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Cooperation creates selection for tactical deception

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Conditional social behaviours such as partner choice and reciprocity are held to be key mechanisms facilitating the evolution of cooperation, particularly in humans. Although how these mechanisms select for cooperation has been explored extensively, their potential to select simultaneously for complex cheating strategies has been largely overlooked. Tactical deception, the misrepresentation of the state of the world to another individual, may allow cheaters to exploit conditional cooperation by tactically misrepresenting their past actions and/or current intentions. Here we first use a simple game-theoretic model to show that the evolution of cooperation can create selection pressures favouring the evolution of tactical deception. This effect is driven by deception weakening cheater detection in conditional cooperators, allowing tactical deceivers to elicit cooperation at lower costs, while simple cheats are recognized and discriminated against. We then provide support for our theoretical predictions using a comparative analysis of deception across primate species. Our results suggest that the evolution of conditional strategies may, in addition to promoting cooperation, select for astute cheating and associated psychological abilities. Ultimately, our ability to convincingly lie to each other may have evolved as a direct result of our cooperative nature.

1. Introduction

Though there are multiple routes through which cooperation can evolve [1,2], conditional cooperation has become a major focus for studies on the evolution of cooperation in taxa of relatively advanced cognitive capabilities, particularly primates, and especially humans. As a result, myriad mechanisms of conditional behaviour that facilitate the evolution of cooperation have been identified, including direct reciprocity [3,4], indirect reciprocity [5,6], generalized reciprocity [7,8], partner choice [9–11], punishment [12,13] and reward [14,15]. 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 [16–18]. 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 recognizing 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 [19–23]. If individuals can use tactical deception to avoid their cheating being detected (e.g. by misdirecting a social partner's attention or misrepresenting 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 eliciting cooperation at lower cost may help select for tactical deception in species with more frequent, and more diverse, forms of cooperation. Here we will 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.

2. Game-theoretic model

We 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 consider only conditional strategies that modify their cooperation in response to their partner's cooperation, though the general logic of our model also applies to cooperation based on punishment or reward. For simplicity we will assume that individuals can take one of the three fixed strategies for this game: conditional cooperator (CC), tactical deceiver (TD) or honest defector (HD). CCs aim to cooperate only with other cooperative individuals and not cooperate with defectors, whereas HDs simply always defect. We assume that TDs 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 . We 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 CCs will cooperate with HDs in proportion s of their interactions. As TDs attempt to conceal their defection, CCs fail to recognize them as defectors with probability q , meaning that a CC will cooperate with a TD in a proportion $q + s - qs$ of their interactions. Following our assumptions the average payoffs per round (π_i) for each of the three strategies are: $\pi_{CC} = (b - c)x_{CC} - c(q + s - qs)x_{TD} - csx_{HD}$ for CCs; $\pi_{TD} = b(q + s - qs)x_{CC} - d$ for TDs; and $\pi_{HD} = bsx_{CC}$ for HDs, 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 $b - c > sb > 0$, $q > 0$, $s < 1$ and $c > d > 0$, meaning that there is bistability between CCs and HDs (neither can invade the other from rarity), CCs do not dominate TDs and HDs dominate TDs (as TDs pay the cost of deception against HDs, while not receiving any benefit of eliciting cooperation). In this scenario, there are two qualitatively different outcomes possible, which are illustrated using the replicator equation $dx_i/dt = x_i(\pi_i - \sum_j \pi_j x_j)$ [24] in figure 1a,b. First, if $b(q + s - qs) - d > b - c$, then TDs dominate CCs. In this case, transient invasion of the TD strategy into a monomorphic population of CCs undermines the stability of the pure CC equilibrium, making honest defection the only Nash equilibrium and causing the collapse of cooperation (figure 1a). Beginning

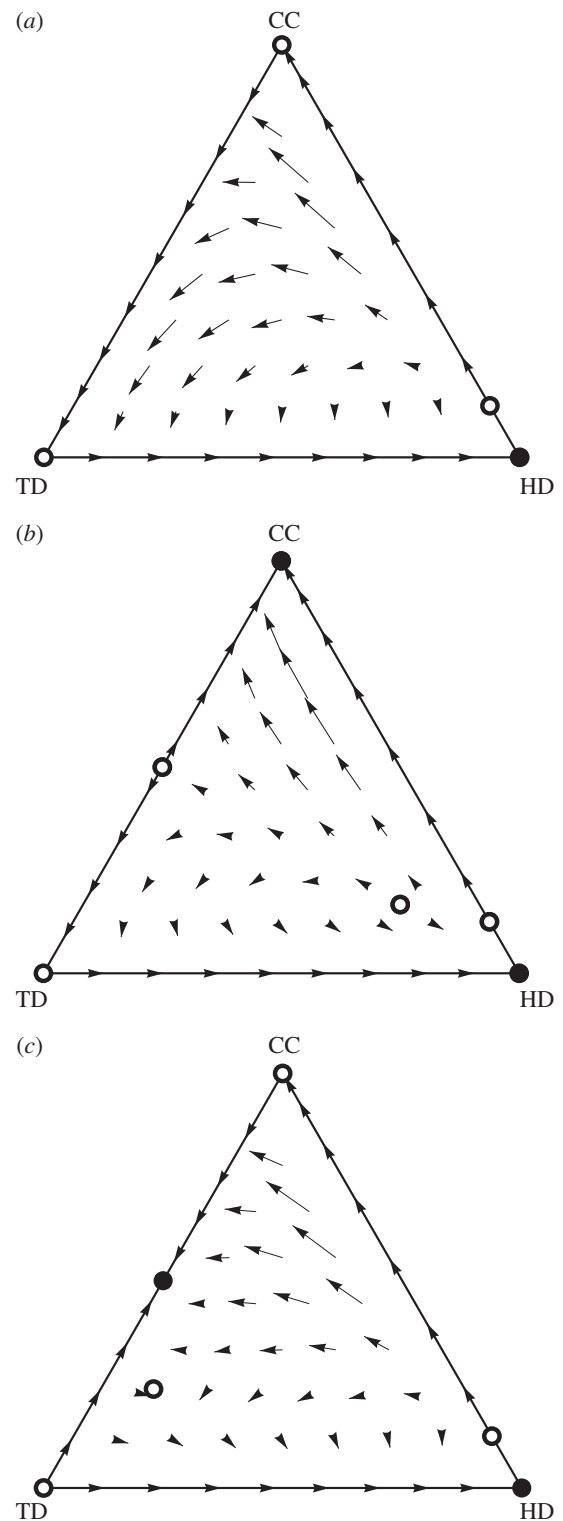


Figure 1. The dynamics of deception and cooperation. Shown are the evolutionary dynamics of the three strategies for the model with (a,b) constant and (c) negatively frequency-dependent efficiency of deception. Solid and open circles represent stable and unstable equilibria, respectively. Parameter values are $b = 1.5$, $c = 0.5$, $s = 0.2$ 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 [25].

from a monomorphic population of CCs, a rare TD will invade and go to fixation. However, this equilibrium will be unstable and can be invaded by a rare HD (as $\pi_{TD} = -d$ and $\pi_{HD} = 0$), which then goes to fixation. Alternatively, if $b(q + s - qs) - d < b - c$, then both conditional cooperation and honest defection are Nash equilibria and the introduction of TDs has little effect (figure 1b), as they cannot invade

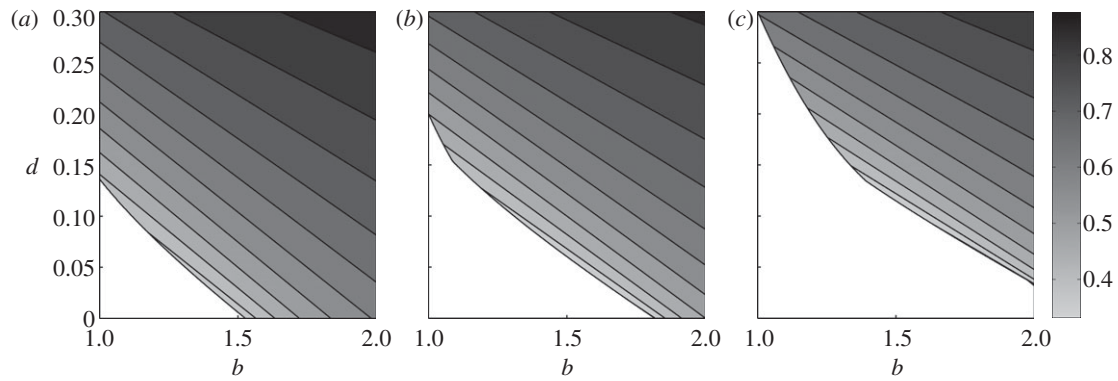


Figure 2. Equilibrium mixture of CCs and TDs. The coloured contour plot shows the frequency of CCs x_{CC}^* at the mixed equilibrium (frequency of TDs is $1 - x_{CC}^*$) as a function of the benefit of cooperation b and the cost of deception d for the model with negative frequency dependence (see figure 1c). Darker (lighter) greys indicate a higher frequency of CCs (TDs) 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) $s = 0.1$, (b) $s = 0.2$ and (c) $s = 0.3$.

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.

In both of the cases above, TDs will only appear transiently before disappearing from the population, so how can TDs persist in the population? One possible factor leading to the coexistence of TDs and CCs is frequency dependence in the efficiency of deception. It would be expected that, as TDs become more common in the population, CCs would become more adept at spotting deception, such as 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 TDs. 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 TD can always invade a monomorphic population of CCs 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 CC will be able to invade a population of TDs when $-cs < -d$. This negative frequency dependence can lead to a stable mixed equilibrium of x_{CC}^* CCs and $1 - x_{CC}^*$ TDs (figure 1c), which can resist invasion by HDs if $b(1 - s)(x_{CC}^*)^2 > d$. The full expressions for the location and stability of this equilibrium are too unwieldy to yield analytical insight, but are numerically explored in figure 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 TDs as their relative advantage over CCs is increased. However, TDs may become victims of their own success; if their equilibrium frequency becomes too high this equilibrium becomes invadable by HDs (i.e. $b(1 - s)(x_{CC}^*)^2 < d$). Increasing the proportion of rounds CCs fail to defect against identified defectors (s) reduces the parameter space in which the mixed equilibrium is stable as the amount of cooperation TDs receive from CCs relative to that received by HDs is reduced (i.e. there is less benefit to outweigh the cost of tactical deception as conditional cooperation becomes less efficient).

3. Comparative analysis

Overall our 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 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 our 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. In essence, new forms of cooperation could add additional dimensions of conditionality in the interactions among individuals, and these additional dimensions could potentially be exploited by deception.

To test this prediction, we used the collation of Byrne & Whiten [26] 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 [26]). While all forms of deception involve the misrepresentation of some information to other individuals, tactical deception implies that this misrepresentation is context-dependent and involves altering one's behaviour in a given context to mislead another individual. As did Byrne & Corp [27], we included all records that were considered by the original observers to meet this definition. This criterion allows the decision on whether tactical deception occurred to be made by the individuals who are best placed to do so: those who made the observations. As much research on tactical deception has occurred since the collation of Byrne & Whiten [26], we supplemented this collation with a literature search for examples of tactical deception. We searched ISI Web of Science using species names (and synonyms) and the term 'deception', and collated all examples where the authors believed that tactical deception occurred (references are included in the electronic supplementary material). Though these more recent examples of deception may suffer from additional biases to those in the collation of Byrne & Whiten

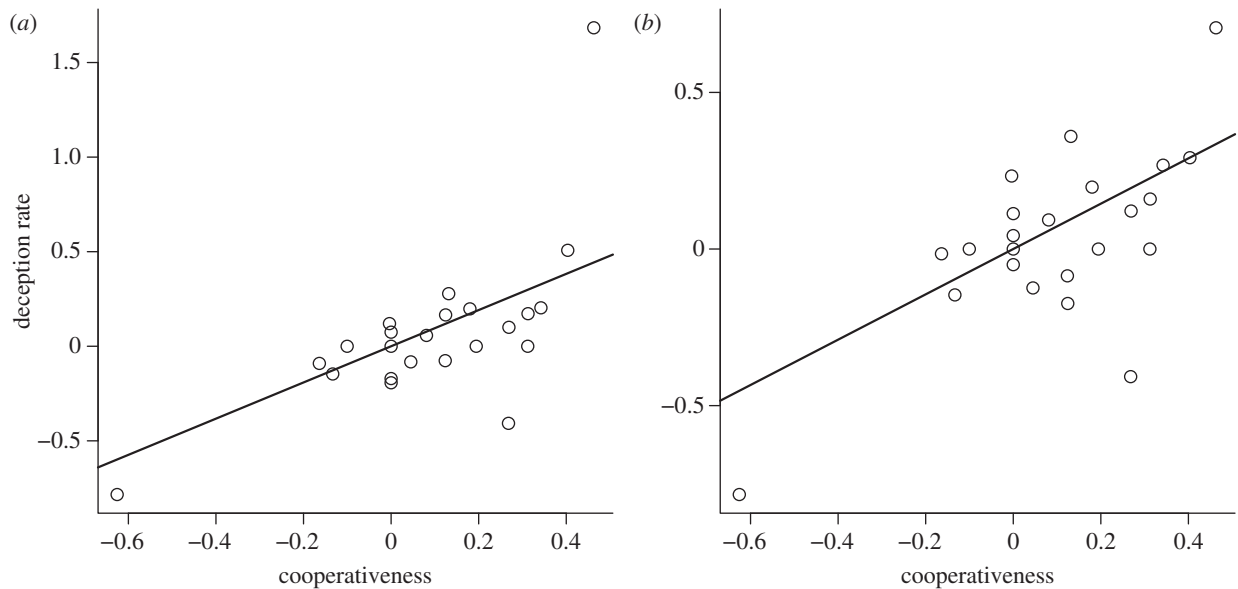


Figure 3. The relationship between deception and cooperation in non-human primates. The data points are independent contrasts for the rate of deception and cooperativeness scores with the effects of neocortex ratio and research effort partialled out for the (a) free-ranging and (b) full datasets. Lines are the predicted values from the models reported in the main text.

(e.g. publication bias), they bring our dataset up to date with our current knowledge on deception in primates. We also note that all of our results hold qualitatively when only the collation of Byrne & Whiten is analysed. We performed two analyses on these frequencies of tactical deception across species. First, following Byrne & Corp [27], we analysed only observations of deception that were made on free-ranging individuals. However, as tactical deception may be more difficult to detect in the field, we also performed an analysis on all data including observations on captive individuals (as in [28]). We used the log of the deception frequency plus one in all analyses.

To assess how cooperativeness affects the frequency of tactical deception across species, we collated data on the presence of three cooperative behaviours that have been important during human evolutionary history: coalition formation, food sharing and alloparenting. We initially used data from the collations in [29–32], supplemented by additional searches for examples of these behaviours that were subsequently published. Searches were carried out using ISI Web of Science with search terms as follows: ‘coalition’, ‘alliance’, ‘ally’ and ‘agonistic support’ for coalition formation; ‘food sharing’ and ‘sharing’ for food sharing; ‘alloparental care’, ‘allomaternal care’, ‘alloparenting’ and ‘allonursing’ (including hyphenated variations) for alloparenting. The additional collated references are given in the electronic supplementary material (note that no additional examples of food sharing were found). We used the unweighted sum of the number of these cooperative behaviours a species is known to engage in, giving a score of cooperativeness between 0 and 3.

As deception has previously been shown to correlate with neocortex size [27] and loads strongly on measures of primate general intelligence [28], it is important to control for cognitive ability. To this end, we included neocortex ratio (size of the neocortex divided by the size of the rest of the brain) as a covariate in our analyses. Data on neocortex ratios were taken from multiple sources [33–36]. 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 [28]. We also performed an additional analysis using the log of the neocortex volume as a measure of cognitive capacity.

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 (data are given in the electronic supplementary material). Analyses were performed using phylogenetic generalized least-squares regression (PGLS) in R [37] with the caper package [38]. As estimation of the level of phylogenetic signal in a dataset becomes unreliable at small sample sizes [39,40], we set Pagel’s $\lambda = 1$, which is equivalent to independent contrasts. We used version 3 of the consensus primate tree from the 10k Trees Project [41] 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, we included a measure of research effort in both analyses. We measured the research effort for all species as the number of papers on a species indexed in ISI Web of Science in the behavioural sciences, psychology, ecology, evolutionary biology, anthropology and zoology, between 1982 and 2012. We included the log of research effort as a covariate in our models.

Our first analysis using neocortex ratio as a measure of cognitive capacity (model structure: $\log(\text{deception rate} + 1) \sim \text{cooperativeness} + \text{neocortex ratio} + \log(\text{research effort})$) showed a significant positive effect of cooperativeness on the rate of tactical deception for both the free-ranging only ($\beta = 0.96$, s.e. = 0.34, $p = 0.010$) and full ($\beta = 0.72$, s.e. = 0.23, $p = 0.005$) datasets (see figure 3). The neocortex ratio had no significant effect on tactical deception in the free-ranging dataset ($\beta = 0.83$, s.e. = 0.63, $p = 0.20$) or the full dataset ($\beta = -0.039$, s.e. = 0.43, $p = 0.93$). Our second analysis using the log of the neocortex volume as a measure of cognitive capacity (model structure: $\log(\text{deception rate} + 1) \sim \text{cooperativeness} + \log(\text{neocortex volume}) + \log(\text{research effort})$) showed a significant positive effect of cooperativeness on the rate of tactical deception for both the free-ranging only ($\beta = 0.97$, s.e. = 0.36, $p = 0.013$) and full ($\beta = 0.69$, s.e. = 0.23, $p = 0.007$) datasets. Neocortex volume had no significant effect on tactical deception

in the free-ranging dataset ($\beta = 0.34$, *s.e.* = 0.72, *p* = 0.64) or the full dataset ($\beta = 0.32$, *s.e.* = 0.47, *p* = 0.51).

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 cooperation provides a major selective benefit to tactical deception. The explanation for this benefit is simple: tactical deception can allow individuals to elicit cooperation (or avoid punishment/gain reward) without paying the costs of cooperation. While there is much debate surrounding the proximate mechanisms involved in tactical deception, it has often been suggested to involve complex psychological abilities such as second-order intentionality and perspective taking [20–22,27,42]. While the taxonomic distribution of these complex proximate mechanisms is highly debatable, our results suggest that, at least in humans, conditional cooperation may have driven the development of many of our other complex psychological abilities by creating selection pressures favouring tactical deception, in addition to selecting for cooperative cognitive capacities such as shared intentionality [43].

Caution must be taken, however, when interpreting the results of our comparative analyses. The collation of tactical deception data of Byrne & Whiten [26] and our additional collations are based almost exclusively on anecdotal accounts of deception, rather than any systematic study. As such they are open to many potential conscious and unconscious biases during observation, and our comparative analyses should be seen as initial support of our hypothesis, rather than an authoritative test. Similarly, our collation of data on cooperation in primates also suffers from potential biases. The treatment of cooperative behaviours as present or absent has obvious pitfalls, and quantitative data are sorely needed. Limited research resources and the difficulty of publishing negative results may exacerbate this problem, though the inclusion of research effort in our analyses should ameliorate these effects to some extent. Further experiments and observational studies of both humans and non-human primates are necessary to ascertain the link between cooperation and tactical deception. These points also highlight important implications of our results for future empirical work on the phylogenetic distribution of deception and the proximate mechanisms underlying it. Deception is notoriously difficult to identify, particularly in the field, and our results suggest that focusing observations on more cooperative species and on individuals during cooperative exchanges may allow for the acquisition of greater volumes of data. Additionally, our model predicts that more costly forms of cooperative behaviour should show higher frequencies of deception, which could be tested by future observational and experimental studies. In addition to testing the evolutionary function of deception, such studies could help increase the amount of data on deception that can be collected with limited resources.

It is also worth noting that not all forms of deception are necessarily deliberate, and deliberate deception is likely to be very rare in non-human species. Individuals need not hold any beliefs regarding the effects of their actions in order to be deceptive. Alternatively, individuals could hold false beliefs about the consequences of their actions in order to deceive others, as has been suggested by Trivers in his theory of the evolution of self-deception in humans [44–48].

The essence of this theory is that the deliberate deception seen in humans 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, non-deliberate deception may not receive the same retribution as deliberate deception, as it may appear to be an ‘accident’ or owing to ignorance. Further empirical research with humans is necessary to ascertain the relative roles of deliberate and non-deliberate deception in eliciting cooperation from others. If Trivers’s 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. However, it is important to stress that for functional tactical deception to occur an individual need not necessarily hold any belief regarding the effect of their actions. Thus, a lack of deliberate deception does not imply that self-deception is occurring.

While our 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 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 [49–51] and/or artificial neural networks [52–54] may be particularly fruitful. Additionally, models of cognitive arms races [55] between TDs and CCs 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 [20,56]. Additionally, it is worth noting some similarity between our results and those in signalling theory. It is a well-known result from signalling theory that dishonesty can only exist in the context of honesty [57]. Indeed conditional cooperation could be understood as a form of honest signalling, pointing to interesting parallels with the mechanisms we explore, which are worthy of further investigation.

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 [58] and Machiavellian capabilities that facilitate selfish ends [20]. 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.

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