$ for the IPD, and $R = 5$, $P = 1$, $T = 8$ and $S = 2$ for the ISD. The fitness penalty for intelligence was set at $0.01i$. The genetic algorithm was implemented as follows:

(1) An initial population of random networks was generated. Individuals were randomly assigned network structures of 0, 1, 2 or 3 hidden layer nodes and were randomly assigned weights and thresholds between 10 and 10, and first moves.

(2) Each individual played every other individual in the population (50 individuals) in an

IPD or ISD.

(3) Each individual network's fitness was calculated as their mean payoff per round minus a fitness penalty of $0.01i$.

(4) Individuals were selected to reproduce asexually with probability proportional to their fitness.

(5) Newly produced offspring underwent mutation with probability 0.1 for network weights, thresholds and first move, and with probability 0.02 for mutations in network structure. Mutations in an individual's first move simply change their first move from cooperate to defect and vice versa. If a weight or threshold of a network was mutated, a random value from a normal distribution with mean 0 and standard deviation 0.5 was added to the current value of the weight or threshold. Mutations in network structure led to the addition or removal of a node with equal probability (see Fig. 2.1). As the number of hidden layer nodes allowed in each network was limited between 0 and 20 (10 cognitive and 10 context) this effectively halves the mutation rate at these boundaries. A context node could not be gained unless a cognitive node without a context node was already present.

(6) The previous generation died.

(7) The algorithm returned to step 2 until 50,000 generations was reached.

During simulations I recorded the frequency of cooperation in the population, individual fitness and intelligence ($\bar{i}$), and assessments of the behaviour of individuals

against a pre-determined test set of moves. I then analyzed the gradients of selection for intelligence across these simulations by taking selection for intelligence as the covariance between fitness and intelligence in any given generation (Price 1970).

As 50 million individual neural networks were simulated in this study, and individuals were not constrained to base their behaviour only on the previous move, the simulations generated a great diversity of strategies. In order to gain a coarse-grained overview of the strategic composition of the population I clustered individuals based on their proximity to four canonical strategy types. Assignment to each of these strategy types was based on which of these four strategies each individual network clustered closest to, based on its behaviour against the test-set. Phenotypes of emergent networks were characterized by playing them against a test-set that was determined before the beginning of all simulations and comparing their behaviour to that of five strategies: always defect, always cooperate, tit-for-tat, tit-for-two-tats and Pavlov. Tit-for-tat is a strategy whereby individuals adopt the action that their opponent carried out in the previous round. Tit-for-two-tats is a similar strategy, where an individual responds to two sequential defections with a defection but otherwise cooperates. Pavlov (also known as win-stay, lose-shift or simpleton) is a strategy by which an individual responds to payoffs of T (defecting while opponent cooperates) and S (cooperating while opponent defects) with defection, and responds to payoffs R (mutual cooperation) and P (mutual defection) with cooperation. Pavlov has been so named as it embodies aspects of Pavlovian conditioning; if your payoff is greater than a given amount stick with the same behavior: if less, then switch behaviors.

The test-set consisted of the moves of theoretical opponents that are characterized simply by their probability of cooperating in each round of the prisoner's dilemma, this probability varying from 0 to 1 in steps of 0.25. The sequence of moves of each of these opponents for 5 replicates of a 20 round IPD or ISD was generated. The networks

were then tested at the end of each generation of the simulations against the test-set and could be clustered with their closest pure strategy (note that tit-for-tat and tit-for-two-tats were pooled for all analyses). A network's closest pure strategy was assessed by assessing the sums of squares between the network's sequence of moves (coded as 0 for defect and 1 for cooperate) and those of each of the pure strategies, treating each move against the test-set as a data point. Networks were then assigned to the strategy type that minimised the sums of squares. While this clustering is only a coarse-grained view, it allows assessment of the effects of shifts towards contingent cooperative strategies on selection for intelligence. Additionally, contingent human cooperation has previously clustered as either tit-for-tat-like or Pavlov-like (Kimmerli *et al.* 2007), though longer-term memory is often included (Fudenberg *et al.* In press).

The relationship between the frequency of cooperative acts and the mean level of intelligence in the population was established by using Spearman's rank correlation test. The relationship between the variance in the frequency of cooperative acts and the mean level of intelligence in the population was established using a modified version of the Breusch-Pagan test. This was done by fitting a binomial model to the relationship between the frequency of cooperative acts and the mean level of intelligence in the population and then regressing the square of the residuals of this model on the mean level of intelligence in the population. A positive slope indicates that variance increases with intelligence. The p-values of these tests were adjusted using Holm's method of correction for multiple comparisons. Spearman's rank correlation test was used to assess the relationship between selection for intelligence and the frequencies of different strategies. Additional analysis was performed by partitioning the data into high (greater or equal to 0.5) and low (less than 0.5) frequencies of cooperation and again using Spearman's rank correlation test. Again, p-values of these tests were adjusted using Holm's method of correction for multiple comparisons. I note that p-values will be significantly deflated

owing to the large sample size, but are presented for completeness.

2.3. Results

My model shows the spontaneous evolutionary emergence of behaviours similar to strategies known to perform well in the IPD and ISD, such as tit-for-tat and Pavlov, as well as simple always-cooperate or always-defect strategies (Fig. 2.2) (see Nowak & Sigmund 1993 for discussion of strategies and their emergence). Though the networks' behaviours are similar to these strategies they often show integration over many previous rounds to decide on their next moves. For example, manual interrogation of networks revealed that, of the tit-for-tat type strategies that emerge, many are tit-for-two(or more)-tats, and many of the Pavlov-like strategies also show a threshold mechanism, switching to constant defection against opponents that show behaviour close to an always-defect strategy. Behaviour was observed that appeared to be close to many other strategies, for example; Grim variants (cooperate until the opponent defects, then defect forever), though often requiring more than one defection to trigger permanent defection; False cooperator (cooperate first then switch to defection), though often giving another cooperative move after many defections; and many other variants of tit-for-tat such as 2-tits-for-1-tat and 2-tits-for-2-tats. It is worth noting that strategies of these types that utilise longer-term memory are observed in behavioural experiments of repeated games with noise (Fudenberg *et al.* In press). These responsive strategies require greater cognitive abilities in order to carry out computations based on payoffs and memorize past rounds and integrate across them to make decisions, in comparison to the lower requirements of simply always cooperating or defecting. I hasten to add however that the strategies emerging only resemble these strategies; the strategies vary in a continuous manner and often incorporate memory over more rounds. The goal here is not to describe the strategies that can emerge in repeated games, as there is already extensive literature on

this topic (see Table 2.1 in Dugatkin 1997), but rather to elucidate the potential effects of their evolution on selection for cognitive capacities.

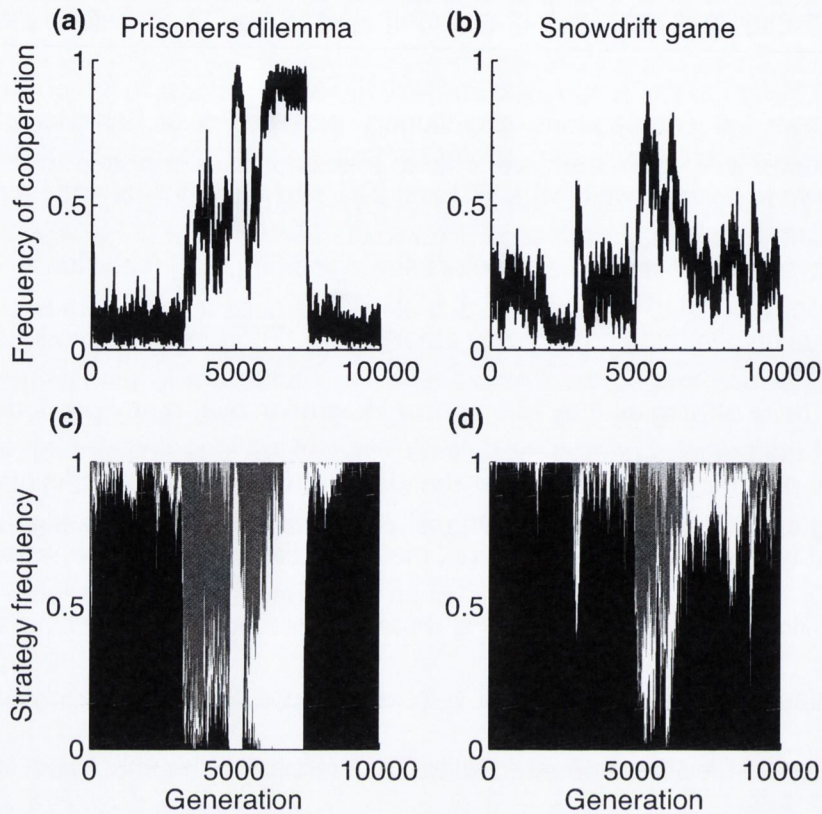


Figure 2.2: The emergence of intelligent strategies. Shown are the dynamics during 10,000 generation subsets of the simulations for the prisoner's dilemma (a and c) and the snowdrift game (b and d). a and b show sample cycles in the frequency of cooperative acts in the population. b and d show the frequencies of different strategy types (always-defect-like black, always-cooperate-like white, tit-for-tat-like dark grey, Pavlov-like light grey) as determined by clustering individuals with their nearest pure strategy (see methods section and electronic supplementary material for details). Transitions to cooperation are characterized by high numbers of contingent strategies, followed by the invasion of the always cooperate strategy.

In order to elucidate the causal factors leading to the evolution of more complex strategies, I analysed the gradient of selection for intelligence in response to population features such as the prevalence of cooperative acts. I found that selection for intelligence is maximized as the level of cooperation in the population moves above the single interaction Nash equilibria towards more cooperative regimes (Fig. 2.3). In the

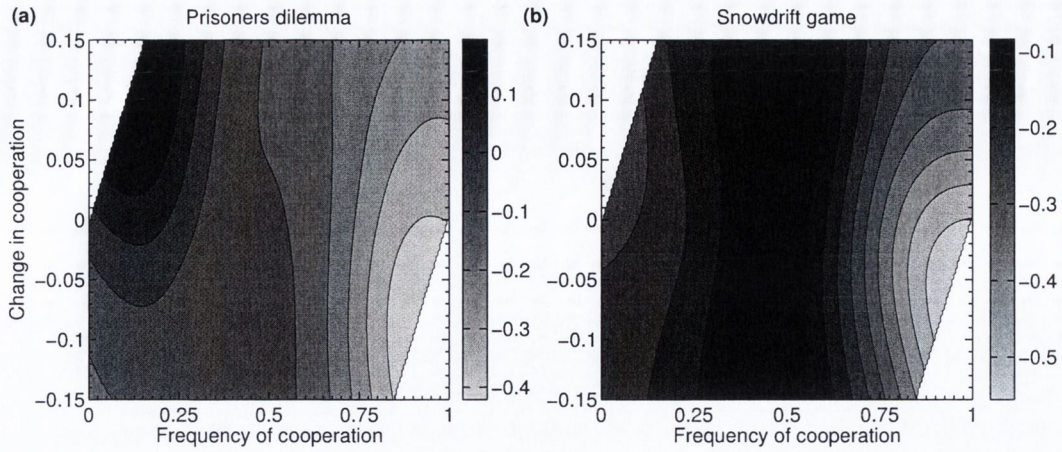


Figure 2.3: Selection for intelligence and transitions to cooperation. Shown is the level of selection for intelligence, taken as the covariance between fitness and intelligence, against the frequency of cooperation in the current generation and the change in the frequency of cooperation since the last generation. Darker shades indicate greater selection for intelligence. White areas indicate impossible value combinations. Selection for intelligence is maximized during transitions away from single-interaction equilibria, which are no cooperation for the IPD (a) and a frequency of cooperation of 0.23 for the ISD (b). Values displayed were smoothed using a Gaussian kernel.

IPD this maximum occurs during increases in cooperation from the single-interaction Nash equilibrium, whereas in the ISD selection for intelligence is maximised at levels of cooperation just above the single-interaction Nash equilibrium. This discrepancy between the games is explained by the different natures of their single-interaction Nash equilibria. In the IPD this equilibrium is zero, meaning that declining cooperation near this equilibrium is caused by increases in the frequency of individuals that always defect, requiring only little cognitive ability. In the ISD the equilibrium frequency of cooperation is non-zero (0.23 in these simulations), meaning that decreases in cooperation back towards the equilibrium can be caused by meaner contingent strategies (e.g. 2-tits-for-1-tat and false cooperator variants), as well as individuals that always defect. As a result, transitions back to the single-interaction Nash equilibrium in the ISD can in principle select for intelligence as some cooperation is still occurring that can be exploited, while this is very unlikely in the IPD.

I also find that increasing intelligence decreases the mean frequency of cooperative acts in the IPD (Spearman's rank correlation test; $\rho = -0.2333$, $p < 0.0001$; Fig. 2.4a), while slightly increasing cooperation in the ISD (Spearman's rank correlation test; $\rho = 0.0089$, $p < 0.0001$, Fig. 2.4b: note that these are increases in rank, the mean values show little trend). Increasing intelligence increases the variance in the frequency of cooperative acts in the population in the both the IPD (Breusch-Pagan test; intercept = 0.0294, slope = 0.0582, $p < 0.0001$; Fig. 2.4a) and the ISD (Breusch-Pagan test; intercept = 0.0309, slope = 0.0384, $p < 0.001$; Fig. 2.4b), showing that intelligence can facilitate greater extremes of cooperation. These results can be explained by assortment of individual's cooperative acts (Fletcher & Doebeli 2009); the contingent strategies facilitated by increased intelligence allow an individual to increase the probability that they assort their cooperative acts with other cooperative acts. This leads to a synergistic process, where this increase in cooperation due to increased intelligence creates further opportunities for intelligent individuals to engage in mutual cooperation. However, as levels of cooperation increase further this feedback can break down, as there may be enough cooperation occurring for unconditional cooperators to increase in the population, allowing in turn for the invasion of unconditional defectors or meaner intelligent strategies (e.g. grim variants, false-cooperator variants, etc.). This results in intelligence facilitating cycles in the levels of cooperation seen in the population (Fig. 2.2), which increases both the variance in, and the maximum level of, cooperation.

In addition to dependency on the prevalence of, and change in, cooperative actions (Fig. 2.3), I find that intelligence can be subject to a Machiavellian runaway process (Byrne & Whiten 1988; Whiten & Byrne 1997). In the ISD as the frequency of contingent (intelligent) strategies increases, so too does selection for intelligence in the population (tit-for-tat-like strategies: Spearman's $\rho = 0.2025$, $p < 0.0001$; Pavlov-like strategies: $\rho = 0.2352$, $p < 0.0001$; see Figs. 5 and 6). In the IPD, increasing frequencies

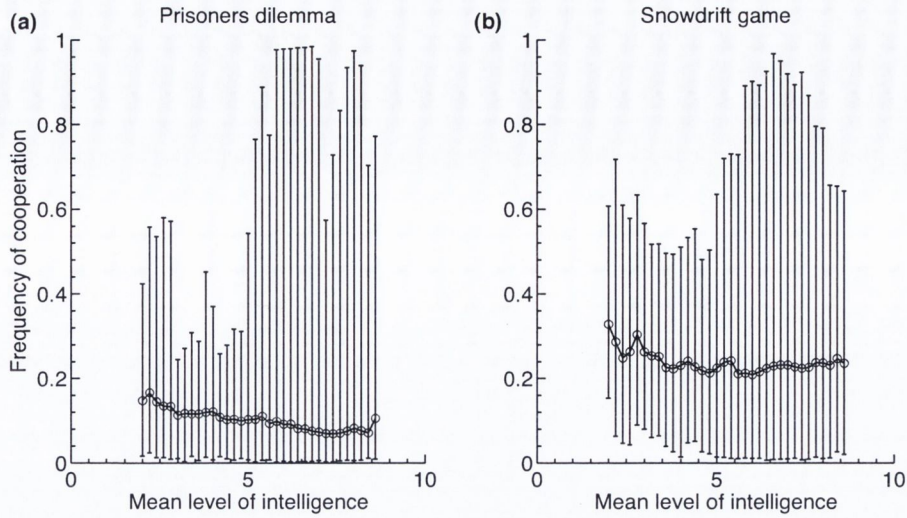


Figure 2.4: Intelligence and the distribution of cooperation. Shown are the relationships between the frequency of cooperative acts in the population and the mean level of intelligence in the population for the prisoner's dilemma (a) and for the snowdrift game (b). Mean values are shown by the open circles and lines, and the ranges of the data are shown by the error bars. Greater intelligence decreases the mean level of cooperation in the IPD, while slightly increasing the mean level of cooperation in the ISD. The maximum and variance in the frequency of cooperative acts increases with intelligence, showing that the evolution of intelligent, contingent strategies leads to greater extremes in the frequency of cooperation.

of tit-for-tat and Pavlov reduces selection for intelligence at low levels of cooperation (frequency of cooperation < 0.5 ; tit-for-tat: $\rho = -0.0945$, $p < 0.0001$; Pavlov: $\rho = -0.0529$, $p < 0.0001$), but does increase selection for intelligence when cooperation is more frequent (frequency of cooperation ≥ 0.5 ; tit-for-tat: $\rho = 0.5491$, $p < 0.0001$; Pavlov: $\rho = 0.3187$, $p < 0.0001$). The reason for this distinction between the IPD and ISD is that there must already be some cooperation occurring for cooperative contingent strategies to be favored via their ability to assort cooperative acts. In the ISD, the partially cooperative single-interaction equilibrium provides sufficient baseline cooperation for tit-for-tat and Pavlov to be favored, whereas in the IPD the single-interaction equilibrium of zero cooperation means that unless contingent strategies (or random drift) have already increased cooperation, tit-for-tat-like and Pavlov-like strategies cannot be favored, and

hence cannot lead to an arms race. Note that it is still the case that intelligence is selected for in the IPD when cooperative acts are rare yet increasing (Fig. 2.3a). However, the cooperative acts that drive selection for intelligence in this case are generated by less cooperative contingent strategies, which cluster with always-defect as their closest pure strategy ($\rho = 0.1095$, $p < 0.0001$; see Fig. 2.6). This means that there is a succession in the arms race in the IPD, with mean contingent strategies initially increasing selection for intelligence at low cooperation, and kind contingent strategies increasing selection for intelligence as cooperation increases.

It is not any particular single strategy that drives these arms races; rather as the complexity of the strategies in the population increases there is selection for other complex strategies to outwit them. Unlike previous analyses where fixed strategies or strategies with constrained memory were used, my open-ended system allows for near infinite strategic variations to outwit opponents. In this way, selection for intelligence occurs owing to a constantly shifting strategic environment, where the best response to the population of strategies can be shifting from generation to generation. Increases in memory allow for the potential of the recognition of opponents' strategies, allowing for the alteration of one's own strategy in response (e.g. Pavlov-like strategies that can recognise individuals that always defect). In turn this can allow for attempts to deceive opponents regarding one's own strategy (e.g. false cooperators).

2.4. Discussion

It is important here to note the closed nature of the model system; individuals can only choose within one social task (whether to cooperate or defect against another individual based on their behaviour in previous interactions with them). However, my results may apply in principle to other social scenarios where individuals use strategies to decide who to cooperate with or when to cooperate, such as indirect reciprocity (Nowak &

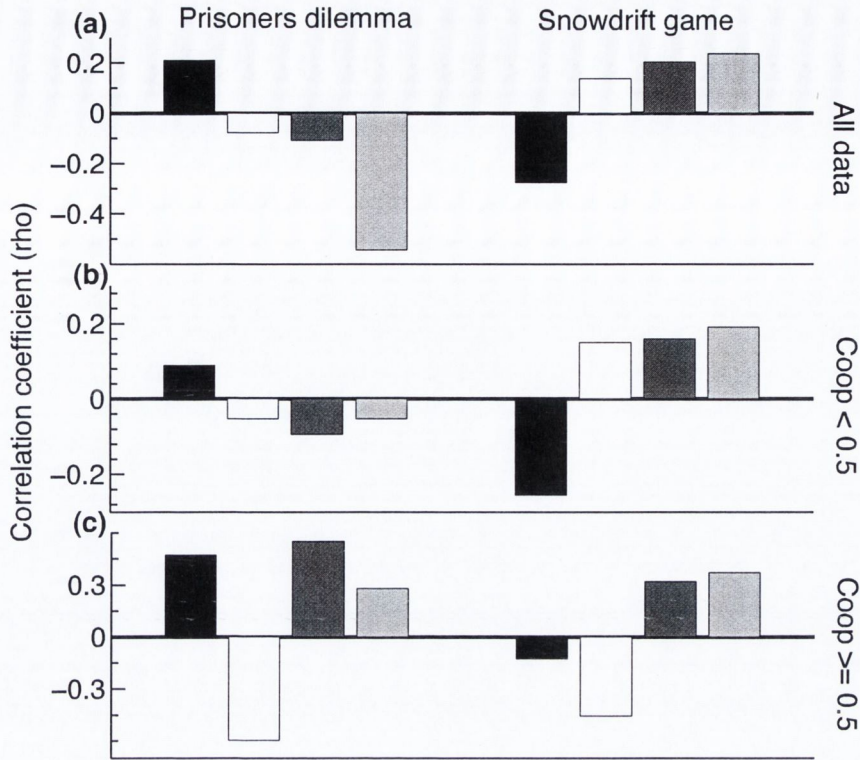


Figure 2.5: Strategic composition and selection for intelligence. The barplots show the Spearman rank correlation (ρ ; all $p < 0.0001$) between the frequency of each of the four strategy types and selection for intelligence for (a) all levels of cooperation, (b) low cooperation (frequency of cooperative acts < 0.5), and (c) high cooperation (frequency of cooperative acts ≥ 0.5). Tit-for-tat-like and Pavlov-like strategies always increase selection for intelligence in the ISD, but only when cooperation is high in the IPD. Colours correspond to: black - "always defect-like", white - "always cooperate-like", dark grey - "tit-for-tat-like", light grey - "Pavlov-like". For further details see Fig. 2.6.

Sigmund 1998; Nowak & Sigmund 2005), policing/punishment (Boyd *et al.* 2003; Hauert *et al.* 2007) and partner choice (Roberts 1998; Sheratt & Roberts 1998; McNamara *et al.* 2008). Along with kin selection these are the major mechanisms thought to lead to transitions to cooperative groups. As the intelligence of an individual increases it is likely that more of these behavioural repertoires will be become available to them, with increased intelligence acting as a pre-adaptation. For example, increased intelligence owing to selection for direct reciprocity could facilitate the evolution of indirect reciprocity

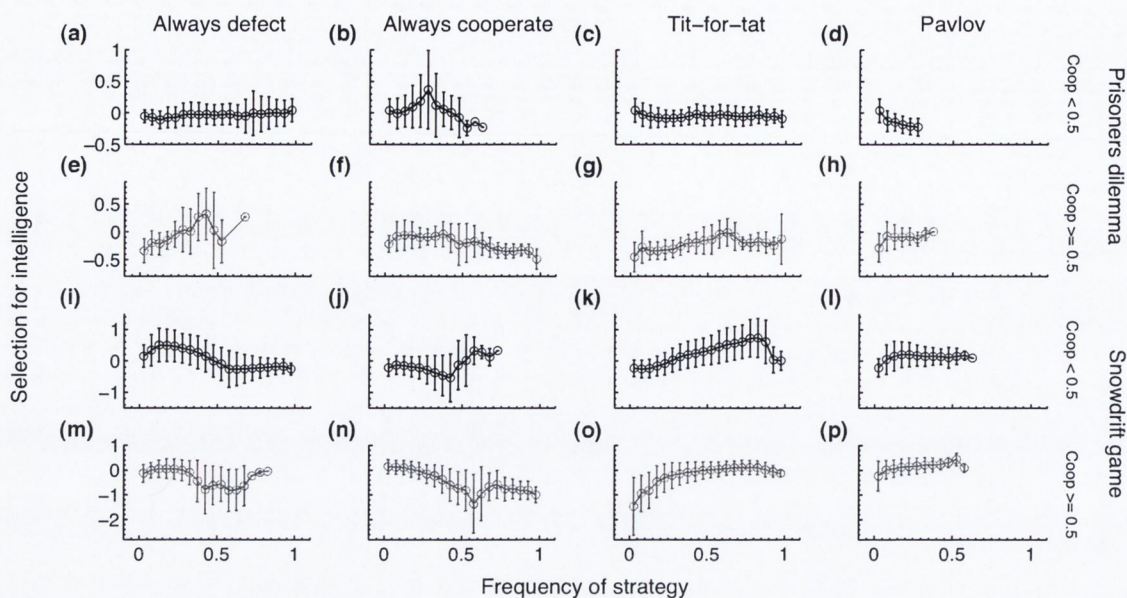


Figure 2.6: Strategic composition and selection for intelligence. Shown are the relationships between selection for intelligence and four main strategy types; always defect (a,e,i,m), always cooperate (b,f,j,n), tit-for-tat (c,g,k,o) and Pavlov (d,h,l,p), for the IPD (a-h) and ISD (i-p). The data are also split between low (< 0.5 ; a-d,i-l; black) and high (≥ 0.5 ; e-h,m-p; gray) frequencies of cooperation. Mean values are shown by the open circles and the solid line, and error bars show one standard deviation of the data.

or partner choice, highlighting the contingent nature of social evolution in multiple strategic dimensions (Brown & Taylor 2010). The facilitation of new social behaviours due to emergent intelligence could allow for a perpetuated Machiavellian arms race leading to ever-greater levels of intelligence. Additionally, in my simulations populations evolved to play only a single game, either the IPD or ISD. The simultaneous play of multiple games could greatly increase strategic complexity, with the possibility of the integration of information from previous interactions in games with different payoff structures into the decision-making process.

It has previously been suggested that the pinnacles of cooperative behaviour in nature show a bimodal distribution with intelligence, with the most cooperative species displaying either limited cognition (e.g. microbes, social hymenoptera), or exceptional intelligence

(e.g. humans and other primates, certain cetaceans and birds) (Brosnan *et al.* 2010). It is clear in the former case that cooperation has evolved primarily due to combinations of kin selection and ecological factors (West *et al.* 2007). However, in the latter case, kin selection is not the only, and may not even be the most important mechanism leading to cooperation. A recent study has in fact suggested that relatedness was too low in human hunter-gatherer groups for kin selection to drive the evolution of human cooperation (Hill *et al.* 2011). In highly intelligent species, contingent behaviours (reciprocity, partner choice, etc.) appear to have been important in the evolution of cooperation (Brosnan *et al.* 2010). My results may help to explain this pattern by showing that selection for appropriate behavioural assortment of cooperative acts can lead to selection for greater cognitive abilities and Machiavellian arms races, and that intelligence facilitates greater extremes of cooperation. Additionally, although kin selection is still of importance in highly intelligent taxa, high relatedness may hinder the evolution of intelligence by driving unconditional cooperation to fixation in the population, without any need of contingent behaviours.

A trait as complex as advanced intelligence is unlikely to have a single causal factor but is likely to have evolved owing to a combination of several factors (Reader *et al.* 2011). Along with the social intelligence hypothesis, many other theories attempting to explain the evolution of advanced intelligence have been suggested, among them that intelligence is an adaptation for tool use (Oakley 1949; Wynn 1988), that intelligence is an adaptation for social learning and the accumulation of culture (Whaiten & van Schaik 2007; Moll & Tomasello 2007; Van Schaik & Burkart 2011), and that intelligence is the result of sexual selection (Miller 2000). All of these theories are supported by evidence from at least some of the most intelligent animals. However, the difficulty lies in disentangling the traits that are causal factors in the evolution of intelligence from those that are by-products of advanced intelligence. The combination of game theoretic

frameworks and artificial neural network models presented here may provide a framework for the evaluation of the mechanistic strengths of these different hypotheses. While previous models have sought to relate cooperation and intelligence the focus has most frequently been on the cognitive requirements of cooperation, rather than on selection for intelligence. Many of these models have lacked an explicit brain structure (e.g. Rubinstein 1986; Abreu & Rubenstein 1988; Gilboa & Samet 1989; Fogel 1993; Ho 1996; Miller 1996), and among those studies that have used artificial neural networks I know of no examples where the network structure was allowed to freely evolve or implications of selection for decision-making strategies, for the evolution of intelligence were directly addressed (Harald & Fogel 1996; Chellapilla & Fogel 1999). While artificial neural networks are not real brains, relying on abstraction of the activity of millions of real neurons down to a manageable number of artificial neurons, they can provide insight into the dynamics of cognitive evolution and allow for the flexible evolution of behaviour (Enquist & Ghirlanda 2005). My results show that, in a freely evolving system, selection for efficient decision-making in social interactions can give rise to selection pressures for advanced cognition and supports the view that the transition to the cooperative groups seen in the most intelligent taxa may be the key to their intellect.

Chapter 3

Bigger brains and longer lives facilitate the evolution of cooperation

This chapter is being prepared for submission for publication

Authors: McNally L, Brown SP, Jackson AL & Kümmerli R

Authors' contributions: LM conceived the idea; LM developed and analysed the model with guidance from SB; LM collated and analysed data with assistance from RK; LM, SB, AJ and RK interpreted results; LM wrote the manuscript with suggestions from SB, AJ and RK

3.1. Introduction

Explaining the evolution of cooperative behaviour is a central challenge in evolutionary biology. A cooperative act often has immediate costs for a cooperative individual, leading to a paradox of how it can evolve as, all else being equal, it will reduce an individual's relative fitness (Lehmann & Keller 2006; West *et al.* 2007). However, many solutions have been proposed to the problem of costly cooperation, all of which rely on correlation, or assortment, among the phenotypes of social partners (Frank 1998; Woodcock & Heath 2002; Henrich 2004). This correlation among the phenotypes of interacting individuals leads to cheaters either being denied cooperation or having a cost imposed on them (e.g. punishment), thus increasing a cooperator's relative fitness.

There are two major factors known to create this necessary correlation: population structure and conditional behaviour (e.g. behaviour dependent on a partner's phenotype). If populations are viscous, i.e. dispersal is limited, high levels of relatedness among group mates can arise, favouring cooperation (Hamilton 1964, though see Taylor 1992). Other factors, such as low levels of promiscuity, that increase relatedness in family groups can also combine with population structure to favour cooperation (Hughes *et al.* 2008; Cornwallis *et al.* 2010). While population structure can help favour costly cooperation, it is not inherently necessary for its evolution. If individuals adjust their levels of cooperation in response to some aspect of the phenotype of their social partners that reliably indicates their future behaviour, this can also create the required assortment (Frank 1998; Henrich 2004).

While there is a wealth of theory on cooperation based on conditional behaviour (Nowak 2006; Lehmann & Keller 2006; West *et al.* 2007), we know surprisingly little regarding the organismal traits that facilitate its evolution. However, two promising candidate traits have been suggested: cognitive capacity and lifespan. As conditional

cooperation requires individuals to assess the behaviour/phenotype of others, commit this information to memory and then make accurate decisions based on this information, it has been suggested that increased cognitive capacities/brain size may favour its evolution (Trivers 1971; Brosnan & de Waal 2002; Stevens & Hauser 2004; Barrett & Henzi 2005; Stevens *et al.* 2005; Hauser *et al.* 2009; Melis & Semmann 2010; Brosnan *et al.* 2010; McNally *et al.* 2012; Chapter 2). Also owing to the inherently predictive nature of conditional cooperation, i.e. past actions are used to infer future actions, it has been suggested that a longer lifespan may favour conditional cooperation as individuals' current actions will be more likely to have future effects and/or individuals have more time to assess the behaviour/phenotype of others (Trivers 1971; Axelrod & Hamilton 1981; McNamara *et al.* 2008).

Here I develop a general illustrative model for the effects of cognition and lifespan on assortment via conditional behaviour and consider specific models for five specific forms of conditional cooperation: partner choice, direct reciprocity, indirect reciprocity, cooperation in response to punishment and kin discrimination based on phenotypic or environmental cues. I then present a comparative analysis showing that non-human primate species with bigger brains and longer lives are more likely to engage in two forms of cooperation: coalition formation and food sharing.

3.2. Theoretical models

Let us assume that an actor's mean fitness payoff from an interaction with others (w) is a function of their mean investment in cooperation per interaction ($\bar{x}$), and that of their social partners ($\bar{X}$). The gradient of selection with respect to an individual's level of cooperation can then be written as $dw/d\bar{x} = \partial w/\partial \bar{x} + (\partial w/\partial \bar{X})(d\bar{X}/d\bar{x})$. $\partial w/\partial \bar{x}$ is the marginal fitness effect of actor phenotype, which we will assume to be negative (i.e. cooperating has a cost), and $\partial w/\partial \bar{X}$ is the marginal effect of partner phenotype, which we will assume to

be positive (i.e. receiving cooperation has a benefit). Note however that the signs for these marginal values need not hold for all possible values of $\bar{x}$ and for a social dilemma to exist, it is only necessary that they hold for some region of possible phenotypic values. The final term $d\bar{X}/d\bar{x}$ is a measure of the phenotypic assortment between individuals, i.e. how partner phenotype changes with actor phenotype. The condition for an increase in actor cooperation to be favoured by selection is then $\partial w/\partial \bar{x} + (\partial w/\partial \bar{X})(d\bar{X}/d\bar{x}) > 0$. This condition is equivalent to Queller's (2011) formulation of 'kin selection': selection on social traits that exhibit phenotypic feedback between partners. While there are many similarities between this formulation and Hamilton's rule, the causal process is accounted for in a substantially different manner. The phenotypic association term can contain effects of both conditional behaviour and interactions among kin, capturing a general measure of phenotypic assortment. For a general discussion of the relationship between this term and relatedness coefficients see Frank (1998) and Queller (2011).

Following our assumptions, the phenotypic assortment term $d\bar{X}/d\bar{x}$ must be greater than the marginal cost to benefit ratio $(\partial w/\partial \bar{x})/(\partial w/\partial \bar{X})$ for selection to favour an increase in actor cooperation. This can arise owing to spatial structuring leading to interactions among kin, however here we will concern ourselves with assortment arising from conditional behaviour. If behaviour is conditional, partner cooperation is expected to be some function of previous observations of some aspect of the actor's phenotype and the cognitive abilities of the partner. We can then write partner cooperation in an interaction at time t as $X_t = f(\mathbf{x}, c)$, where $\mathbf{x}$ is a vector containing information on the actor's phenotype of interest in all previous rounds and c represents the cognitive capacities of the species. We ignore variation in, and selection on, c for clarity and analytical tractability. The function f could represent many different forms of conditional cooperative behaviour such as partner choice or some form of reciprocity. We can now

the write the mean level of cooperation received by the actor per round as

$$\bar{X} = \left(\sum_{t=1}^{\infty} f(\mathbf{x}, c)(s^2 p^2)^{t-1} \right) (1 - s^2 p^2), \quad (3.1)$$

where s is the probability that an individual survives until the next interaction and p is the probability that individuals do not leave the group owing to sources other than mortality (e.g. dispersal). The term $(s^2 p^2)^{t-1}$ is the probability that the two individuals interact at round t (assuming that they interact at $t = 1$), and the term $(1 - s^2 p^2)$ is the inverse of the average number of rounds of interaction.

Given this, what are the expected effects of cognition and survival on selection for cooperation? Successful strategies of conditional cooperation all have the property of increasing investment in cooperation based on some measure of their partner's phenotype (Frank 1998). As long as increased cognitive capacity facilitates more accurate decisions based on the behaviour of others and the probability of repeated interaction is non-zero ($s^2 p^2 > 0$), we then expect increased cognitive capacity to increase the magnitude of phenotypic assortment. Similarly, as long as partner investment in cooperation is a function of previous observations of the actor's phenotype and individuals have some memory of this, the magnitude of phenotypic assortment will also increase with survival rate. We illustrate this general argument with specific examples below.

(a) Partner choice

First we consider the case of partner choice. Partner choice favours the evolution of cooperation by individuals rejecting and accepting partners based on their investment in cooperation (Roberts 1998; Sheratt & Roberts 1998; McNamara *et al.* 2008). This differs from reciprocity as all interaction ceases, rather than cooperation simply being withheld. We will assume that investment in cooperation can take values between 0 and

1. We consider a resident phenotype that invests maximally in cooperation but aims to cease interactions with individuals investing less than maximally in cooperation (i.e. they reject them as partners). We further assume that the cognitive capacity c of an individual and the extent of the deviation from maximal cooperation of the actor influences the probability that a resident ceases interaction. Following these assumptions we can write the probability that a resident ceases interaction with the actor after a given round as $q = (1 - x)(1 - e^{-\alpha c})$, where x is the investment in cooperation per round by the actor if interaction occurs, and α is a scaling factor on the effect of cognition. As residents are assumed to invest maximally in cooperation, the actor will never choose to cease interaction with them. It follows that the expected number of rounds of interaction without the actor being rejected by the resident is $1/(1 - (1 - q)s^2p^2)$. Using equation 3.1 we can then write the mean investment in cooperation by the resident as

$$\bar{X} = \frac{1 - s^2p^2}{1 - (1 - (1 - x)(1 - e^{-\alpha c}))s^2p^2}, \quad (3.2)$$

and by the actor as

$$\bar{x} = \frac{x(1 - s^2p^2)}{1 - (1 - (1 - x)(1 - e^{-\alpha c}))s^2p^2}. \quad (3.3)$$

Both equations 3.2 and 3.3 are the products of three quantities: the expected number of rounds of interaction before rejection $1/(1 - (1 - (1 - x)(1 - e^{-\alpha c}))s^2p^2)$, the inverse of the expected number of possible rounds $1 - s^2p^2$, and the investment in cooperation by each individual during each round of interaction (1 and x for the resident and actor respectively). We can now use $d\bar{X}/dx = (d\bar{X}/dx)(dx/d\bar{x})$ to write

$$\frac{d\bar{X}}{d\bar{x}} = \frac{(1 - e^{-\alpha c})s^2p^2}{1 - e^{-\alpha c}s^2p^2}. \quad (3.4)$$

We can then evaluate the effects of c and s on assortment as

$$\frac{d(d\bar{X}/d\bar{x})}{dc} = \frac{\alpha e^{-c}s^2p^2(1 - s^2p^2)}{(e^{-\alpha c}s^2p^2 - 1)^2} \quad (3.5)$$

and

$$\frac{d(d\bar{X}/d\bar{x})}{ds} = \frac{2(1 - e^{-\alpha c})sp^2}{(e^{-\alpha c}s^2p^2 - 1)^2} \quad (3.6)$$

which are both strictly positive meaning that assortment is monotonically increasing with both cognitive capacity and survival rate.

(b) Direct reciprocity

Direct reciprocity occurs when individuals adjust their investment in cooperation with a partner in response to the levels of cooperation previously received from that partner (Trivers 1971; Axelrod & Hamilton 1981). Again we will assume that investment in cooperation can take values between 0 and 1. We will consider a resident strategy that initially invests maximally in cooperation but will subsequently attempt to match the contribution of the actor (x) if this is less than 1. We will further assume for simplicity and clarity that reciprocity only acts in a downward direction, i.e. that the actor will never invest more than x . The probability with which an individual can detect investment lower than their own and adjust their investment is decided by their cognitive ability according to $1 - e^{-\alpha c}$. From these assumptions it follows that the actor will invest x in cooperation in all rounds and the resident will invest 1 in the first round and $x(1 - e^{-\alpha c}) + e^{-\alpha c}$ on average in all subsequent rounds. From equation 3.1 and following the same procedure as before we can then write the mean investment in cooperation by the resident per round as

$$\bar{X} = 1 - s^2 p^2 + (x(1 - e^{-\alpha c}) + e^{-\alpha c})(s^2 p^2), \quad (3.7)$$

while the average investment for the actor is simply $\bar{x} = x$. We can then calculate assortment as $d\bar{X}/d\bar{x} = (1 - e^{-\alpha c})s^2 p^2$. The effects of c and s on assortment are then

$$\frac{d(d\bar{X}/d\bar{x})}{dc} = \alpha e^{-\alpha c} s^2 p^2 \quad (3.8)$$

and

$$\frac{d(d\bar{X}/d\bar{x})}{ds} = 2(1 - e^{-\alpha c}) s p^2, \quad (3.9)$$

which are both strictly positive meaning that assortment is monotonically increasing with

both cognitive capacity and survival rate.

(c) Indirect reciprocity

Indirect reciprocity operates by individuals adjusting their levels of cooperation in response to their partner's previous cooperation with other individuals (Alexander 1987; Nowak & Sigmund 1998). Following previous analyses (Nowak & Sigmund 1998, Lehmann & Keller 2006) we consider the simple scenario of indirect reciprocity based on image scoring. Image scoring works by individuals basing their decision to cooperate on a score of their partner's cooperativeness (the image score), information on which is obtained based on the partner's interactions with others (Nowak & Sigmund 1998). We again assume that investment in cooperation can take values between 0 and 1, and that an individual's image score can take values between 0 and 1, representing their investment in cooperation. We will consider strategies defined by their maximal investment in cooperation: x for the focal individual and X for the resident. Again we will assume that the resident is fully cooperative ($X = 1$) and that reciprocity acts only in a downward direction, i.e. that the resident will attempt to match their contribution to the image score of the focal individual but that the focal individual will never invest more than x . We assume that an observer of the focal individual's behaviour during the previous round of interaction assigns them an image score of x with probability $1 - e^{-\alpha c}$, or assigns them the default image score of 1 with probability $e^{-\alpha c}$, where α is again a scaling factor on the effect of cognitive capacity on error. We denote the probability that the focal individual's partner in the current round observed their behaviour in the previous round as h . The probability that the focal individual's partner assigns them the correct image score based on their own observation is then $h(1 - e^{-\alpha c})$. There is also the possibility that the actor's partner may learn of their image score via gossip (Nowak & Sigmund

1998). We denote the probability that a partner gains information on the focal individual's image score via gossip as g , and scale this by $1 - e^{-\beta c}$, where β is a scaling factor on the effect of cognitive capacity on the efficiency of gossip. Given these assumptions and using equation 3.1 we can now write the mean level of cooperation per round received by the focal individual as

$$\bar{X} = 1 - s^2 p^2 + x(h(1 - e^{-\alpha c}) + g(1 - e^{-\beta c}))s^2 p^2, \quad (3.10)$$

while the average investment for the actor is simply $\bar{x} = x$. We can then calculate assortment as $d\bar{X}/d\bar{x} = (h(1 - e^{-\alpha c}) + g(1 - e^{-\beta c}))s^2 p^2$. The effects of c and s on assortment are then

$$\frac{d(d\bar{X}/d\bar{x})}{dc} = (h\alpha e^{-\alpha c} + g\beta e^{-\beta c})s^2 p^2 \quad (3.11)$$

and

$$\frac{d(d\bar{X}/d\bar{x})}{ds} = 2(h(1 - e^{-\alpha c}) + g(1 - e^{-\beta c}))sp^2, \quad (3.12)$$

which are both strictly positive meaning that assortment is monotonically increasing with cognitive capacity and survival rate.

(d) Punishment

Punishment in response to cheating can act as a mechanism favouring investment in cooperation by adding a cost to cheating (Boyd & Richerson 1995; Gardner & West 2004). We will consider a strategy defined by two traits: investment in cooperation with a partner that is known to punish (x) and a tendency to punish (y) in response to the deviation of an individual from maximal cooperation. We will assume that individuals are initially cautious and do not cooperate if they do not know that (or how much) an individual punishes. We will consider a resident that employs a strategy of $X = 1$ and $Y = 1$ (i.e. a kind of strong reciprocator) and assume that individuals only gain information on an

individual's tendency to punish from direct interactions with them. Again the response of an individual to punishment is constrained by cognition, with the probability of the correct response in each round being $1 - e^{-\alpha c}$, i.e. they fail to recognise or remember the actor as a punisher with probability $e^{-\alpha c}$. As punishment may occur directly following or during an interaction we will assume for simplicity and clarity of presentation that punishment is apportioned without error. Using equation 3.1 we can then write the mean investment in cooperation by the resident per round as

$$\bar{X} = y(1 - e^{-\alpha c})s^2p^2, \quad (3.13)$$

and by the actor as

$$\bar{x} = (x(1 - e^{-\alpha c}) + e^{-\alpha c})s^2p^2 \quad (3.14)$$

We can also then write the investment in punishment by a resident as

$$\bar{Y} = \left(1 + \frac{((1 - x)(1 - e^{-\alpha c}) + e^{-\alpha c})s^2p^2}{1 - s^2p^2}\right) (1 - s^2p^2), \quad (3.15)$$

and by the actor as

$$\bar{y} = \left(y + \frac{ye^{-\alpha c}s^2p^2}{1 - s^2p^2}\right) (1 - s^2p^2). \quad (3.16)$$

As conditional cooperation in response to punishment is inherently two-trait in nature there are two key forms of assortment necessary for it's evolution (Gardner & West 2004): a negative relationship between punishment received and cooperation given ($d\bar{Y}/d\bar{x} < 0$) and a positive relationship between cooperation received and one's tendency to punish ($d\bar{X}/d\bar{y} > 0$). Using $d\bar{Y}/d\bar{x} = (d\bar{Y}/d\bar{x})(d\bar{x}/d\bar{x})$ it is easy to show that $d\bar{Y}/d\bar{x}$ reduces to -1 . This is the case as we have assumed that punishment can occur during or immediately following an interaction (so probability of repetition has no effect) and that error in punishment is vanishingly small (cognition has no effect). However, for conditional cooperation in response to punishment to be favoured there must also be selection for a tendency to punish, which relies on assortment term $d\bar{X}/dy$, which is

$$\frac{d\bar{X}}{dy} = (1 - e^{-\alpha c})s^2p^2. \quad (3.17)$$

The effects of c and s on assortment are then

$$\frac{d\bar{X}/dy}{dc} = \alpha e^{-\alpha c} s^2 p^2 \quad (3.18)$$

and

$$\frac{d\bar{X}/dy}{ds} = 2(1 - e^{-\alpha c}) s p^2, \quad (3.19)$$

which are both strictly positive meaning that assortment based on an actor's tendency to punish is monotonically increasing with both cognitive capacity and survival rate.

(e) Kin discrimination

Kin discrimination operates based on the preferential helping of related individuals (Hamilton 1964), thus leading to cooperation being returned by one's relatives. For simplicity we will consider a scenario where individuals aim to distinguish a class of highly related individuals (e.g. siblings), of average relatedness r_1 , from random group members, of average relatedness r_2 . We concern ourselves here with kin discrimination based on behavioural and/or environmental cues (Komdeur & Hatchwell 1999; Russell & Hatchwell 2001; McDonald & Wright 2011) rather than those based on genetic recognition systems. We will assume that the processing of these cues to determine kinship relies on cognitive processing and that the iterative accumulation of information from cues leads to more accurate assignment (e.g. via associative learning). Following these assumptions we write the relatedness between a focal individual and the partners they choose to cooperate with at time t as

$$R_t = (1 - e^{-\alpha c \gamma t}) r_1 + e^{-\alpha c \gamma t} r_2. \quad (3.20)$$

where α and γ are scaling factors for the effect of cognition on cue discrimination and how cue information accumulates during associative learning. Here the error in assignment

$(e^{-\alpha c \gamma t})$ is a declining function of the product of effective cognitive power (αc) and accumulated cue information (γt). We can then write assortment as

$$\frac{d\bar{X}}{d\bar{x}} = \left(\sum_{t=1}^{\infty} R_t (s^2 p^2)^{t-1} \right) (1 - s^2 p^2) = \frac{r_1 (e^{\alpha c \gamma} - 1) + r_2 (1 - s^2 p^2)}{e^{\alpha c \gamma} - s^2 p^2}. \quad (3.21)$$

The effects of c and s on assortment are then

$$\frac{d(d\bar{X}/dx)}{dc} = \frac{\alpha \gamma e^{\alpha c \gamma} (1 - sp)(1 + sp)(r_1 - r_2)}{(e^{\alpha c \gamma} - s^2 p^2)^2} \quad (3.22)$$

and

$$\frac{d(d\bar{X}/dx)}{ds} = \frac{2(e^{\alpha c \gamma} - 1)(r_1 - r_2)s^2 p^2}{(e^{\alpha c \gamma} - s^2 p^2)^2} \quad (3.23)$$

which are both strictly positive (as $r_1 > r_2$), meaning that, as long as the processing of kinship cues relies on cognition and the accumulation of information over time, increasing cognitive capacity and survival rate are expected to increase assortment via kin discrimination.

3.3. Comparative analysis

My theoretical models suggest that increased cognitive capacities and lifespan should facilitate the evolution of cooperation by increasing the potential for assortment via conditional behaviours. To test my theoretical predictions I performed a comparative analysis on the distribution of two forms of cooperation in non-human primates: coalition formation (i.e. agonistic support) and food sharing. As quantitative data are not currently available, I collected presence/absence data on the occurrence of coalition formation and food sharing for both sexes for all available primate species. Data on coalition formation were taken from Plavcan *et al.* (1995) and Jaeggi & van Schaik (2011) and data on food sharing were taken from Jaeggi & van Schaik (2011). Data on food sharing between males and females or between parents and offspring was not included as these are adequately explained by the food-for-sex' hypothesis and parental care, respectively. For

food sharing, only data from interactions among non-relatives were included, suggesting that conditional behaviour will be the likely mechanism of assortment. For coalition formation no information on relatedness between cooperators was available.

Data on the social system (solitary/mated pair, multi-female single-male or multi-female multi-male groups) of each species were taken from Rowe (1996) and www.theprimata.com. Species that are solitary or live in mated pairs were omitted from the analyses, as intra-sex cooperation could not occur. I collated data on the mean endocranial volume, which is isomorphic with brain size in primates (Isler *et al.* 2008), and body weight for each species from Isler *et al.* (2008). The residuals of a log-log regression of endocranial volume on body weight were taken as a measure of body-mass-corrected cognitive capacity. I used maximum-recorded lifespan as a proxy for species' average lifespan, which was taken from the AnAge database (de Magalhaes & Costa 2009), supplemented using Rowe (1996). Finally, data on social group size were also collated for each species from Nunn & van Schaik (2002). Group size may affect competition for food and may influence the benefit of coalitionary support in agonistic interactions. Given this possibility and the strong correlation between group size and relative brain size in primates (Dunbar 1998), group size was included as a covariate in the analyses as a potential confounding variable. The version 3 primate consensus tree from the 10k Trees Project (Arnold *et al.* 2010) was used in the analyses to account for the non-independence of species owing to shared ancestry. In total, data were available for 76 species for the coalition formation analysis and 49 species for the food sharing analysis.

I analysed the coalition formation and food sharing data using linear mixed models implemented in the R (R Core Development Team 2012) package MCMCglmm (Hadfield 2010), which uses a Markov chain Monte Carlo algorithm for model fitting. Coalition formation and food sharing were modelled as binomial response variables in separate

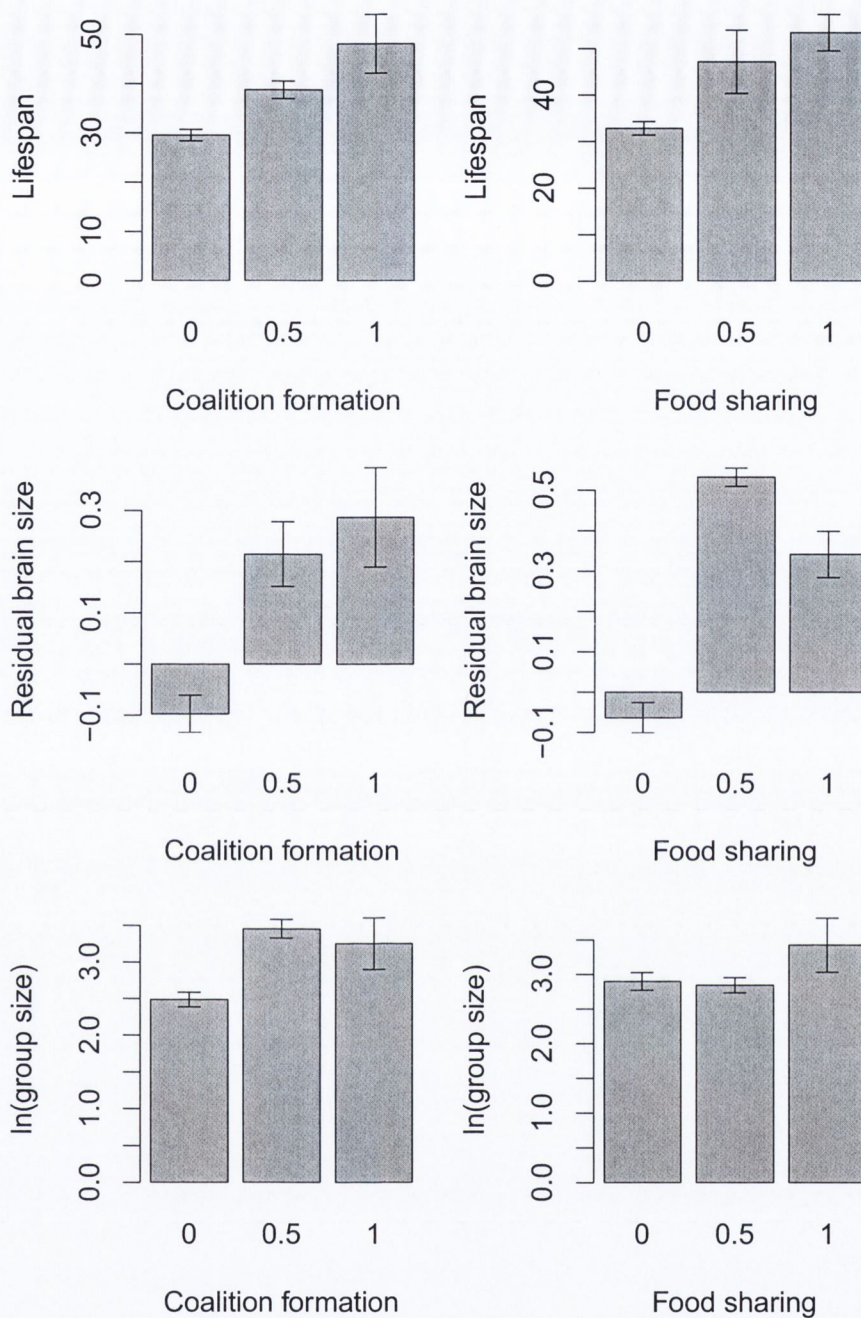


Figure 3.1: The barplots show mean values and their standard error for maximum lifespan, residual brain size and the log of group size for different coalition formation and food sharing scores. Sample sizes (number of species) are 53, 20 and 3 for coalition formation and 44, 2 and 3 for food sharing for scores of 0, 0.5 and 1, respectively. The cooperation scores correspond to the proportion of sexes with multiple individuals per group that cooperate for each species.

analyses, with the number of sexes cooperating in each species acting as the number of successes, and with the number of trials taken as 1 for species with single-male/multi-

female groups and 2 for species with multi-male/multi-female groups. This gives each species a measure of cooperation of (number of sexes cooperating)/(number of sexes with multiple individuals per group), giving a score of 0, 0.5 or 1. This binomial approach helps take account of the qualitative nature of the available data on cooperation by weighing species where both sexes cooperate more heavily than species where only one sex does so. The primate phylogeny was included as a random effect and lifespan, residual brain size and the log of group size were included as predictors. All predictors were mean standardised prior to analysis. Priors for both the residual and phylogenetic variances were set using an inverse-Wishart distribution with variance of 1 and degree of belief of 0.002 (code: $R=list(V=1, nu=0.002)$, $G=list(V=1, nu=0.002)$). Priors for the fixed effects were set using a normal distribution with mean of 0 and variance of $4.3 + \pi^{2/3}$, which is approximately uniform on the probability scale, fulfilling the requirement of a weakly informative prior. Priors of larger variance show high densities near probabilities of 0 and 1, which can cause problems for mixing behaviour (Hadfield 2010). Models were run for 2,100,000 with the first 100,000 iterations discarded as a burn-in and with a thinning interval of 100. To avoid autocorrelation in the posterior samples.

Table 3.1: Results of comparative analyses

Explanatory variable	Parameter estimate	95% credible interval
Coalition formation		
Lifespan	0.828	[0.195, 1.473]
Residual brain size	0.741	[0.164, 1.376]
ln(group size)	0.868	[0.163, 1.605]
Food sharing		
Lifespan	2.363	[0.658, 4.374]
Residual brain size	1.996	[0.343, 3.823]
ln(group size)	0.035	[-2.167, 2.259]

Table 3.1 shows the posterior parameter estimates (mode) and 95% credible intervals

for both the coalition formation and food sharing models (see also Fig. 3.1). For both forms of cooperation, lifespan and residual brain size had significant positive effects on cooperation (95% credible intervals do not overlap with zero), supporting the model predictions that increased cognitive capacity and lifespan should facilitate the evolution of cooperation. Group size had a significant positive effect on coalition formation, suggesting that agonistic support may be of more importance under stronger competition in larger groups, though it had no significant effect on food sharing.

3.4. Discussion

Both the theoretical models and comparative analysis suggest that cognition and lifespan play an important role in the evolution of conditional cooperation. Increased cognitive capacities facilitate conditional cooperation by allowing for the accurate assessment of a partner's phenotype/behaviour, its committal to memory and future use in decision-making. Increased lifespan facilitates conditional cooperation by increasing the opportunity for current investment in cooperation to affect the future actions of one's partners and/or allowing more time for the assessment of the behaviour/phenotype of others. However, it is important to note that my models consider a best-case scenario for the effect of cognition on cooperation. While large brains may facilitate assortment via conditional behaviour they may also facilitate deception (Byrne & Whiten 1988; Byrne & Corp 2004), which may allow individuals to conceal or misrepresent their actions, undermining conditional cooperation (see Chapter 4). Nonetheless, as long as deception does not completely undermine cooperation, increased cognitive abilities should facilitate the evolution of cooperation.

My results highlight important links between morphology, life history and social behaviour. The facilitation of conditional cooperation that increased cognition provides may be an important selective factor in the evolution of large brains (Brosnan *et al.* 2010;

Chapter 2; McNally *et al.* 2012). Additionally, theory and comparative analyses suggest that brain size and lifespan coevolve and positively reinforce each other, as the fitness benefits of increased brain size are likely to be manifest as increased survival and the benefits of the learning that big brains facilitate are likely to take time to accumulate (Kaplan & Robson 2002; Robson & Kaplan 2003; Gonzalez-Lagos *et al.* 2010; van Schaik *et al.* 2012). This also points to the importance of sources of extrinsic mortality, such as predation, in the evolution of cooperation. High extrinsic mortality will obviously reduce lifespan, but is also expected to reduce the benefits of increased brain size (as these are expected to accumulate over time: van Schaik *et al.* 2012), and thus limit the potential for the evolution of conditional cooperation.

There is growing evidence for the importance of conditional behaviour in the evolution of primate sociality, mainly in the forms of partner choice (Schino & Aurelli 2009; Fruteau *et al.* 2011; Sabbatini *et al.* 2012), direct reciprocity (Brosnan & de Waal 2002; Silk 2005), punishment (Clutton-Brock & Parker 1995; Silk 2005) and kin discrimination (Silk 2009). My theoretical and comparative results suggest the coevolution of brain size and lifespan has played a key role in the evolution of primate sociality, and in the evolution of the human socio-cognitive niche', and ultimately resulted in our global colonisation (Pinker 2010; Whiten & Erdal 2012). Our big brains and long lifespan may have driven the emergence of human society.

Chapter 4

Cooperation creates selection for tactical deception

This chapter is in revision for resubmission for publication.

Authors: McNally L & Jackson AL.

Authors' contributions: LM conceived the idea; LM developed and analysed the model, and collated and analysed the data; LM and AJ interpreted results; LM wrote the manuscript with input from AJ

4.1. Introduction

Though there are multiple routes through which cooperation can evolve (Lehmann & Keller 2006; West *et al.* 2007), conditional cooperation has become a major focus for studies on the evolution of cooperation in taxa of relatively advanced cognitive capabilities, particularly primates, and even more so humans. As a result, myriad mechanisms of conditional behaviour that facilitate the evolution of cooperation have been identified, including direct reciprocity (Trivers 1971; Axelrod & Hamilton 1981), indirect reciprocity (Alexander 1987; Nowak & Sigmund 1998), generalised reciprocity (Pfeiffer *et al.* 2005; Barta *et al.* 2011), partner choice (Roberts 1998; Sheratt & Roberts 1998; McNamara *et al.* 2008), punishment (Boyd & Richerson 1992; Gardner & West 2004), and reward (Oliver 1980; Rand *et al.* 2009). While the details of how these mechanisms favour the evolution of cooperation differ, they all share the implicit requirement of correlation between the behaviours of interacting individuals (Frank 1998; Woodcock & Heath 2002; Henrich 2004). This correlation leads to cooperative individuals receiving more cooperation, less punishment, and/or more rewards than cheats, thus giving them a fitness advantage.

For this correlation to arise an individual's behaviour must be either directly or indirectly conditional on their partner's behaviour, e.g. by accounting for their past actions or recognising some cue of their current intentions. Almost all models for the evolution of conditional cooperation implicitly assume that the past or current actions of others can be assessed accurately and that cheats act passively during this assessment (i.e. they do not conceal their cheating). One possible mechanism by which cheats could avoid detection is tactical deception - the misrepresentation of the state of the world to another individual (Whiten & Byrne 1988; Byrne & Whiten 1988; Byrne & Whiten 1991; Byrne & Whiten 1992; Lewis & Carolyn 1993). If individuals can use tactical deception to avoid their

cheating being detected (e.g. by misdirecting a social partner's attention or lying about their past actions or current intentions), they could circumvent enforcement mechanisms, gaining a fitness benefit.

Of course, deception may have benefits in many spheres of animal behaviour other than cooperative interactions, e.g. mating behaviour, aggressive encounters, etc. Regardless, the benefit of illiciting cooperation at lower cost may help select for the psychological and cognitive capabilities necessary for tactical deception in species with more frequent, and more diverse forms of, cooperation. Here I first present a theoretical model exploring the evolution of tactical deception as a strategy in cooperative interactions before presenting a comparative analysis to test the relationship between deception and cooperation in primates.

4.2. Game theoretic model

I consider the scenario of an iterated prisoner's dilemma between pairs of individuals in an infinite, well-mixed population. In any given interaction individuals can choose to cooperate, bestowing a fixed benefit b on their partner at a fixed cost c to themselves, or to defect, bestowing no benefit and paying no cost. Here we will only consider conditional strategies that modify their cooperation in response to their partner's cooperation, though the general logic of the model also applies to cooperation based on punishment or reward. For simplicity we will assume that individuals can take one of three fixed strategies for this game: conditional cooperator (CC), tactical deceiver (TD), or honest defector (HD). Conditional cooperators aim to only cooperate with other cooperative individuals and not cooperate with defectors, while honest defectors simply always defect. We assume that tactical deceivers always defect but attempt to hide that defection from others in some manner (e.g. by waiting until they are unobserved or manipulating their reputation by lying), and that this deception carries a cost d . I do not specify the mechanism

(e.g. partner choice or some form of reciprocity) by which conditional cooperation is achieved, but assume that conditional cooperation is somewhat constrained by repetition probability (i.e. current behaviour is somehow based on previous partner behaviour) and/or individual cognition (mistakes are sometimes made) so that conditional cooperators will cooperate with honest defectors in a proportion p of their interactions. As tactical deceivers attempt to conceal their defection, conditional cooperators fail to recognise them as defectors with probability q , meaning that a conditional cooperator will cooperate with a tactical deceiver in a proportion $q + p - qp$ of their interactions. Following our assumptions the average payoffs per round (π_i) for each of the three strategies are: $\pi_{CC} = (b - c)x_{CC} - c(q + p - qp)x_{TD} - cp x_{HD}$ for conditional cooperators; $\pi_{TD} = b(q + p - qp)x_{CC} - d$ for tactical deceivers; and $\pi_{HD} = bp x_{CC}$ for honest defectors, where x_i denotes the current frequency of strategy i in the population.

Initially we will assume that q is a constant, but will later consider the case where q is frequency dependent. We will constrain our analysis to the scenario where $b - c > pb > 0, q > 0, p < 1$, and $c > d > 0$, meaning that there is bistability between conditional cooperators and honest defectors (neither can invade the other from rarity), conditional cooperators do not dominate tactical deceivers, and honest defectors dominate tactical deceivers. In this scenario there are two qualitatively different outcomes possible, which are illustrated using the replicator equation $dx_i/dt = x_i(\pi_i - \sum_j \pi_j x_j)$ (Weibull 1995) in Fig. 4.1a and b. Firstly, if $b(q + p - qp) - d > b - c$ then tactical deceivers dominate conditional cooperators. In this case transient invasion of the tactical deceiver strategy into a monomorphic population of conditional cooperators undermines the stability of the pure conditional cooperator equilibrium, making honest defection the only Nash equilibrium and causing the collapse of cooperation (Fig. 4.1a). Beginning from a monomorphic population of conditional cooperators, a rare tactical deceiver will invade and go to fixation. However, this equilibrium will be unstable and can be invaded by a rare

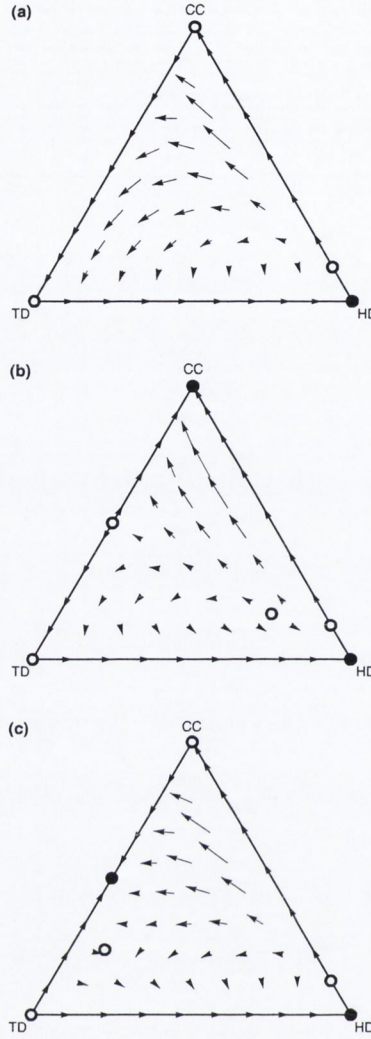


Figure 4.1: The dynamics of deception and cooperation. Shown are the evolutionary dynamics of the three strategies for the model with constant (a,b) and negatively frequency dependent (c) efficiency of deception. Solid and open circles represent stable and unstable equilibria respectively. Parameter values are $b = 1.5$, $c = 0.5$, $p = 0.2$ for all plots and (a) $q = 0.8$, (b) $q = 0.5$, and (c) $q = 1 - x_{TD}$. Graphical output based on the Dynamo software (Sandholm *et al.* 2012).

honest defector (as $\pi_{TD} = -d$ and $\pi_{HD} = 0$), which then goes to fixation. Alternatively, if $b(q + p - qp) - d < b - c$, then both conditional cooperation and honest defection are Nash equilibria and the introduction of tactical deceivers has little effect (Fig. 4.1b), as they cannot invade either monomorphic population. Note that in both scenarios there will be no stable mixed equilibrium owing to the lack of any negative frequency dependence among strategies.

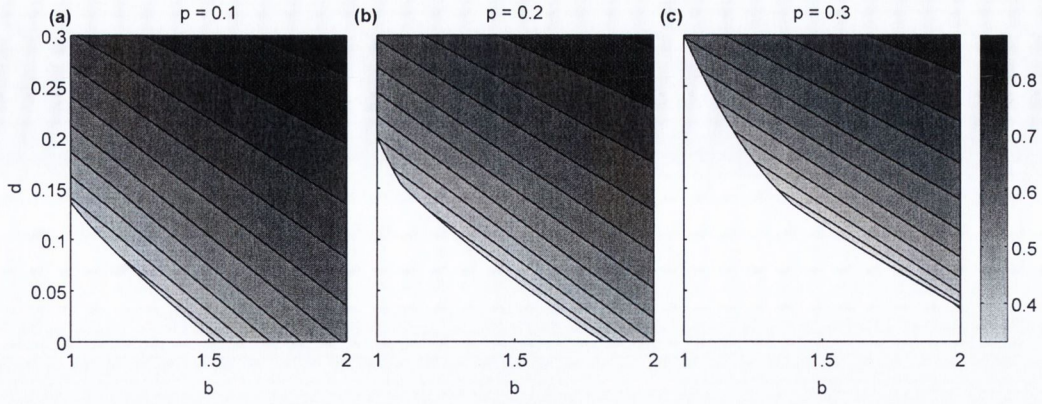


Figure 4.2: Equilibrium mixture of conditional cooperators and tactical deceivers. The coloured contour plot shows the frequency of conditional cooperators x_{CC}^* at the mixed equilibrium (frequency of tactical deceivers is $1 - x_{CC}^*$) as a function of the benefit of cooperation b and the cost of deception d for the model with negative frequency dependence (see Fig. 4.1c). Darker (lighter) greys indicate a higher frequency of conditional cooperators (tactical deceivers) at the equilibrium. White areas indicate parameter values where there is no stable mixed equilibrium and the population converges on honest defection. Parameter values are $c = 0.5$, $q = 1 - x_{TD}$ for all plots and (a) $p = 0.1$, (b) $p = 0.2$, and (c) $p = 0.3$.

In both of the cases above tactical deceivers will only appear transiently before disappearing from the population, so how can tactical deceivers persist in the population? One possible factor leading to the coexistence of tactical deceivers and conditional cooperators is frequency dependence in the efficiency of deception. It would be expected that as tactical deceivers become more common in the population conditional cooperators would become more adept at spotting deception, likely via associative learning. The necessary negative frequency dependence for a mixed equilibrium may exist if the efficiency of deception q declines with increasing frequencies of tactical deceivers. Here we will consider the simplest scenario where $q = 1 - x_{TD}$, so that deception is seldom detected when very rare, but is almost always detected when deception is the norm. In this scenario a rare tactical deceiver can always invade a monomorphic population of conditional cooperators as they will have payoffs $\pi_{TD} = b - d$ and $\pi_{CC} = b - c$, and we have assumed that the cost of deception is less than that of cooperation ($d < c$). Additionally a

rare conditional cooperator will be able to invade a population of tactical deceivers when $-cp < -d$. This negative frequency dependence can lead to a stable mixed equilibrium of x_{CC}^* conditional cooperators and $1 - x_{CC}^*$ tactical deceivers (Fig. 4.1c), which can resist invasion by honest defectors if $b(1 - p)(x_{CC}^*)^2 > d$. The full expressions for the location and stability of this equilibrium are too unwieldy to yield analytical insight but are numerically explored in Fig. 4.2. Extensive numerical exploration showed no other stable mixed equilibria. Increasing cost to benefit ratio (c/b) and decreasing costs of deception (d) increase the equilibrium frequency of tactical deceivers as their relative advantage over conditional cooperators is increased. However, tactical deceivers may become victims of their own success as if their equilibrium frequency becomes too high this equilibrium becomes invadable by honest defectors (i.e. $b(1 - p)(x_{CC}^*)^2 < d$). Increasing the proportion of rounds conditional cooperators fail to defect against identified defectors (p) reduces the parameter space in which the mixed equilibrium is stable as the amount of cooperation tactical deceivers receive from conditional cooperators relative to that received by honest defectors is reduced (i.e. there is less benefit to outweigh the cost of tactical deception as conditional cooperation becomes less efficient).

4.3. Comparative analysis

Overall my theoretical results suggest that conditional cooperation can create selection pressures favouring investment in tactical deception. However, some form of negative frequency dependence in the efficacy of deception, possibly owing to associative learning, is necessary for tactical deception to be maintained at equilibrium. From these results we can now ask what will happen as a species begins to cooperate in more ways (i.e. begin to play more games where some cooperation occurs). From the model we can predict that, given the requisite negative frequency dependence, adding more cooperative behaviours will lead to more tactical deception as conditional cooperation

and tactical deception will coexist. As more cooperative behaviours (games) evolve this is expected to increase selection for deception, which should be manifest as a positive relationship between the frequency of tactical deception and the number of cooperative behaviours a species engages in.

To test this prediction I used the collation of Byrne & Whiten (1990) of the frequencies of tactical deception across non-human primates. This catalogue is based on a survey of expert researchers of a wide range of primate species and includes all records known at the time, that conform to the following definition of tactical deception: “acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent” (p. 3 of Byrne & Whiten 1990). While all forms of deception involve the misrepresentation of some information to other individuals, tactical deception implies that this misrepresentation is context-dependent and, at least in a functional sense, involves deliberately altering one’s behaviour in a given context to mislead another individual. As in Byrne & Corp (2004), we included all records which were considered by the original observers to meet this definition. I performed two analyses on these frequencies of tactical deception across species. Firstly, following Byrne & Corp (2004), I only analysed observations of deception which were made on free-ranging individuals. However as tactical deception may be more difficult to detect in the field I also performed an analysis on all data including observations on captive individuals (as in Reader *et al.* 2011). I used the log of the deception frequency plus one in all analyses.

In order to assess how cooperativeness affects the frequency of tactical deception across species I collated data on the presence of three cooperative behaviours that have been important during human evolutionary history: coalition-formation, food-sharing and alloparenting from Plavcan *et al.* (1995), Jaeggi & van Schaik (2011) and Riedmann (1982). Food-sharing between males and females and parents and offspring were not

included as these are easily explained by the “food for sex’ hypothesis” and simple parental care (Jaeggi & van Schaik 2011). I used the unweighted sum of the number of these cooperative behaviours a species engages in, giving a score of cooperativeness between 0 and 3. To avoid the possibility of inherent correlation between deception and cooperation owing simply to the fact that more behaviours are being performed in more cooperative species, examples of deceptive behaviours directly relating to the forms of cooperation considered here were removed from the data. Thus my analysis tests for an association between a species level of cooperativeness and their general propensity towards deception.

As deception is generally considered an indicator of intellectual capabilities (Whiten & Byrne 1988; Byrne & Whiten 1988; Byrne & Whiten 1991; Byrne & Whiten 1992; Lewis & Carolyn 1993), and has been previously been shown to correlate with neocortex size (Byrne & Corp 2004) and load strongly on measures of primate general intelligence (Reader *et al.* 2011), it is important to control for cognitive ability. To this end, I included neocortex ratio (size of the neocortex divided by the size of the rest of the brain) as a covariate in the analyses. Data on neocortex ratios were taken from multiple sources (Stephan *et al.* 1981; Zilles & Redkamper 1988; Macleod *et al.* 2003; Bush & Allman 2004). Volumes calculated using serial sections were supplemented with volumes calculated using magnetic resonance imaging for species where no serial section volume was available as these do not differ significantly within the primates (Reader *et al.* 2011).

In total, data for all variables were available for 24 species spanning a wide taxonomic distribution: 3 prosimians, 7 new world monkeys, 10 old world monkeys, and 4 apes. Analyses were performed using phylogenetic generalised least squares regression (PGLS) in R (R Core Development Team) with the caper package (Orme *et al.* 2012). As estimation of the level of phylogenetic signal in a dataset becomes unreliable at small sample sizes (Freckleton *et al.* 2002; Mönkenmüller *et al.* 2012), I set Pagel’s

$\lambda = 1$, which is equivalent to independent contrasts. I used version 3 of the consensus primate tree from the 10k Trees Project (Arnold *et al.* 2010) to control for the phylogenetic relationships among species.

As the number of reports of deception may be influenced by the research effort a species receives, I included a measure of research effort in both analyses. I used the research effort measure of Reader *et al.* (2011), which is based on the counts of published papers on each species in the Zoological Record. I took two approaches to controlling for research effort in our analyses. Firstly I included the log of research effort as a covariate in our models. This analysis showed a significant positive effect of cooperativeness on the rate of tactical deception for both the free-ranging only ($\beta = 0.66, S.E. = 0.22, p = 0.006$) and full ($\beta = 0.61, S.E. = 0.13, p < 0.0001$) datasets (see Fig. 4.3). Neocortex ratio bordered on significance in the free-ranging dataset ($\beta = 1.22, S.E. = 0.64, p = 0.07$), but was not significant in the full dataset ($\beta = 0.29, S.E. = 0.37, p = 0.44$).

I also repeated the analysis using a more conservative approach of first taking the residuals of a log-log regression of deception frequency on research effort (free-ranging: $\beta = 0.32, S.E. = 0.12, p = 0.04$; all data: $\beta = 0.42, S.E. = 0.18, p = 0.03$), and then performing a PGLS as before with cooperativeness and neocortex ratio as predictors. This analysis yields similar results to the previous analysis for both the free-ranging (cooperativeness: $\beta = 0.62, S.E. = 0.20, p = 0.006$; neocortex ratio: $\beta = 1.04, S.E. = 0.57, p = 0.08$) and complete (cooperativeness: $\beta = 0.51, S.E. = 0.13, p = 0.001$; neocortex ratio: $\beta = -0.11, S.E. = 0.37, p = 0.77$) datasets.

4.4. Discussion

Both our theoretical model and the results of our comparative analysis provide strong support for the hypothesis that the presence of conditional mechanisms to enforce

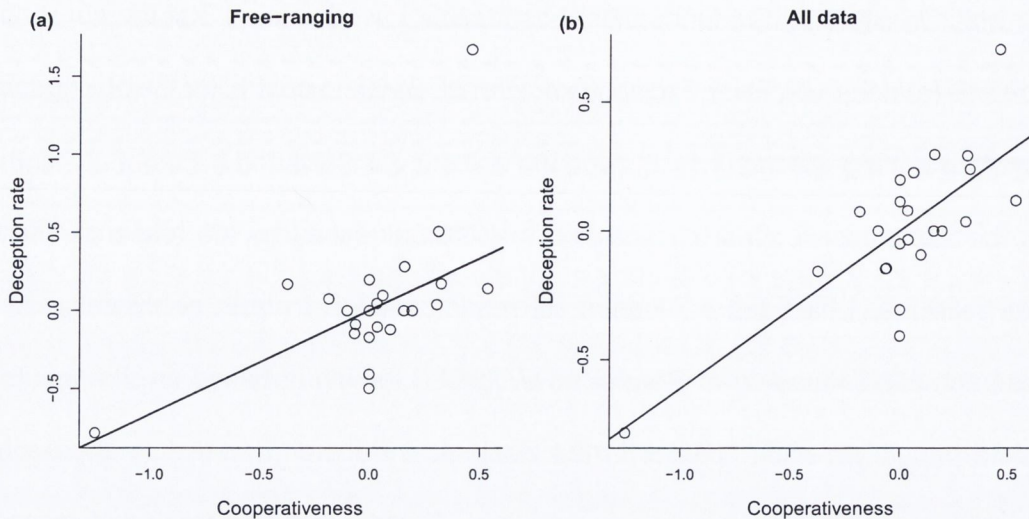


Figure 4.3: The relationship between deception and cooperation in non-human primates. The data points are independent contrasts for the rate of deception and cooperativeness scores with the effects of neocortex ratio and research effort partialled out for the free-ranging (a) and full (b) datasets. Lines are the predicted values from the models reported in the main text.

cooperation provides a major selective benefit to tactical deception. The explanation for this benefit is simple; tactical deception can allow individuals to illicit cooperation (or avoid punishment/gain reward) without paying the costs of cooperation. The ability to deliberately deceive others is generally held as a pinnacle of intelligence, exhibiting complex psychological abilities such as second order intentionality and theory of mind (Premack & Woodruff 1978; Byrne & Whiten 1988, 1991, 1992; Byrne & Corp 2004). Our results suggest that, in addition to selecting for capacities such as shared intentionality (Moll & Tomasello 2007), conditional cooperation may have driven the development of many of our other complex psychological abilities by creating selection pressures favouring tactical deception.

It is also worth noting however, that not all forms of deception are necessarily intentional; individuals could also deceive others by deceiving themselves. Trivers has recently advanced a theory for the evolution of self-deception as a means to better deceive others (Trivers 1991, 2000, 2010, 2011; von Hippell & Trivers 2011). The essence

of this theory is that conscious deception has a high "cognitive load" leading to tell-tale signs that an individual is deceiving you, such as signs of nervousness. By reducing this cognitive load, self-deception may allow deception of others to go unnoticed. Additionally, unconscious deception may not receive the same retribution as conscious deception, as it may appear to be an "accident" or owing to ignorance. Although our model applies in principle to intentional and un-intentional deception the deception catalogue collated by Byrne & Whiten (1990) is restricted to cases of deception that show the appearance of deliberate manipulation. Further empirical research is necessary to ascertain the relative roles of conscious and unconscious deception in eliciting cooperation from others. However, if Trivers' thesis holds, the ability to elicit cooperation (or avoid punishment/gain reward) without paying the costs of cooperation may have also been a major selective factor in the evolution of self-deception in humans.

While my simple model provides a general overview of the coevolution of deception and conditional cooperation, much further theoretical investigation of this relationship is required. Our model does not explicitly account for the underlying behavioural dynamics of conditional cooperation and there is great potential for more mechanistic models. The inclusion of the possibility of tactical deception could lead to greater nuance in strategy evolution, with individuals showing different responses to the detection of honest cheating (e.g. possibly eliciting than to attempted deception. Given the infinite strategy space and complex dynamics of iterated games, and the additional complexity of the possibility of deception, approaches based on finite state automata (Rubenstein 1986; Ho 1996; van Veelen *et al.* 2012) and/or artificial neural networks (Harald & Fogel 1996; Mitri *et al.* 2009; McNally *et al.* 2012) may be particularly fruitful. Additionally, models of cognitive arms races (Gavrillits & Vose 2006) between tactical deceivers and conditional cooperators owing to selection for more subtle forms of deception and its detection could help shed further light on the drivers and evolutionary history of human cognitive evolution

(Byrne & Whiten 1988; Dunbar & Schultz 2007).

Great progress has been made in recent years in elucidating both the proximate psychology of, and the ultimate explanations for, human cooperation. However, human psychology shows a mixture of conformance to moral/social norms that favour cooperation (Fehr & Fischbacher 2003) and Machiavellian capabilities that facilitate selfish ends (Byrne & Whiten 1988). Explaining how evolutionary forces have balanced these tendencies is a major theoretical and empirical challenge. Our results suggest that studying the evolution of deception in the context of social interactions could provide a key window into the origins of this balance. Ultimately this most Machiavellian element of human behaviour may be the product of one of our most beneficent characteristics - our tendency to seek mutually cooperative relationships.

Chapter 5

Assortment, coevolutionary feedback and the evolution of culture.

This chapter is being prepared for submission for publication.

Authors: McNally L & Jackson AJ

Authors' contributions: LM conceived the idea; LM developed and analysed the model, and collated and analysed the data with advice from AJ; LM and AJ interpreted results; LM wrote the manuscript with input from AJ

5.1. Introduction

The human capacity to produce innovations and transmit them is generally held to be key in humans' evolutionary success and our near global colonisation (Boyd & Richerson 1985, Boyd *et al.* 2011). The desire to identify the selective pressures responsible for the evolution of these capabilities is manifest in large numbers of theoretical and empirical studies of the strategies used by humans and other animals to acquire novel behaviours. The diverse learning abilities that underlie culture are frequently grouped into two main categories (Boyd & Richerson 1985); innovation (i.e. individual learning) and social learning (i.e. learning from others). Theoretical developments in this area have largely been based on a trade-off between these two forms of learning (Rogers 1988). The trait of interest in these models is the ratio of learning time invested in innovation, and social learning, though often the analyses are restricted to pure strategies (e.g. Rogers 1988; Lehmann & Feldman 2009; Rendell *et al.* 2010). These models have lead to many predictions regarding the factors governing the balance of innovation and social learning such as the role of temporal variability (e.g. Feldman *et al.* 1996; Aoki *et al.* 2005; McElreath & Strimling 2008) and details of the social learning strategy that is used (e.g. Boyd & Richerson 1995; Kameda & Nakanishi 2003; Laland 2004, Enquist *et al.* 2007). However, while these analyses can tell us a great deal about how the balance of time investment in innovation and social learning is affected by ecological factors and the resultant impacts on cultural evolution, they tell us little regarding the selective factors that drive the evolution of investment in learning.

A new paradigm has recently emerged in the study of primate cognitive evolution: the cultural intelligence hypothesis' (Reader & Laland 2002; Whiten & van Schaik 2007; Van Schaik & Burkhardt 2011; Reader *et al.* 2011; van Schaik *et al.* 2012). This hypothesis holds that primate cognitive evolution is driven by selection for improved

general learning capacities, which as a by-product also endows species with a general-purpose' intelligence (Reader *et al.* 2011; van Schaik *et al.* 2012). From the perspective of the cultural intelligence hypothesis, humans' increased investment in culture, compared to other primates, is proximately achieved by investment in increased brain size, an idea which is well supported by comparative analyses (Reader & Laland 2002). However, viewing increased brain size as the proximate mechanism by which learning capabilities are increased, rather than as an ultimate explanation for them, begs the question of what shapes the costs and benefits of this investment? The main factors identified as determinants of these costs and benefits have been life-history filters (reviewed in van Schaik *et al.* 2012). The essence of the argument here is that brains are energetically costly and take time to develop, meaning that fitness benefits will likely accrue through increased survival rate. Life-history factors which constrain lifespan will therefore also constrain brain size, and hence investment in learning.

Here I present a general model for the evolution of investment in innovation and social learning based on the logic of the cultural intelligence hypothesis. I focus on how phenotypic assortment, either owing to interactions with kin (Hamilton 1964) or partner choice (Roberts 1998; Sheratt & Roberts 1998; McNamara *et al.* 2008), modulates the costs and benefits of investment in learning.

It has previously been suggested that culture may be viewed as a public good, as individuals produce novel behaviours by innovation, which can then be acquired by others via social learning (Lehmann *et al.* 2010). Much theory and empirical research suggests that assortment, where the phenotypes of interacting individuals are correlated, is key in the evolution of public goods investment as increases in investment by one individual will then result in increases in investment by their social partners (Frank 1998). Here I first present a theoretical model examining the effects of assortment on investment in innovation and social learning, and then present a comparative analysis of culture in

primates in support of my theoretical results.

5.2. Theoretical model

I take the direct fitness approach (Taylor & Frank 1996; Frank 1998), commonly used in kin selection analyses, to model the joint evolution of investment in innovation and social learning. Here I present a general illustrative model, but I also present a model with explicit description of the learning dynamics and fitness function below. We denote total investment by a focal mutant in innovation as x and in social learning as y . The trait values for the focal individual's resident group-mates are denoted as X and Y , respectively. Here the values of x and y represent total cognitive investment in learning multiplied by the proportion of learning effort invested in innovation and social learning, respectively. Therefore the total cognitive investment in learning is $x + y$. We assume that the number of cultural traits that an individual holds, A , is a function of their phenotype and that of their social partners. For simplicity we will also assume global competition, though our general conclusions should be robust to this assumption. From these assumptions we can write the fitness of a focal individual as

$$w = B(A(x, y, X, Y)) - C(x + y), \quad (5.1)$$

where B is a benefit function for the number of cultural adaptations an individual holds and C is the cost function for investment in cognition. Assuming no linkage between traits ($dx/dy = dy/dx = 0$) we can use the chain rule to write the gradient of selection with respect to x and y as

$$\frac{dw}{dx} = \frac{\partial B(A)}{\partial x} + \frac{\partial C}{\partial x} + \frac{\partial B(A)}{\partial X} \frac{dX}{dx} + \frac{\partial B(A)}{\partial Y} \frac{dY}{dx} \quad (5.2)$$

and

$$\frac{dw}{dy} = \frac{\partial B(A)}{\partial y} + \frac{\partial C}{\partial y} + \frac{\partial B(A)}{\partial Y} \frac{dY}{dy} + \frac{\partial B(A)}{\partial X} \frac{dX}{dy}, \quad (5.3)$$

respectively. In all cases the partial derivatives indicate marginal fitness effects. The derivatives dX/dx and dY/dy capture the effects of changes in the focal individual's investment in innovation and social learning on investment in the same trait in that individual's social partners - i.e. assortment. These associations may be positive if individuals interact with genealogical relatives, in which case they are equivalent to the standard Hamilton's coefficient of relatedness (Hamilton 1964). However, it is worth noting that a positive phenotypic association may arise owing to other factors such as partner choice. The remaining derivatives dY/dx and dX/dy capture the effects of changes in the focal individual's investment in innovation and social learning on investment in the other trait in that individual's social partners. Interactions with relatives are not expected to produce positive values of these derivatives in the absence of trait linkage, though they may increase via partner choice if individuals assess the values of both traits when deciding which individuals to interact with (discussed below).

Obviously, in the absence of phenotypic correlation the gradient of selection for both traits is simply decided by the direct effects of an individual's own phenotype ($\partial B(A)/\partial x - \partial C/\partial x$ for innovation and $\partial B(A)/\partial y - \partial C/\partial y$ for social learning). Here the benefit and cost functions B and C are likely to be determined by life history filters, factors limiting what life histories are possible, that influence the costs of investment in cognition and the benefit that can be accrued from learned behaviours. Specifically, it has previously been predicted that low extrinsic mortality is expected to increase the benefits of learning by allowing for a longer lifespan to accrue its benefits, and also reduce the costs of investment in cognition by allowing for a longer developmental period (van Schaik *et al.* 2012). However, here I will focus on how correlations among the phenotypes of social partners are expected to affect selection for innovation and social learning. Three main expectations arise from the model:

(a) All forms of positive assortment should increase selection for innovation and social learning. We will first consider the effects of assortment on selection for innovation (dw/dx). The third term in equation 5.2 is $(\partial B(A)/\partial X)(dX/dx)$, which is the product of the fitness benefit of increased innovation by a focal individual's social partners and the derivative of partner investment in innovation on that of a focal individual. As long as the innovations of others can be acquired through social learning we expect increasing values of dX/dx to increase selection for innovation. The fourth term in equation 5.2 is $(\partial B(A)/\partial Y)(dY/dx)$, which is the product of the fitness benefit of increased social learning by a focal individual's social partners and the derivative of partner investment in social learning on the investment in innovation by a focal individual. As long as the social learning of others helps spread innovations to a focal individual, we expect increasing values of dY/dx to increase selection for innovation. Identical logic applies to the third and fourth terms of equation 5.3, leading us to expect selection for social learning to increase monotonically with increases in the assortment terms dY/dy and dX/dy . Thus increased innovation and social learning are expected to be favoured by assortment.

(b) There is expected to be a positive coevolutionary feedback between innovation and social learning, which is increased by assortment. Here I focus on the terms $\partial B(A)/\partial y$ and $\partial B(A)/\partial X$ and consider the sign of their partial derivatives with respect to X and y , respectively. In both cases this gives the quantity $\partial^2 B(A)/\partial y \partial X$. This quantity is expected to be positive, as the benefit of social learning requires the production of innovations by others. Thus there is positive coevolutionary feedback between investment in innovation and social learning, as the advantage of social learning increases with increasing innovation by social partners. However, the term $\partial B(A)/\partial X$ is weighted by the assortment measures dX/dx and dX/dy in equations 5.2 and

5.3, respectively. Thus increases in these two forms of assortment are expected to create selection for simultaneous increases in innovation and social learning via this coevolutionary feedback.

(c) Increasing group size may increase selection for innovation and social learning via this coevolutionary feedback, depending on the form of assortment present.

Here I consider the effect of group size (N) on the term $\partial B(A)/\partial y$. As previously stated $\partial B(A)/\partial y$ is expected to increase with X as higher levels of innovation will mean that there are more adaptive behaviours to be gained by social learning. Following this logic we might expect that, holding X constant, increased group size will increase the benefit of social learning, as more individuals will be producing innovations (i.e. $\partial^2 B(A)/\partial y \partial N > 0$). Note that this relies on the assumption that the effective social contact rate, at a minimum, declines sub-linearly (or does not decline) with group size. By increasing the benefit of social learning, increasing group size will strengthen the coevolutionary feedback outlined above (i.e. $\partial^3 B(A)/\partial y \partial N \partial X > 0$). However, it is worth noting that group size may also have effects on assortment, in particular if this assortment is via interactions with kin owing to limited dispersal. For example, if we consider the case of haploid asexual individuals in an infinite island model with dispersal rate d between groups and group size N , the expected relatedness between a focal individual and their social partners is $(1-d)^2/(N-(1-d)^2(N-1))$ (Taylor 1992), which declines with N . Thus increased group size may decrease assortment based on limited dispersal. However, other mechanisms of assortment, such as partner choice, could, in principle, maintain assortment even with increasing group size.

Overall this illustrative theoretical analysis suggests that innovation and social learning should be favoured by increased assortment, and that there will be a positive

coevolutionary feedback between innovation and social learning. The results also suggest that increasing group size may increase selection for social learning, and consequently innovation via coevolutionary feedback, as long as increasing group size does not have a strong negative effect on assortment. To complement these results I now present a mechanistic model with explicit cultural dynamics.

Explicit cultural model. I consider a scenario where all individuals in a group interact and individuals sample from the total pool of cultural traits present in the group. The number of cultural traits n an individual possesses follows the differential equation

$$\frac{dn}{dt} = \alpha x + \beta y m - \gamma n, \quad (5.4)$$

where m is the number of cultural traits present in the group that have not been learned by the focal individual, α and β are scaling factors for the efficiency of innovation and social learning, and γ is the rate at which cultural traits become obsolete. Similarly the number of traits not yet learned by the focal individual follows the differential equation

$$\frac{dm}{dt} = \alpha X - \beta y m - \gamma m. \quad (5.5)$$

If we assume that the learning dynamics occur on a much faster timescale than the evolutionary dynamics, we can take the steady-state values of n^* , which is given by

$$n^* = \frac{\alpha(xy\beta + x\gamma + yX\beta(N-1))}{\gamma(y\beta + \gamma)}. \quad (5.6)$$

I use the following fitness function to model the evolution of investment in learning:

$$w = a + bn^* - c(x + y)^2, \quad (5.7)$$

assuming accelerating costs of brain size and linear benefits of cultural traits. Unfortunately, even such a simple representation of the cultural dynamics leads to the model quickly becoming analytically intractable. However, Fig. 5.1 illustrates the

evolutionarily stable trait values for a representative numerical solution of the model, illustrating that both increased assortment and group size select for increases in investment in innovation and social learning.

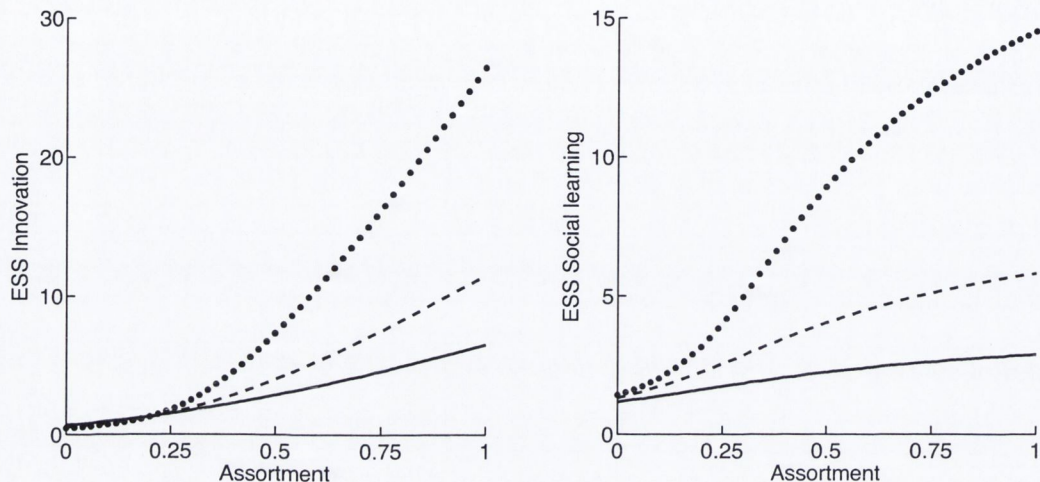


Figure 5.1: Shown are evolutionarily stable levels of investment in innovation (left panel) and social learning (right panel) from the model with explicit, as a function of assortment (dX/dx). Solid lines are for $N = 10$, dashed lines $N = 20$, and dotted lines for $N = 50$. Other parameter values are: $c = 0.1$, $b = 0.5$, $\alpha = 0.15$, $\beta = 0.5/(N - 1)$ and $\gamma = 0.2$.

5.3. Comparative analysis

To test my model predictions I analysed the frequencies of innovation and social learning across primate species using comparative phylogenetic methods. Data on the frequencies of innovation and social learning for each species were taken from Reader *et al.* (2011). These data are based on comprehensive counts of the frequencies of occurrences of innovation and social learning in the primatological literature (see Reader & Laland 2002, and Reader *et al.* 2011 for details). As these data could show pseudoreplication, which could increase the correlation between innovation and social learning, all examples of behaviours present in both innovation and social learning for a given species were removed. To avoid excessive biasing of our analysis by large numbers of species for which no observations of culture have been made, we restricted

our dataset to species for which at least one occurrence of innovation or social learning has been recorded, giving a total of 49 species. As in Reader *et al.* (2011) I corrected the frequencies of innovation and social learning for research effort by taking the residuals of a log-log regression of these frequencies on a research effort measure based on counts of published studies on each species (see Reader & Laland 2002 and Reader *et al.* 2011 for details).

As cooperative behaviours should be favoured by phenotypic assortment (Frank 1998, West *et al.* 2007), I used a measure of the cooperativeness of each species as a proxy for assortment. To measure the cooperativeness of species I collated data on the presence/absence of three cooperative behaviours that have been important during human evolutionary history: coalition-formation, food-sharing and alloparenting. Data were taken from Plavcan *et al.* (1995) and Jaeggi & van Schaik (2011) for coalition-formation; Jaeggi & van Schaik (2011) for food-sharing between adults of the same sex; and Riedman (1982) for alloparenting. Food-sharing between males and females and parents and offspring were not included as these are easily explained by the food for sex' hypothesis and parental care (Jaeggi & van Schaik 2011). We used the unweighted sum of the number of these cooperative behaviours a species engages in, giving a score of cooperativeness between 0 and 3. To assess the effect of group size on innovation and social learning, data on social group size were taken from the compilation of Nunn & van Schaik (2002). To control for the phylogenetic relationships among species I used the consensus primate tree from the 10k Trees Project (Arnold *et al.* 2010). Fig. 5.2 shows bivariate plots of all data used in the models. Note that I do not include brain size measures in our models, as in our theoretical model investment in cognition is the proximate mechanism via which innovation and social learning are achieved. It would therefore not be appropriate to include brain size measures as explanatory variables, as they are considered latent proximate variables within our framework (i.e. we would be

explaining the response variable using the proximate mechanism via which it is achieved).

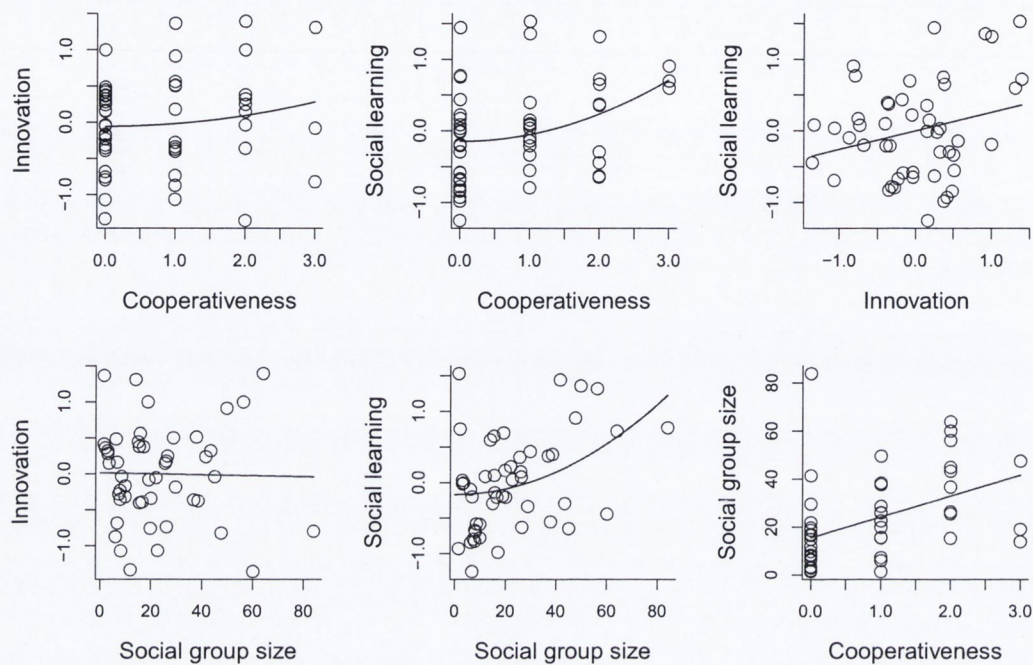


Figure 5.2: Bivariate plots of the data used in the models are shown. Lines are simply added for illustrative purposes and were fit using linear models. Innovation and social learning frequencies have had the effect of innovation removed.

We implemented multiple response models using the R (R Core Development Team) package MCMCglmm (Hadfield 2010). MCMCglmm uses a Markov chain Monte Carlo algorithm to fit generalised linear mixed models. We modelled both innovation and social learning as gaussian response variables. This approach allows us to estimate both residual and phylogenetic correlation between innovation and social learning while simultaneously estimating the effects of cooperativeness and group size on each of them. We modelled the effect of phylogeny as a random effect. We used inverse-Wishart distributions for the priors for both the residual and phylogenetic covariance matrices. We set prior variances for the residual and phylogenetic covariance matrices at 0.5 and covariances at 0, with a degree of freedom parameter of 2 for each matrix (code: `R = list(V = 0.5*diag(2), n = 2), G = list(V = 0.5*diag(2), n = 2))`). The prior value of 0.5 for the variance parameters corresponds to the prior belief that the variance is split evenly

between the residual and phylogenetic effects as both innovation and social learning were standardised to unit variance. Setting the prior covariances to 0 implies a priori independence of innovation and social learning. In our initial model we estimated both the residual and phylogenetic covariances and fit separate effects of cooperativeness and group size on both innovation and social learning, but attempted to simplify our models based on the deviance information criterion (DIC, a generalised Bayesian equivalent of the Akaike information criterion AIC). We ran each model for 600,000 iterations with a burn-in period of 100,000 and a thinning interval of 100.

The maximal model had cooperativeness and group size as predictors with separate slopes for their effects on innovation and social learning, and had estimated covariances for both the residual and phylogenetic covariance matrices. Using the square of both cooperativeness and group size improved model fit ($\Delta\text{DIC} = 3.53$), so these transformations were used in all subsequent analyses. The simplification step of fitting a shared slope for the effect of cooperativeness on innovation and social learning also led to an improvement in DIC ($\Delta\text{DIC} = 1.74$) so was retained as a more parsimonious model. Fitting a shared slope for the effect of group size significantly reduced model fit so was rejected ($\Delta\text{DIC} = -4.22$). Finally, we attempted model simplification by fixing the different covariance terms to 0. While fixing the phylogenetic covariance led to a disimprovement in DIC ($\Delta\text{DIC} = -10.03$), fixing the residual covariance at 0 showed a significant improvement in DIC and was retained ($\Delta\text{DIC} = 6.61$), indicating that the relationship between innovation and social learning is adequately explained by their correlated evolution.

Fig. 5.3 illustrates the structure and results of the minimal adequate model. The model shows a significant (95% credible intervals of posterior distribution do not overlap with zero) positive effect of cooperativeness on innovation and social learning. As cooperation is also expected to be favoured by phenotypic assortment this result provides

support for our main theoretical conclusion. The model also shows a significant positive phylogenetic correlation between innovation and social learning, suggesting coevolutionary feedback between innovation and social learning. We also find a significant positive effect of social group size on social learning, though the effect of group size on innovation was not significant at the 95% probability level. However, an indirect effect of group size on innovation via the coevolutionary feedback with social learning is expected.

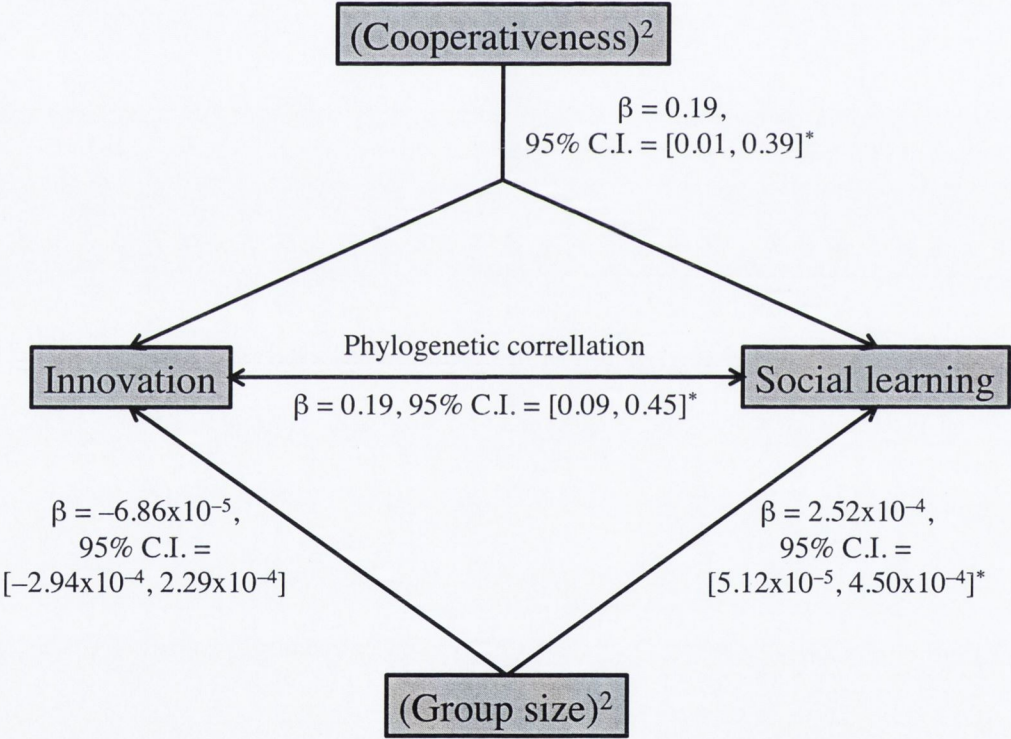


Figure 5.3: The diagram illustrates the structure of the minimal adequate model. The branching arrow for the effect of cooperativeness indicates the shared effect on both innovation and social learning. The double-headed arrow between innovation and social learning indicates phylogenetic correlation. Modal posterior parameter estimates (β) and 95% credible intervals (95% C.I.) are shown. Significant effects are denoted with an asterisk.

5.4. Discussion

My results have strong implications for our understanding of the evolution of culture and cognition in primates. The coevolution of innovation and social learning shares much in common with the evolution of public goods investment. The logic of our model shows many similarities to models for the coevolution of investment in public goods production and exploitation (Brown & Taylor 2010), with innovation being viewed as public goods production and social learning being somewhat akin to exploitation. However, there are important differences between social learning and exploitation of public goods. Cultural adaptations are generally judged to be non-rival (Lehmann & Feldman 2009), i.e. their use by one individual does not generally erode their value to another individual, thus meaning that social learning does not have the same negative impact as other forms of exploitation. Additionally, as discussed in our illustrative model, social learning may be considered cooperative if it secondarily helps spread innovations to others. Both our theoretical and empirical results support this view that culture evolves with dynamics similar to those of public goods production.

Both the results of our theoretical model and the significant effect of cooperativeness on innovation and social learning suggest that assortment may have been a key factor in the evolution of human culture. However, the mechanism, or mixture of mechanisms, leading to assortment based on investment in culture is still unclear. Interactions among kin owing to limited dispersal have previously been suggested as an important mechanism (Lehmann *et al.* 2010), though as stated previously large group sizes may ameliorate this effect. Alternatively, partner choice, i.e. choosing to interact with individuals that invest more in learning, could provide such assortment. There is now a wealth of evidence for the importance of partner choice in maintaining cooperation in humans (Barclay 2004; Sylwester & Roberts 2010; Rockenbach & Milinski 2011; Fehl *et*

al. 2011; Rand *et al.* 2011; Wang *et al.* 2012), and evidence is also accumulating for the importance of partner choice in non-human primates (Schino & Aurelli 2009; Fruteau *et al.* 2011; Sabbatini *et al.* 2012). In principle partner choice can achieve assortment even in large groups (Baumard *et al.* In Press), thus allowing for the maintenance of assortment while simultaneously gaining the benefit of providing access to a large number of individuals from which to learn.

My results do not prove causation and much further theoretical and empirical work is necessary to ascertain the role of assortment in the evolution of culture and cognition. There is much scope for the development of theory on the evolution of partner choice in the context of investment in learning. Recently, sophisticated experimental protocols have been developed to study the role of partner choice in human cooperation (e.g. Rand *et al.* 2011; Wang *et al.* 2012). These protocols could likely be adapted to games of innovation and social learning, such as the game used in the recent social learning strategies tournament' (Rendall *et al.* 2010).

It is also worth noting that causation between assortment and investment in culture may not be unidirectional. The cognitive investment necessary for the evolution of cultural learning capacities may itself allow for assortment by improving assessment of the phenotypes of others via their past actions (Brosnan *et al.* 2010; McNally *et al.* 2012). This points to a potential synergy between the cultural intelligence' and social intelligence' hypotheses. The social intelligence hypothesis holds that a major benefit of a large brain is the ability to negotiate complex social scenarios by modifying one's behaviour in response to others and seeking out the best social partners (Dunbar 1998; Dunbar & Schultz 2007). The coevolution of these abilities to create phenotypic assortment and the investment in culture that they favour may have been important factors in the evolution of human intelligence.

Finally, it is worth noting the possible implications of my results for our understanding

of the nature of the human brain as an adaptation. As I have argued, investment in culture may be seen as investment in a public good. If, as is held by the cultural intelligence hypothesis, increased brain size is the proximate mechanism via which investment in culture is achieved, our brains may have largely evolved as a public good. The evolution of social learning gives us access to each other's creative investments, transferring the benefits across our social groups. The element of humans that seems most private, our minds, may have evolved, in a proximate sense, for the benefit of others.

Chapter 6

General discussion

In this chapter I briefly review the results of the preceding chapters before synthesising some general implications for our understanding of primate cognitive evolution.

6.1. Overview of results

Chapter 2: Cooperation and the evolution of intelligence.

In chapter 2, I developed a model to test the mechanistic validity of the social intelligence hypothesis (Humphrey 1976; Byrne & Whiten 1988; Dunbar 1998). Specifically, I assessed the role of the demands of decision-making in two social dilemmas in selecting for increased brain size. The model consisted of individuals endowed with artificial neural networks playing each other in two social dilemmas: the iterated prisoner's dilemma and the iterated snowdrift game. A genetic algorithm was used to evolve the size, structure and the weights between nodes of the networks, allowing for the flexible evolution of decision-making strategies. The model showed that transitions towards cooperative groups maximise selection for large brains, supporting the predictions of the social intelligence hypothesis. Additionally, my results showed that higher frequencies of intelligent contingent strategies increase selection for intelligence, leading to a Machiavellian arms race (Byrne & Whiten 1988). Overall the results of this study suggest that selection for conditional cooperation may have played a key role in the evolution of human intelligence. Finally, I argued that these results might help explain the apparent bimodal distribution of the pinnacles of cooperation on intelligence across taxa (Brosnan *et al.* 2010), with interactions among kin owing to population structure driving cooperation at low levels of intelligence (e.g. microorganisms, social hymenoptera) and conditional behaviour driving cooperation at high levels of intelligence (e.g. humans).

Chapter 3: Bigger brains and longer lives facilitate the evolution of cooperation.

In chapter 3, I examined the role of cognition and lifespan in the evolution of conditional cooperation. It had previously been suggested that a bigger brain should favour conditional cooperation by increasing the accuracy of the assessment of social partners (Trivers 1971; Stevens & Hauser 2004; Hauser *et al.* 2009; Melis & Semmann 2010), and that a longer lifespan should favour conditional cooperation as there will be more opportunities for one's current actions to affect the future actions of others (Trivers 1971; Axelrod & Hamilton 1981; McNamara *et al.* 2008). I developed a series of mathematical models to show that the potential assortment created by conditional cooperation increases with cognitive capacity and survival rate for five different mechanisms (partner choice, direct reciprocity, indirect reciprocity, punishment and kin discrimination). These models elucidated the key role of brain size and life history in shaping phenotypic correlations among individuals. I then used comparative analyses to show that bigger brains and longer lives facilitate the evolution of two forms of cooperation in primates - coalition formation and food sharing. The results suggest that the evolution of human cooperation and society was driven by the evolution of our enlarged brains and extended lifespan. I also stressed how these results help elucidate the evolutionary links between brain size, life history and sociality, and the inhibition of cooperation by sources of extrinsic mortality, via its effects on these traits (van Schaik *et al.* 2012).

Chapter 4: Cooperation creates selection for tactical deception.

In chapter 4, I turned my attention to a possible negative consequence of conditional cooperation: selection for tactical deception (Byrne & Whiten 1988; Whiten & Byrne

1988). I used a simple game theoretic model to show that conditional cooperation can create selection for tactical deception, as it erodes the assortment that conditional cooperation creates. I showed that tactical deception can undermine an otherwise stable population of conditional cooperators, dooming the population to a state of defection. I also showed that associative learning could lead to the stable coexistence of conditional cooperators and tactical deceivers owing to negative frequency dependence in the efficiency of deception. I then used data from the primate deception database of Byrne & Whiten (1990) to show that primate species that engage in more forms of cooperation also deceive each other more frequently. Trivers' argument that self-deception evolved as a mechanism to better conceal deception from others (Trivers 2011) was used to illustrate the potential role of cooperation in selecting for self-deception. As the ability to deceive others is generally viewed as a major benefit of theory of mind and second order intentionality (Premack & Woodruff 1978; Byrne & Whiten 1991), I argued that conditional cooperation may have been important in the evolution of these psychological capabilities in humans by creating selection for deception. Finally, this study has interesting implications for the evolution of moral behaviour in humans. Cooperation and self-sacrifice' are generally viewed as bedrocks of our morality, while deception is seen as one of our most immoral behaviours. That this most noble aspect of human behaviour could have selected for dishonesty and manipulateness paints an intriguing picture of selection balancing moral extremes.

Chapter 5: Assortment, coevolutionary feedback and the evolution of culture.

In chapter 5, I applied social evolution theory to the coevolution of cognitive investment in innovation and social learning, and considered culture as a form of public good. I built a general illustrative model using the direct fitness approach (Taylor & Frank

1996; Frank 1998), which showed that assortment could be of key importance in the evolution of culture. Assortment leads to increased investment in innovation and/or social learning resulting in increased investment by one's social partners, which can then be exploited via social learning. As social learning allows the acquisition of the innovations of others there is a positive coevolutionary feedback between innovation and social learning, which is strengthened by assortment. Assortment of investment in innovation and social learning could arise owing to interactions with kin or partner choice, though I argued that interactions with kin could be of less relative importance. A comparative analysis of rates of innovation and social learning in primates yielded general support for the model predictions. The analysis highlights that assortment of different types of cognitive abilities may be a driving force in primate brain evolution. Interestingly, if the resultant intelligence is general domain (Reader *et al.* 2011), increased cognitive investment in culture may create further assortment by allowing for more efficient partner choice (chapter 2). The general conclusion of this study is that, to the extent that the cultural intelligence hypothesis holds true (van Schaik & Burkhardt 2011; van Schaik *et al.* 2012), our brains evolved as a form of public goods investment. This highlights the key role of social learning in turning our cognition from a private to a public good, by giving us access to the innovations of others.

6.2. Conclusions

The cultural intelligence hypothesis is really social.

The cultural intelligence hypothesis is quickly becoming the most popular explanation for human cognition (Whiten & van Schaik 2007; van Schaik & Burkhardt 2011; van Schaik *et al.* 2012). As result the popularity of the social intelligence hypothesis has somewhat waned. However, my results suggest that these explanatory frameworks are

more interconnected than previously thought. Assortment creates selection favouring cognitive investment in culture (chapter 5). However, this assortment can be increased by cognition (chapter 3). The ability to create assortment can facilitate cooperation as well as culture (chapters 2 and 3), which in turn could select for further investment in cognition (chapter 2). When viewed from the perspective of social evolution theory the social and cultural intelligence hypotheses are intimately connected in terms of ultimate explanation.

The human mind is inherently social.

The confluence of the social and cultural intelligence hypotheses suggests social forces have been the major factors determining human cognitive evolution. Our brains seem to be at once a form of public goods investment and a tool for creating assortment. Conditional cooperation facilitated by a powerful intellect creates selection for tactical deception, thus likely selecting for theory of mind and second (and higher) order intentionality. Our very consciousness and self-awareness is likely an adaptation to our social environment.

Life history is crucial.

While only formally considered in chapter 3, it is clear that life history, and the extrinsic mortality rate in particular, is a crucial factor shaping selection on cognition. Longer lives increase the potential for assortment via conditional behaviours (chapter 3), which is an important benefit of cognition (chapter 2; Brosnan *et al.* 2010). However, we also expect lower extrinsic mortality to favour investment in cognition by allowing more time for the benefits of learning to accrue, allowing time for the brain to develop, and allowing for

fitness benefits to manifest as an increased survival rate (van Schaik *et al.* 2012). Much further modelling and comparative analysis is needed to combine social and life history effects to further elucidate their shared influence on cognitive evolution. For example, predation rate is likely to be a major source of extrinsic mortality. This could create selection for increased group size via safety in numbers (Krause & Ruxton 2002) or for alarm calls to warn others, or deter the attack, of approaching predators (Zuberbühler *et al.* 1999). There is great potential for the interaction between ecological factors and the social forces shaping primate brain evolution.

Social evolution theory can enrich our understanding of cognitive evolution.

Throughout this thesis, assortment, the central quantity in social evolution theory (Frank 1998), has been shown to have profound effects on cognitive evolution. Increased cognitive capabilities increase the potential for assortment via conditional cooperation (chapter 3) and the benefits of this assortment can select for bigger brains (chapter 2). While the importance of assortment for the evolution of cooperation is well understood (Frank 1998; West *et al.* 2007), the effects of cognition on this assortment and the potential for assortment to select for bigger brains have almost entirely been overlooked. It is hard to imagine how the view of cognitive investment in learning as a public good favoured by assortment (chapter 5) could be reached without the use of social evolution theory. Similarly, the result that cooperation selects for deception (chapter 4) seems puzzlingly counter-intuitive without the lens of social evolution theory firmly fixed on assortment. While there have been many advances in our understanding of primate cognitive evolution over recent decades (Dunbar & Schultz 2007; van Schaik & Burkhardt 2011; Reader *et al.* 2011; Whiten & Erdal 2012), the field has suffered from a lack of rigorous modelling approaches and often a conflation of proximate and ultimate

explanations. The formal modelling approach of social evolution theory promises great insight in this field, both via the clear expression of the evolutionary logic behind current thinking and the discovery of novel explanatory hypotheses. A trait whose evolution has been primarily shaped by social forces deserves a social theory to explain its evolution.

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Appendix A

This appendix contains the published manuscript from Chapter 2.

Cooperation and the evolution of intelligence

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The high levels of intelligence seen in humans, other primates, certain cetaceans and birds remain a major puzzle for evolutionary biologists, anthropologists and psychologists. It has long been held that social interactions provide the selection pressures necessary for the evolution of advanced cognitive abilities (the 'social intelligence hypothesis'), and in recent years decision-making in the context of cooperative social interactions has been conjectured to be of particular importance. Here we use an artificial neural network model to show that selection for efficient decision-making in cooperative dilemmas can give rise to selection pressures for greater cognitive abilities, and that intelligent strategies can themselves select for greater intelligence, leading to a Machiavellian arms race. Our results provide mechanistic support for the social intelligence hypothesis, highlight the potential importance of cooperative behaviour in the evolution of intelligence and may help us to explain the distribution of cooperation with intelligence across taxa.

Keywords: reciprocity; Machiavellian intelligence; cognition; social brain; prisoner's dilemma; snowdrift game

1. INTRODUCTION

Natural selection never favours excess; if a lower-cost solution is present, it is selected for. Intelligence is a hugely costly trait. The human brain is responsible for 25 per cent of total glucose use, 20 per cent of oxygen use and 15 per cent of our total cardiac output, although making up only 2 per cent of our total body weight [1]. Explaining the evolution of such a costly trait has been a long-standing goal in evolutionary biology, leading to a rich array of explanatory hypotheses, ranging from evasion of predators to intelligence acting as an adaptation for the evolution of culture [2–4]. Among the proposed explanations, arguably the most influential has been the 'social intelligence hypothesis', which posits that it is the varied demands of social interactions that have led to advanced intelligence [4–12].

In recent years, the cognitive demands of reciprocity, one of the mechanisms posited as important in the maintenance of cooperation in humans and other intelligent taxa, have been suggested to be a causal factor in the evolution of advanced intelligence and human language. This has been particularly apparent in the evolutionary game theory literature, where conjecture regarding this relationship is frequent [13–16]. Indeed, there is a rich history of work relating intelligence and reciprocity in the game theory literature, though most of this work has focused on the cognitive abilities required for the evolution of cooperation, rather than the possible role that the negotiation of these interactions has in the evolution of intelligence [17–24]. As well as the cognitive abilities

required for the coordination of partners during cooperative acts, both direct (decisions based on what you do to me) and indirect (decisions based on what you do to others) reciprocity have additional demands in terms of the ability to remember previous interactions and to integrate across these interactions to make decisions in cooperative dilemmas [25–31]. These cognitive demands, combined with the occurrence of cooperative behaviour between unrelated individuals in intelligent taxa, suggest that selection for these mechanisms of cooperation could, at least in part, be responsible for advanced cognitive abilities [26].

The many subfields within the social intelligence hypothesis have shown a rich elaboration of verbal arguments, and data from comparative studies support many of their predictions [32–34]. However, verbal reasoning and comparative analysis alone are not sufficient to assess the relative merit of competing hypotheses [35]; mechanistic models are needed to assess the plausibility of these different explanations for advanced cognition.

Here, we use an artificial neural network model to focus on the potential for direct reciprocity, a behaviour that is widespread in humans, to select for advanced cognitive abilities. Rather than manufacturing some form of functional relationship between intelligence and fitness, we allow this relationship to emerge based on the demands of decision-making in two social dilemmas, and analyse the consequences for the evolution of intelligence.

2. MATERIAL AND METHODS

(a) *The social dilemmas*

In order to consider the dynamics of cooperative social interactions, we use the framework of two classic social dilemmas: the iterated prisoner's dilemma (IPD) and the iterated

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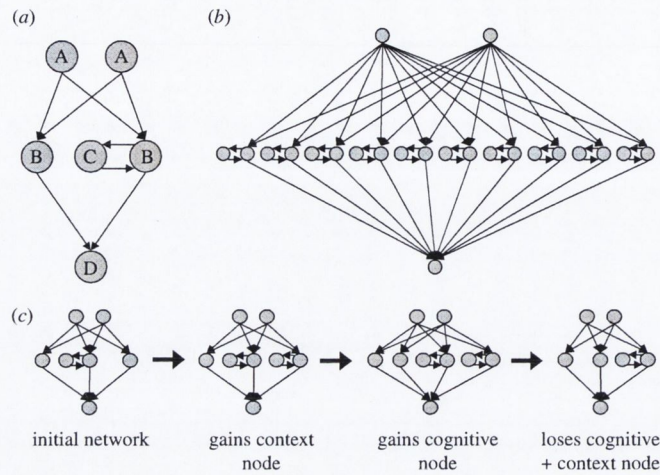


Figure 1. The artificial neural network model. (a) A schematic to aid in the understanding of our network structures is shown. Input nodes, which receive the payoffs of both players in the previous round, are labelled A. Cognitive nodes, which can receive input from both input and context nodes, are labelled B. Context nodes, which store the previous state of their cognitive node and return this state (times a weight) as input in the next round, are labelled C. The output node that receives inputs from the cognitive nodes and gives the individual's decision to cooperate or defect is labelled D. The most complex artificial neural network allowed in our simulations is shown in (b), possessing 10 cognitive nodes and 10 context nodes. A sample of a possible sequence of mutations to network structure is shown in (c). Individuals gain and lose cognitive and context nodes by random mutation. If a cognitive node with a connection to a context node is lost by mutation, the context node is also lost.

snowdrift game (ISD). In both games, two players must choose between cooperation and defection during repeated rounds. In the event of mutual cooperation or mutual defection, both players receive payoffs R or P , respectively, while a defector exploiting a cooperator gets T and the cooperator gets S . In the prisoner's dilemma, the benefit of an individual's cooperative behaviour goes to their opponent, while they pay all of the costs (e.g. food sharing, reciprocal coalitional behaviour). This results in a payoff order of $T > R > P > S$. Here, the worst possible outcome for an individual is to cooperate while their opponent defects, while the best outcome is to defect while the opponent cooperates. In the snowdrift game, the benefits of cooperative behaviours are shared between opponents, and the costs are shared if both individuals cooperate (e.g. cooperative hunting, coalitional behaviour with shared benefits). This results in a payoff order of $T > R > S > P$. Again, the best outcome for an individual is to defect while their opponent cooperates, though the worst possible outcome for an individual is for neither them nor their opponent to cooperate. In both games, the overall payoff (sum of both individual's payoffs) is greatest for mutual cooperation and lowest for mutual defection.

All of this means that the equilibrium frequency of cooperation for a single interaction (single-interaction Nash equilibrium) will be zero in the prisoner's dilemma but will be non-zero for a single-interaction snowdrift game [36]. These single-interaction Nash equilibria provide a useful benchmark against which to assess the effects of contingent behaviours (i.e. those that depend on the behaviour of others) in repeated interactions.

(b) The neural network model

Any attempt to define a metric of intelligence will always be a contentious matter. However, comparative studies across taxa have usually focused on two main classes of brain

properties as proxies of intelligence: metrics based on relative or absolute size of the brain or certain brain regions, and metrics based on more specific properties such as numbers of cortical neurons [37]. It is with this tradition in mind that we develop our artificial neural network model, with evolving network structure, using the number of neurons, i , as our proxy for intelligence. Each individual can display varying levels of intelligence, from simply being characterized by a binary response of always cooperate or always defect to large neural networks that possess complex neuronal structure, allowing for computations to inform decisions based on payoffs and the integration of longer-term memory into their current decision-making processes.

Each individual in our simulated populations possesses a neural network that determines their behaviour in social dilemmas (illustrated in figure 1). The networks each have two input nodes (which receive the payoffs of the individual and their opponent in the previous round as inputs) and one output node (giving the probability that they cooperate during their next interaction). The hidden layer of each individual's network has an evolving structure, possessing different numbers of cognitive and context nodes [38] (figure 1). Cognitive nodes allow for computation based on the values of network inputs and context nodes, which in turn allow for the build-up of memory based on previous states of their associated cognitive nodes.

Computation in the network is implemented via synchronous updating of nodes. The value of each input node is passed to each of the network's cognitive nodes, multiplied by the weight linking the two nodes. Each cognitive node is also passed the current value of their associated context node (if they possess one) multiplied by the weight linking the two nodes. The cognitive nodes sum across all of the weighted values that they receive and pass this value through a sigmoidal squashing function, resulting in a value between 0 and 1, analogous to a probability of activation. All context

nodes are then passed the value of their associated cognitive nodes. This allows the context nodes to build up memory of previous interactions without having to store the actual sequence of events that have occurred. The internal states of these context nodes could be considered analogous to emotional states. Finally, the values at all cognitive nodes are then passed to the output node (multiplied by their weights), summed and again passed through a sigmoidal squashing function. This output gives the probability that the individual will cooperate in the current round. As the sigmoidal function asymptotes to 0 at $-\infty$ and 1 at ∞ , there will always be inherent noise in the network's probabilistic decision. This property of the function also means that it is easy to minimize noise in the network's behaviour if that behaviour shows a lack of contingency (as the node can always be near one of the asymptotes), while contingent behaviour will show greater noise (as switching is more difficult to achieve near the asymptotes). This formulation has intuitive appeal over simply adding extraneous noise to individual decisions, as in nature we would expect individuals to make few mistakes when their behaviour is non-contingent, while more complex decisions would be expected to be more error-prone. As the network cannot make decisions without an input, each individual has an additional trait encoding whether they cooperate or defect in the first round.

We allowed networks to evolve according to natural selection using a genetic algorithm where fitness is the mean payoff per round from the iterated games minus a penalty for the individual's intelligence, i . When individuals reproduce, mutations allow for the gain and loss of nodes from the hidden layer of their network with a fixed probability. Context nodes could only be gained if there was already a cognitive node present without an associated context node. The loss of a cognitive node with an associated node resulted also in the loss of the associated context node.

The addition of extra cognitive nodes gives networks the potential to perform complex computation based on payoffs by increasing the dimensions of internal representation of the network. The addition of context nodes gives the potential for the integration of longer-term memory of previous interactions in these computations. If an individual possessed no hidden layer nodes in its network, its behaviour in all rounds was decided by its first round move (i.e. they either always cooperated or always defected). The weights of each node in the network (arrowed lines in figure 1) and the threshold of each node (see the electronic supplementary material) were encoded as continuous genetic traits, again subject to mutation during reproduction. This means that, while the number of nodes in the network constrains the possible behavioural repertoire, it is the way that the constituent parts of the network interact that actually decides the individual's behaviour. In this way, our metric of intelligence assesses the potential for complex behaviour that the individual possesses, rather than the appropriateness or 'wisdom' of their behaviour, similarly to the measures of intelligence used in comparative studies.

(c) Model implementation

In order to elucidate when selection favoured intelligence, we ran 10 replicates of our model for both the IPD and ISD, with each replicate lasting 50 000 generations. The payoff values used for all simulations were $R = 6$, $P = 2$, $T = 7$ and $S = 1$ for the IPD, and $R = 5$, $P = 1$, $T = 8$ and $S = 2$ for

the ISD. The genetic algorithm was implemented as follows (see the electronic supplementary material for further details):

- an initial population of random networks was generated;
- each individual played every other individual in the population (50 individuals) in an IPD or ISD;
- each individual network's fitness was calculated as their mean payoff per round minus a fitness penalty for their level of intelligence, i ;
- individuals were selected to reproduce asexually with probability proportional to their fitness;
- newly produced offspring underwent mutation of their network weights, node thresholds and network structure with constant probabilities;
- the previous generation died; and
- the algorithm returned to step 2 until 50 000 generations was reached.

During simulations we recorded the frequency of cooperation in the population, the intelligence of individuals (i) and assessments of the behaviour of individuals against a pre-determined test set of moves (see the electronic supplementary material). We then analysed the gradients of selection for intelligence across these simulations by taking selection for intelligence as the covariance between fitness and intelligence in any given generation [39]. As 50 million individual neural networks were simulated in our study, and individuals were not constrained to base their behaviour only on the previous move, our simulations generated a great diversity of strategies. In order to gain a coarse-grained overview of the strategic composition of the population, we clustered individuals based on their proximity to four canonical strategy types: always-defect-like, always-cooperate-like, tit-for-tat-like (do what your opponent did to you) and Pavlov-like (if your payoff is over a threshold, repeat your previous move). Assignment to each of these strategy types was based on which of these four strategies each individual network clustered closest to based on its behaviour against the test set. While this clustering is only a coarse-grained view, it allows assessment of the effects of shifts towards contingent cooperative strategies on selection for intelligence. Additionally, contingent human cooperation has previously clustered as either tit-for-tat-like or Pavlov-like [40], though longer-term memory is often included [41]. For full details of our data analysis, we direct readers to the electronic supplementary material.

3. RESULTS

Our model shows the spontaneous evolutionary emergence of behaviours similar to strategies known to perform well in the IPD and ISD, such as tit-for-tat and Pavlov, as well as simple always-cooperate or always-defect strategies (figure 2) [42]. Although our networks' behaviours are similar to these strategies, they often show integration over many previous rounds to decide on their next moves. For example, manual interrogation of networks revealed that, of the tit-for-tat type strategies that emerge, many are tit-for-2(or more)-tats, and many of the Pavlov-like strategies also show a threshold mechanism, switching to constant defection against opponents that show behaviour close to an always-defect strategy. Behaviour was observed that appeared to be close to many other strategies—for example, grim variants

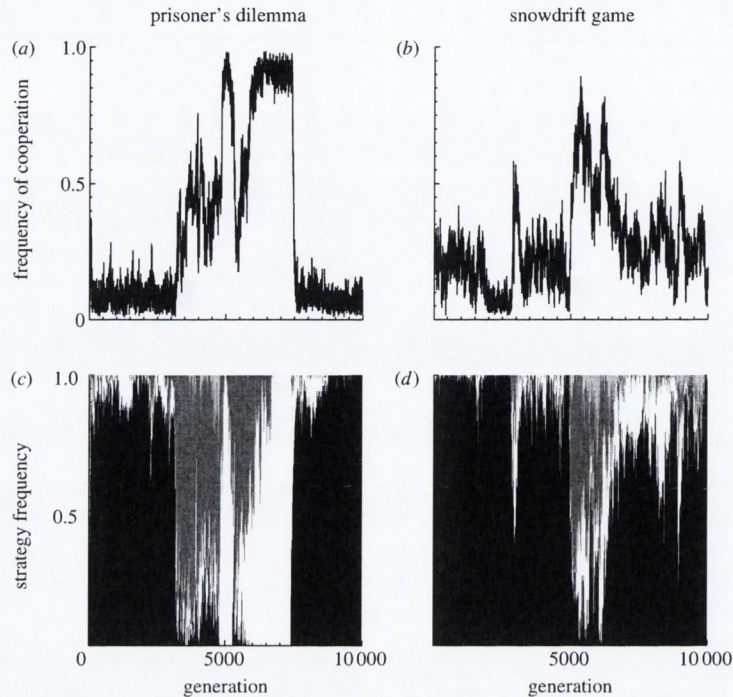


Figure 2. The emergence of intelligent strategies. Shown are the dynamics during 10 000 generation subsets of our simulations for the (a,c) prisoner's dilemma and the (b,d) snowdrift game. (a,b) Sample cycles in the frequency of cooperative acts in the population. (b,d) Frequencies of different strategy types (black, always-defect-like; white, always-cooperate-like; dark grey, tit-for-tat-like; light grey, Pavlov-like) as determined by clustering individuals with their nearest pure strategy (see §2 and electronic supplementary material for details). Transitions to cooperation are characterized by high numbers of contingent strategies, followed by the invasion of the always-cooperate strategy.

(cooperate until the opponent defects, then defect forever), though often requiring more than one defection to trigger permanent defection; false cooperators (cooperate first then switch to defection), though often giving another cooperative move after many defections; and many other variants of tit-for-tat such as 2-tits-for-1-tat and 2-tits-for-2-tats. It is worth noting that strategies of these types that use longer-term memory are observed in behavioural experiments of repeated games with noise [41]. These responsive strategies require greater cognitive abilities in order to carry out computations based on pay-offs, memorize past rounds and integrate across them to make decisions, in comparison with the lower requirements of simply always cooperating or defecting. We hasten to add, however, that the strategies emerging only resemble these strategies; the strategies vary in a continuous manner and often incorporate memory over more rounds. Our goal here is not to describe the strategies that can emerge in repeated games, as there is already extensive literature on this topic (see table 2.1 in [43]), but rather to elucidate the potential effects of their evolution on selection for cognitive capacities.

In order to elucidate the causal factors leading to the evolution of more complex strategies, we analyse the gradient of selection for intelligence in response to population features such as the prevalence of cooperative acts. We find that the selection for intelligence is maximized as the level of cooperation in the population moves above the single-interaction Nash equilibria towards more

cooperative regimes (figure 3). In the IPD, this maximum occurs during increases in cooperation from the single-interaction Nash equilibrium, whereas in the ISD selection for intelligence is maximized at levels of cooperation just above the single-interaction Nash equilibrium. This discrepancy between the games is explained by the different natures of their single-interaction Nash equilibria. In the IPD, this equilibrium is zero, meaning that declining cooperation near this equilibrium is caused by increases in the frequency of individuals that always defect, requiring only little cognitive ability. In the ISD, the equilibrium is non-zero (0.23 in our simulations), meaning that decreases in cooperation back towards the equilibrium can be caused by 'meaner' contingent strategies (e.g. 2-tits-for-1-tat and false-cooperator variants), as well as individuals that always defect. As a result, transitions back to the single-interaction Nash equilibrium in the ISD can in principle select for intelligence, while this is very unlikely in the IPD.

We also find that increasing intelligence decreases the mean frequency of cooperative acts in the IPD (Spearman's rank correlation test; $\rho = -0.2333$, $p < 0.001$; figure 4a), while slightly increasing cooperation in the ISD (Spearman's rank correlation test; $\rho = 0.0089$, $p < 0.0001$, figure 4b). Increasing intelligence increases the variance in the frequency of cooperative acts in the population in both the IPD (Breusch–Pagan test; intercept = 0.0294, slope = 0.0582, $p < 0.0001$; figure 4a) and the ISD (Breusch–Pagan test; intercept = 0.0309, slope = 0.0384, $p < 0.001$; figure 4b),

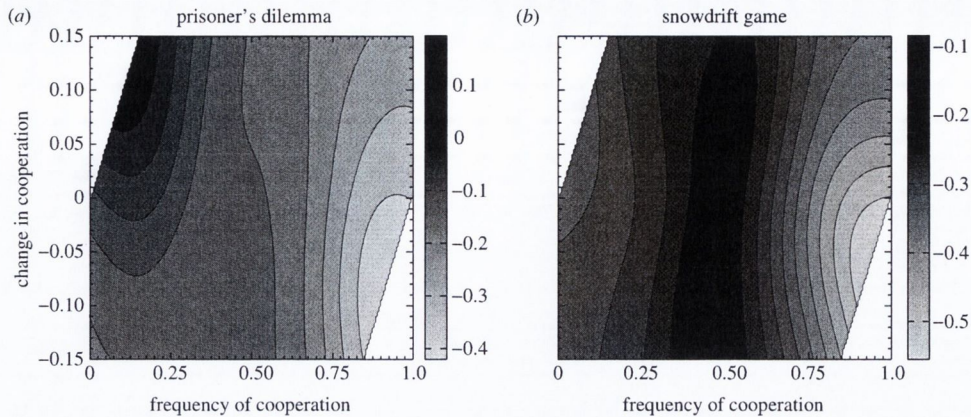


Figure 3. Selection for intelligence and transitions to cooperation. Shown is the level of selection for intelligence, taken as the covariance between fitness and intelligence, against the frequency of cooperation in the current generation and the change in the frequency of cooperation since the last generation. Darker shades indicate greater selection for intelligence. White areas indicate impossible value combinations. Selection for intelligence is maximized during transitions away from single-interaction equilibria, which are no cooperation for the IPD (a), and a frequency of cooperation of 0.23 for the ISD (b). Values displayed were smoothed using a Gaussian kernel.

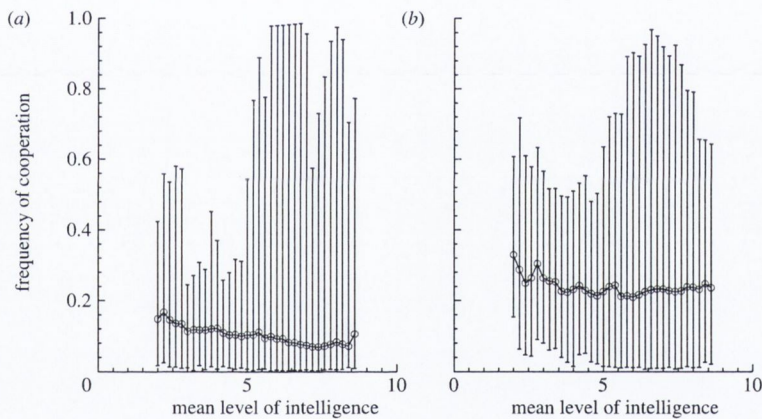


Figure 4. Intelligence and the distribution of cooperation. Shown are the relationships between the frequency of cooperative acts in the population and the mean level of intelligence in the population (a) for the prisoner's dilemma and (b) for the snowdrift game. Mean values are shown by the open circles and lines, and the ranges of the data are shown by the error bars. Greater intelligence decreases the mean level of cooperation in the IPD, while slightly increasing the mean level of cooperation in the ISD. The maximum and variance in the frequency of cooperative acts increases with intelligence, showing that the evolution of intelligent, contingent strategies leads to greater extremes in the frequency of cooperation.

showing that intelligence can facilitate greater extremes of cooperation. These results can be explained by assortment of individuals' cooperative acts [44]; the contingent strategies facilitated by increased intelligence allow an individual to increase the probability that they assort their cooperative acts with other cooperative acts. This leads to a synergistic process, where this increase in cooperation due to increased intelligence creates further opportunities for intelligent individuals to engage in mutual cooperation. However, as levels of cooperation increase further this feedback can break down, as there may be enough cooperation occurring for unconditional cooperators to increase in the population, allowing in turn for the invasion of unconditional defectors or 'meaner' intelligent strategies (e.g. grim variants, false-cooperator variants, etc.). This results in intelligence-facilitating cycles in the levels of cooperation

seen in the population (figure 2), which increases both the variance in, and the maximum level of, cooperation.

In addition to dependency on the prevalence of, and change in, cooperative actions (figure 3), we find that intelligence can be subject to a Machiavellian runaway process [11,12]. In the ISD, as the frequency of contingent (intelligent) strategies increases, so too does selection for intelligence in the population (tit-for-tat-like strategies: Spearman's $\rho = 0.2025$, $p < 0.0001$; Pavlov-like strategies: $\rho = 0.2352$, $p < 0.0001$; see figure 5; electronic supplementary material, table S1 and figure S1). In the IPD, increasing frequencies of tit-for-tat and Pavlov reduces selection for intelligence at low levels of cooperation (frequency of cooperation < 0.5 ; tit-for-tat: $\rho = -0.0945$, $p < 0.0001$; Pavlov: $\rho = -0.0529$, $p < 0.0001$), but does increase selection for intelligence when cooperation

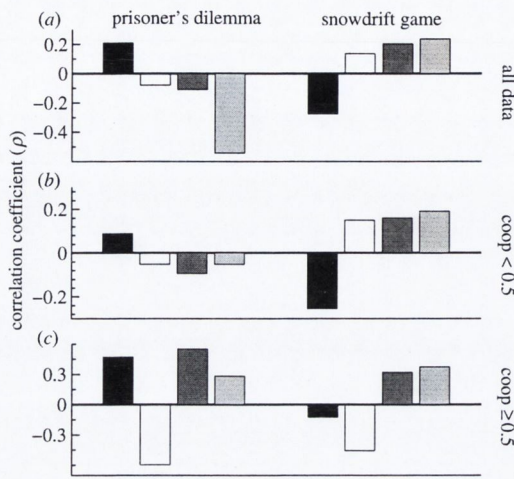


Figure 5. Strategic composition and selection for intelligence. The barplots show the Spearman rank correlation (ρ) between the frequency of each of our four strategy types and selection for intelligence for (a) all levels of cooperation, (b) low cooperation (frequency of cooperative acts less than 0.5) and (c) high cooperation (frequency of cooperative acts greater than or equal to 0.5). Tit-for-tat-like and Pavlov-like strategies always increase selection for intelligence in the ISD, but only when cooperation is high in the IPD. For further details, see electronic supplementary material, figure S1 and table S1.

is more frequent (frequency of cooperation ≥ 0.5 ; tit-for-tat: $\rho = 0.5491$, $p < 0.0001$; Pavlov: $\rho = 0.3187$, $p < 0.0001$). The reason for this distinction between the IPD and the ISD is that there must already be some cooperation occurring for cooperative contingent strategies to be favoured via their ability to assort cooperative acts. In the ISD, the partially cooperative single-interaction equilibrium provides sufficient baseline cooperation for tit-for-tat and Pavlov to be favoured, whereas in the IPD the single-interaction equilibrium of zero cooperation means that unless contingent strategies (or random drift) have already increased cooperation, tit-for-tat-like and Pavlov-like strategies cannot be favoured, and hence cannot lead to an arms race. Note that it is still the case that intelligence is selected for in the IPD when cooperative acts are rare yet increasing (figure 3a). However, the cooperative acts that drive selection for intelligence in this case are generated by less cooperative contingent strategies, which cluster with always-defect as their closest pure strategy ($\rho = 0.1095$, $p < 0.0001$; see electronic supplementary material, table S1 and figure S1). This means that there is a succession in the arms race in the IPD, with 'mean' contingent strategies initially increasing selection for intelligence at low cooperation, and 'kind' contingent strategies increasing selection for intelligence as cooperation increases.

It is not any particular single strategy that drives these arms races; rather, as the complexity of the strategies in the population increases, there is selection for other complex strategies to outwit them. Unlike previous analyses where fixed strategies or strategies with constrained memory were used, our open-ended system allows for near infinite strategic variations to outwit opponents. In

this way, selection for intelligence occurs owing to a constantly shifting strategic environment, where the 'best response' to the population of strategies can be shifting from generation to generation. Increases in memory allow for the potential of the recognition of opponents' strategies, allowing for the alteration of one's own strategy in response (e.g. Pavlov-like strategies that can recognize individuals that always defect). In turn this can allow for attempts to deceive opponents regarding one's own strategy (e.g. false cooperators).

4. DISCUSSION

It is important here to note the closed nature of our model system; individuals can only choose within one social task (whether to cooperate or defect against another individual based on their behaviour in previous interactions with them). However, our results may apply in principle to other social scenarios where individuals use strategies to decide who to cooperate with or when to cooperate, such as indirect reciprocity [17,18], policing/punishment [45,46] and partner choice [47–49]. Along with kin selection, these are the major mechanisms thought to lead to transitions to cooperative groups. As the intelligence of an individual increases, it is likely that more of these behavioural repertoires will become available to them, with increased intelligence acting as a pre-adaptation. For example, increased intelligence owing to selection for direct reciprocity could facilitate the evolution of indirect reciprocity or partner choice, highlighting the contingent nature of social evolution in multiple strategic dimensions [50]. The facilitation of new social behaviours due to emergent intelligence could allow for a perpetuated Machiavellian arms race leading to ever-greater levels of intelligence. Additionally, in our simulations populations evolved to play only a single game (either the IPD or ISD). The simultaneous play of multiple games could greatly increase strategic complexity, with the possibility of the integration of information from previous interactions in games with different payoff structures into the decision-making process.

It has previously been suggested that the pinnacles of cooperative behaviour in nature show a bimodal distribution with intelligence, with the most cooperative species displaying either limited cognition (e.g. microbes, social hymenoptera) or exceptional intelligence (e.g. humans and other primates, certain cetaceans and birds) [26]. It is clear in the former case that cooperation has evolved primarily owing to combinations of kin selection and ecological factors [51]. However, in the latter case, kin selection is not the only mechanism leading to cooperation, and may not even be the most important. A recent study has in fact suggested that relatedness was too low in human hunter–gatherer groups for kin selection to drive the evolution of human cooperation [52]. In highly intelligent species, contingent behaviours (reciprocity, partner choice, etc.) appear to have been important in the evolution of cooperation [26]. Our results may help us to explain this pattern by showing that the selection for appropriate behavioural assortment of cooperative acts can lead to selection for greater cognitive abilities and Machiavellian arms races, and that intelligence facilitates greater extremes of cooperation. Additionally, although kin selection is still of importance

in highly intelligent taxa, high relatedness may hinder the evolution of intelligence by driving unconditional cooperation to fixation in the population, without any need of contingent behaviours.

A trait as complex as advanced intelligence is likely to have evolved owing to a combination of several factors rather than a single factor [4]. Along with the social intelligence hypothesis, many other theories attempting to explain the evolution of advanced intelligence have been suggested, among them that intelligence is an adaptation for tool use [53,54], that intelligence is an adaptation for social learning and the accumulation of culture [55–57], and that intelligence is the result of sexual selection [58]. All of these theories are supported by evidence from at least some of the most intelligent animals. However, the difficulty lies in disentangling the traits that are causal factors in the evolution of intelligence from those that are by-products of advanced intelligence. The combination of game theoretic frameworks and artificial neural network models presented here may provide a framework for the evaluation of the mechanistic strengths of these different hypotheses. While previous models have sought to relate cooperation and intelligence, the focus has most frequently been on the cognitive requirements of cooperation, rather than on the selection for intelligence. Many of these models have lacked an explicit brain structure [17–22], and among those studies that have used artificial neural networks, we know of no examples where the network structure was allowed to freely evolve or implications of selection for decision-making strategies for the evolution of intelligence were directly addressed [23,24]. While artificial neural networks are not real brains, relying on abstraction of the activity of millions of real neurons down to a manageable number of artificial neurons, they can provide insight into the dynamics of cognitive evolution and allow for the flexible evolution of behaviour [59]. Our results show that, in a freely evolving system, selection for efficient decision-making in social interactions can give rise to selection pressures for advanced cognition, supporting the view that the transition to the cooperative groups seen in the most intelligent taxa may be the key to their intellect.

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