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Cite this article: Lie-Panis J, André J-B. 2022 Cooperation as a signal of time preferences. *Proc. R. Soc. B* **289**: 20212266. https://doi.org/10.1098/rspb.2021.2266

Received: 12 October 2021
Accepted: 25 March 2022

Subject Category:
Behaviour

Subject Areas:
behaviour, evolution, theoretical biology

Keywords:
cooperation, trust, time preferences, evolution, costly signalling

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5923872.

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Cooperation as a signal of time preferences

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Many evolutionary models explain why we cooperate with non-kin, but few explain why cooperative behaviour and trust vary. Here, we introduce a model of cooperation as a signal of time preferences, which addresses this variability. At equilibrium in our model (i) future-oriented individuals are more motivated to cooperate, (ii) future-oriented populations have access to a wider range of cooperative opportunities, and (iii) spontaneous and inconspicuous cooperation reveal stronger preference for the future, and therefore inspire more trust. Our theory sheds light on the variability of cooperative behaviour and trust. Since affluence tends to align with time preferences, results (i) and (ii) explain why cooperation is often associated with affluence, in surveys and field studies. Time preferences also explain why we trust others based on proxies for impulsivity, and, following result (iii), why uncalculating, subtle and one-shot cooperators are deemed particularly trustworthy. Time preferences provide a powerful and parsimonious explanatory lens, through which we can better understand the variability of trust and cooperation.

1. Introduction

Human cooperation is inherently variable. Cooperation varies with the individual. We are not all equally likely to help an unrelated stranger in the field or in the laboratory, and report differing levels of cooperative behaviour in surveys [1–15]. Cooperation is also a function of historical and social context. Social trust tends to be lower in poorer countries, and in the aftermath of conflict or other dramatic events [16–21]. For the same interaction, the norm may even be to cooperate in one society, and defect in another [22,23]. Finally, the value of cooperation itself is variable. We place more trust in spontaneous and inconspicuous cooperators than we do in individuals who help others in deliberate or overt fashion [24–30].

Evolutionary biologists and game theoreticians explain the evolution of cooperation with non-kin based on the principle of reciprocity. We trust and help those who have helped us [31,32] or others, and have thus acquired a trustworthy reputation [33–36]. These approaches, however, are chiefly concerned with explaining the existence of cooperation, and rarely attend to its variable nature. In most models helpful behaviour varies because of exogenous noise [37–40]. Cooperative variability remains an open question: we are unable to predict who is more prone to help, where cooperation is more likely to emerge, and what determines its informational value.

The variable nature of cooperation may be studied following a framework introduced by Leimar [41]. His model is based on the assumption that individuals derive differing pay-offs from cooperation, and may thus be differentially motivated to help others (see also [42]). In line with honest signalling theory [43,44], an individual's behaviour in cooperative encounters will then reveal her private pay-offs, and therefore her future cooperative intentions—making it reasonable to trust others based on past behaviour [41,45,46].

Leimar's model provides the general framework for our study. At first glance however, his central assumption seems unrealistic. Virtually all the resources or services that we acquire on our own may be obtained via cooperative exchanges; it is therefore difficult to conceive that some of us could systematically benefit more from cooperation than others. In order to better understand the who, the where and the what of cooperation, we must first explain why individual pay-offs should vary *in general*.

One answer to these questions may lie in differences in individual time preferences. Laboratory and field experiments performed in a diversity of contexts reveal that individuals can be distinguished according to their level of preference for immediate versus future rewards [47–50]. These time preferences are stable in the short to medium term [51,52], and across similar decisions [53,54].

Interindividual differences could originate from adaptive phenotypic plasticity, as harsher environments make future rewards more uncertain and/or present needs more pressing, and select for stronger preference for the present [55–61]. At a fundamental level, cooperation entails paying immediate costs (to help others) and, following the principle of reciprocity, receiving delayed benefits (in the form of future help) [34,41,45,46,62]. In theory, an individual's time preferences should equivalently affect *all* the pay-offs she derives from cooperative encounters.

In this paper, we formally explore the hypothesis that time horizon is the underlying cause of the variability of human cooperation. We develop a mathematical model of cooperation in which individuals are characterized by a hidden discount rate, which remains constant throughout their life, and affects all future pay-offs. Individuals face strangers in a cooperative setting, and may use their reputation to discriminate between trustworthy and exploitative partners. Help emerges as an honest signal of time preferences in our model. Variation of time horizon ensures behavioural variability at evolutionary equilibrium, which stabilizes cooperation [63–67]. In addition, assuming that individual time preferences vary allows us to account for all three dimensions of cooperative variability.

First, we predict that more future-oriented individuals should be more prone to help. At equilibrium in our model, trustworthy partners are individuals whose time horizon surpasses a certain threshold. This result conforms with empirical data. Many studies report a positive correlation between individual time horizon and cooperation [68–72], although it should be noted that some of the evidence is inconclusive [9,62]. Our first result also helps explain interindividual cooperative variability. In surveys and field studies, individual cooperation is associated with environmental affluence [2,6,7,11,12,15]—a variable that closely aligns with time horizon [48–50,53,73–76]. Time preferences have been found to mediate the relationship between environmental affluence and individual investment in collective actions [12].

Second, we predict that more future-oriented populations should have access to a wider range of stable cooperative opportunities. In surveys and field studies, average cooperation and trust are associated with collective wealth [6,11,12,16,18]. Our model offers two complementary explanations for these observations. Following our first result, we expect higher aggregate cooperation when many individuals are future-oriented. Following our second result, we expect cooperation and trust to emerge in a wider range of contexts when the population distribution of time preferences shifts towards the future.

Third, we predict that cooperation should be a more informative signal of time preferences when observation is unlikely, or when the cost–benefit ratio is low. Our theory may explain why we place more trust in helpful partners who maintain a low profile or make impromptu decisions [24–30]. Inconspicuous cooperators are indeed less likely to be observed and, since spontaneous cooperators help more frequently [28,30,77], they stand to gain less from the average encounter. Both behaviours reveal strong preference for the future in our model, and therefore strong cooperative motivation.

Table 1. Pay-offs for the trust game.

		Signaller	
		cooperate	defect
Chooser	accept	$(b, r-c)$	$(-h, r)$
	reject	$(0, 0)$	$(0, 0)$

2. Cooperating with strangers

We model cooperative encounters following a trust game with two roles (adapted from [78]). The game consists in two stages: in the first, the 'Chooser' may either accept the 'Signaller' or reject partnership with that prospective partner, putting an early end to the interaction. Accepted Signallers reap reward r.

Partnership is only advantageous with trustworthy Signallers. In the second stage, the Signaller may cooperate with the Chooser, or opt to defect. Cooperation costs c and benefits the Chooser, who earns b. By contrast, defection is free and harms the Chooser, who loses h. We assume cooperation is net beneficial for Signallers: $r > c$. Pay-offs are summarized in table 1.

When in the role of Chooser, individuals always face a strange Signaller, with whom they have never interacted before, and of whom they possess no privileged information. Choosers may however condition their play on their partner's reputation. Signallers are observed with probability p, and error σ. Individuals form a trustworthy or exploitative image of Signallers based on the most recent observation (figure 1).

Signallers have varying time preferences. We assume that individuals engage in a large number of cooperative interactions throughout their life, and that lifetime pay-offs can be calculated following a discounted utility model [47]. A Signaller's time preference is represented by her discount rate δ: obtaining pay-off π at future time t is worth $(1/(1+\delta))^t \times \pi$ now. δ is positive and fixed at birth, by drawing in the population distribution of discount rates. The closer δ is to zero, the more an individual is future-oriented.

In the electronic supplementary material, we give a full description of the model, and provide a thorough equilibrium analysis. Below we focus on the conditional trust and trustworthiness (CTT) strategy profile, which is defined in relation to a threshold discount rate $\hat{\delta}$, and whereby, throughout their life, (i) Choosers accept strangers given trustworthy reputation, and reject them given exploitative reputation; and (ii) Signallers cooperate when their discount rate is smaller than $\hat{\delta}$, and defect when their discount rate is larger than $\hat{\delta}$. Demonstrations for this strategy profile are detailed in the Material and methods section.

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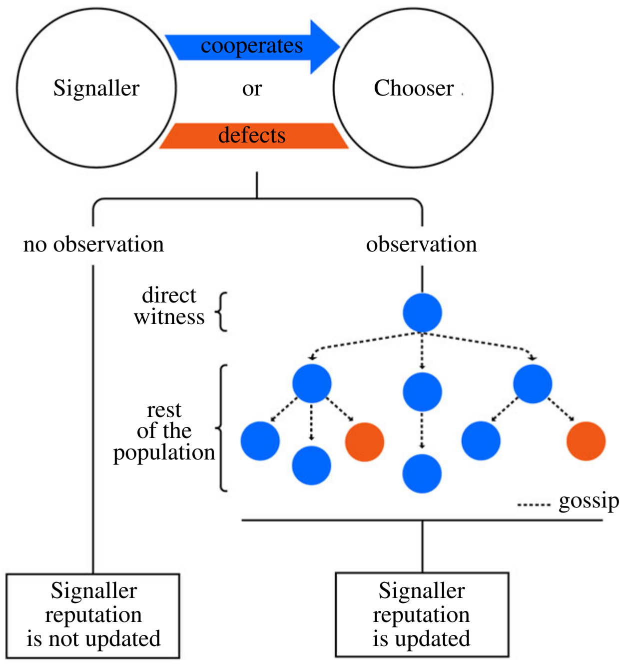

Figure 1. Reputation formation. Signaller behaviour is observed with probability p and error σ by the entire population in our model and $\left(0 < p < 1 \text{ and } 0 < \sigma < \frac{1}{2}\right)$. This may be interpreted to reflect direct observation by one or several witnesses, and rapid social transmission of information (gossip) [34,79,80]. Direct observers mention their observation to several acquaintances, who in turn inform their acquaintances, etc. When this process is rapid relative to social interactions, all individuals receive information by the next trust game. Error σ can thus be seen to reflect the noisiness of social transmission: when a Signaller is observed cooperating, $1-\sigma$ per cent of individuals form a trustworthy image of that Signaller, and σ per cent an exploitative image (and vice-versa with defection). We assume that new information replaces old information, and that individuals never forget. In future trust games, partners of that Signaller may condition their trust on (their private view of) her reputation. (Online version in colour.)

3. Results

(a) Cooperative equilibrium

We show that CTT is an evolutionarily stable strategy (ESS) if and only if [81]:

$$\hat{\delta} = p \times \left[(1-\sigma)\left(\frac{r}{c} - 1\right) - \sigma\frac{r}{c}\right] \tag{3.1}$$

and

$$\frac{\sigma h}{\sigma h + (1-\sigma)b} < \mathbf{P}(\delta < \hat{\delta}) < 1 - \frac{\sigma b}{\sigma b + (1-\sigma)h}. \tag{3.2}$$

Equation (3.1) specifies the strategy profile under study, by specifying the value of the threshold discount rate. Since $\hat{\delta}$ must be positive for cooperation to actually occur, we deduce an upper bound on error σ:

$$\sigma < \frac{(r/c) - 1}{2(r/c) - 1}. \tag{3.3}$$

Cooperation is stabilized by variation of individual time preferences. Following equation (3.2), CTT is an ESS when at least $\sigma h/(\sigma h + (1-\sigma)b)$ per cent of individuals have a discount rate which is smaller than $\hat{\delta}$, and therefore cooperate when in the Signaller role; and at least $\sigma b/(\sigma b + (1-\sigma)h)$ individuals are above that threshold, and therefore defect. Both fractions are positive, increasing functions of error σ: cooperation is evolutionarily stable in our model when behaviour at equilibrium is sufficiently variable [63–67], and error sufficiently small [80].

(b) Who: cooperators are sufficiently future-oriented individuals

At equilibrium, trustworthy Signallers are individuals whose discount rate is inferior to $\hat{\delta}$. When individuals play CTT, Signallers who cooperate pay immediate cost c and increase their chances of facing well-disposed partners in the future, once they have been observed. The value of establishing and maintaining a trustworthy reputation $\hat{\rho}$ depends on the average delay Signallers have to wait before they are observed, which is proportional to $\Delta t = 1/p$, and on the benefit of consistently cooperating instead of defecting after observation, $\hat{\beta} = (1-\sigma)(r-c) - \sigma r$.

We can in fact write: $\hat{\rho} = p[(1-\sigma)(r-c) - \sigma r] = \hat{\beta}/\Delta t$. Since $\sum_{t=1}^{\infty}(1/(1+\delta))^t = 1/\delta$, an individual's social future may be represented by a single trust game whose pay-offs are discounted with rate $1/\delta$. Signallers cooperate at equilibrium if and only if the value they attach to gaining $\hat{\rho}$ their entire future social life exceeds the immediate cost of cooperation c—mathematically, $\delta < \hat{\delta} \Leftrightarrow 1/\delta \times \hat{\rho} > c$. Everything is as if trustworthy Signallers pay c to secure benefit $\hat{\beta}$ in a future trust game which occurs with probability p. (Note that $\hat{\rho}$ tends towards $r-c$ when p tends toward 1 and σ towards 0; when observation is highly faithful and certain, trustworthy Signallers pay c in order to gain approximately $r-c$ their entire future life, with quasi-certainty.)

(c) Where: future-oriented populations have access to a wider range of cooperative opportunities

When average discount rates are low, equation (3.2) is verified for a wide range of possible parameter values, including when $\hat{\delta}$ is small—i.e. when the cost–benefit ratio r/c of cooperation is low, and/or when observation is unlikely (small p) or unreliable (large σ). Even the most demanding forms of cooperation are stable in sufficiently future-oriented populations.

(d) What: cooperation reveals underlying time preferences

Cooperation evolves as a signal of time preferences. At equilibrium, when a Signaller cooperates, she reveals that her discount rate is under $\hat{\delta}$. What's more, cooperation emerges as a signal, and not merely a cue, of Signaller time preferences [82]. Cooperation is selected because it affects Choosers' behaviour: future-oriented Signallers cooperate in order to increase their chances of being trusted in the future, effectively paying c now in order to gain $\hat{\rho} > 0$ their entire future life. By contrast, cooperation cannot evolve in the absence of such an effect. If for instance Choosers accept whatever the information they are presented with, cooperative Signallers do not increase their relative chances of being trusted in the future; in such a case, they would pay c now to gain nothing later.

In addition, the informative value of cooperation increases when $\hat{\delta}$ decreases. When a Signaller helps given small cost–benefit ratio r/c or unlikely observation p, she reveals that her temporal discount rate must be small—and that she could therefore potentially be trusted in a wide array of cooperative interactions.

4. Discussion

In this paper, we have shown that cooperation can be understood as a signal of time preferences, using a formal model. We derived three predictions from our model: (i) future-oriented individuals should be more motivated to cooperate, (ii) future-oriented populations should have access to a wider range of cooperative opportunities, and (iii) cooperators who reveal stronger preference for the future should inspire more trust. These results shed light on the variability of cooperative behaviour and trust.

(a) Environment and cooperation

Results (i) and (ii) help explain why individual and aggregate cooperation are associated with environmental affluence in large representative surveys [6,11,12,16,18], in field studies [2,7,15] and a natural experiment [8]—since people in more privileged circumstances tend to display stronger preferences for the future [48–50,53,73–76] (see also [83]).

Due to adaptive phenotypic plasticity, the environment in which we grow up and live may in fact directly fashion our time preferences; and therefore, fashion our cooperative inclinations [55–57]. Evolutionary models show that it is adaptive to be more present-oriented in adverse circumstances, i.e. when future rewards are uncertain [58,59], or when present needs are pressing [60,61]. Interindividual differences in time preferences and cooperation could thus arise from an adaptive plastic response to one's environment, for either of these reasons. In support of this hypothesis, a recent study finds that present biases partially mediate the relationship between affluence and investment in collective actions [12], while a meta-analytic review finds a negative correlation between early-life stress and self-reported cooperation [14].

It should be noted that the evidence from behavioural experiments is mixed. While some economic games have produced a positive association between affluence and cooperation [2,3,6,11,17,23], other laboratory experiments yield the opposite association [1,4,5,10], or no effect at all [9,13]. The previously mentioned meta-analysis finds no significant overall correlation [14]. In some instances, this discrepancy is attributable to small sample sizes [6,13]. More largely, the generalizability and ecological validity of many laboratory experiments can be questioned; in particular, when only one economic game is performed. Recent studies find that measures derived from a single economic game do not correlate with self-reported cooperation or real-life behaviour, but that a general factor based on several games does [84,85].

(b) Trust depends on revealed time preferences

Result (iii) helps explain why we infer trustworthiness from traits that appear unrelated to cooperation, but happen to predict time preferences. We trust known partners and strangers based on how impulsive we perceive them to be [86,87]; impulsivity being associated with both time preferences and cooperativeness in laboratory experiments [88–93]. Other studies show we infer cooperative motivation from a wide variety of proxies for partner self-control, including indicators of their indulgence in harmless sensual pleasures (for a review see [94]), as well as proxies for environmental affluence [95,96].

Time preferences further offer a parsimonious explanation for why different forms of cooperation inspire more trust than others. When probability of observation p or cost–benefit ratio r/c are small in our model, helpful behaviour reveals large time horizon—and cooperators may be perceived as relatively genuine or disinterested. We derive two different types of conclusion from this principle.

(c) Inconspicuous cooperation

First, time preferences explain why we trust our partners more when they cooperate in an inconspicuous manner (see also [26,29,97,98]). In our model, the average delay cooperators have to wait before help can be profitable varies like $\Delta t = 1/p$. Given smaller probability of observation p, helpful individuals literally reveal they are able to wait for a longer amount of time. By contrast, when immediate rewards are added (e.g. when blood donors are promised payment), help becomes much less informative; and less valuable to the more genuinely prosocial [99].

In particular, only acutely future-oriented individuals will help when observability p is tiny. Their cooperation is akin to a 'message in a bottle': a powerful demonstration of their intrinsic cooperativeness, which, so long as $p \neq 0$, will eventually be received by others. This could explain why some of us cooperate in economic games that are designed to make our help anonymous [100], so long as we assume that anonymity is never absolutely certain (see also [101]).

(d) Spontaneous cooperation

Second, time preferences explain why we trust our partners more when they cooperate spontaneously—when their behaviour appears more natural, unhesitant, intuitive, uncalculating or underlain by emotion [24,25,27,28,30]. Since they help their partners more frequently [28,30,77], including when defection is tempting, more spontaneous cooperators enjoy lower expected pay-offs in the typical encounter (see also [102]). Greater spontaneity could thus indicate willingness to help given smaller values of r/c; and therefore stronger preference for the future.

(e) Time preferences and other partner qualities

Our analysis has fixated on time preferences. This is somewhat arbitrary. Many other characteristics affect our cooperative interests, and are revealed by our social behaviour—underlying costs and benefits [28,78], revelation probability [97], and, when interacting with known associates, specific commitment to the shared relationship [29,62,98,103,104] (this latter dimension is absent in our model). These qualities shape our strategic interests in a given social context: we stand to gain more from cooperation when it involves a partner we know and are committed to; and when it occurs in a social network we value and are embedded in, where we should enjoy higher observability and pay-offs. Yet, context changes fast. We can help a close friend today, and donate anonymously tomorrow.

In contrast to other partner qualities, time preferences appear remarkably stable. Communication of time preferences is likely to be a fundamental element of human cooperation. It may even underlie other facets of our social life. The larger our time horizon, the more likely we are to invest in our social surroundings, via dyadic help as well as collective actions or policing. Contribution to public goods [105] and prosocial punishment [78], which function as signals of cooperative intent, may also rely on communication of time preferences.

5. Material and methods

This section gives a sketch of the evidence regarding the conditional trust and trustworthiness strategy profile, in a simplified setting. For a full description of the model, and a thorough equilibrium analysis, see the electronic supplementary material.

Two types of players engage in a repeated trust game: Choosers and Signallers. In each round, a Chooser faces a Signaller she has never encountered before. She may first accept or reject the Signaller, putting an early end to the interaction. If accepted, the Signaller reaps reward r, and may then cooperate (play action C) or defect (play D). Cooperation involves the Signaller paying cost c for the Chooser to gain b; defection is free, and harms the Chooser, who loses h.

Choosers may condition their strategy on their private view of the Signaller's reputation. Each time a Signaller acts, she is observed with probability p. When a Signaller is observed cooperating, $1-\sigma$ per cent of Choosers receive information $\mathcal{T}$, correctly indicating that the Signaller behaved in a trustworthy manner; and the remaining σ per cent receive information $\mathcal{E}$, falsely indicating exploitative behaviour (and vice-versa with defection). We assume new information replaces old information.

Signallers may condition their strategy on their discount rate δ. To simplify things, we assume here that Signallers play a stationary strategy ('always cooperate', or 'always defect'), and that they are initially certain to be accepted (before the first observation). We relax both these assumptions in the electronic supplementary material, and obtain the same results. δ is fixed at birth, by drawing in a continuous probability distribution which characterizes the Signaller population. Signallers engage in a large number of rounds of the repeated trust game, a pay-off t rounds in the future being discounted by factor $(1/(1+\delta))^t$ now.

According to the conditional trust and trustworthiness (CTT) strategy profile, throughout their life, (i) Choosers accept given trustworthy reputation $\mathcal{T}$, and reject given exploitative reputation $\mathcal{E}$; and (ii) Signallers cooperate if their discount rate is smaller than a certain threshold value $\hat{\delta}$, and defect if their discount rate is larger than $\hat{\delta}$. We show that CTT is an evolutionarily stable strategy (ESS) [81] under the conditions set by equations (3.1)–(3.2), by computing equilibrium and deviation pay-offs for Signallers first, and Choosers second.

(a) Signaller equilibrium pay-offs

We consider a Signaller of discount rate δ. Let Π_C and Π_D be the lifetime discounted pay-off she can expect from playing always cooperate and always defect, respectively. We show that when the value of $\hat{\delta}$ is given by equation (3.1), the Signaller stands to strictly lose from deviation from CTT.

Let us first calculate Π_C. When the Signaller always cooperates, she gains $r-c$ every round she is accepted. She will eventually be observed, from which point she can expect to be accepted $1-\sigma$ per cent of the time in equilibrium, in rounds where she is paired with a Chooser who has (correctly) received information $\mathcal{T}$. In other words, she eventually gains pay-off $\Pi_C^\infty = \sum_{t=0}^{\infty}(1/(1+\delta))^t(1-\sigma)(r-c) = ((1+\delta)/\delta)(1-\sigma)(r-c)$, starting from the point of first observation.

In the initial round however, she is certain to be accepted, and gain $r-c$. Observation affects her pay-offs starting in the next round, which are discounted by factor $1/(1+\delta)$: if she is observed, she gains Π_C^∞ starting the next round, if not, she continues to gain pay-off Π_C. In other words, we have:

$$\Pi_C = r - c + \frac{p \times \Pi_C^\infty + (1-p) \times \Pi_C}{1+\delta}.$$

From which we deduce:

$$\Pi_C = \left(r - c + \frac{p \times \Pi_C^\infty}{1+\delta}\right) \times \frac{1+\delta}{p+\delta}.$$

We can apply an analogous reasoning to calculate Π_D. When the Signaller always defects, she gains r every round she is accepted. After the first observation, the Signaller can expect to be accepted σ per cent of the time, when paired with a Chooser who has (incorrectly) received information $\mathcal{T}$. She eventually gains: $\Pi_D^\infty = \sum_{t=0}^{\infty}(1/(1+\delta))^t \sigma r = ((1+\delta)/\delta)\sigma r$. Starting from the initial round, she therefore gains:

$$\Pi_D = r + \frac{p \times \Pi_D^\infty + (1-p) \times \Pi_D}{1+\delta}.$$

Which yields:

$$\Pi_D = \left(r + \frac{p \times \Pi_D^\infty}{1+\delta}\right) \times \frac{1+\delta}{p+\delta}.$$

By comparing both expressions, we deduce that the Signaller strictly benefits from cooperation if and only if the cost of cooperating now is smaller than the benefit of receiving Π_C^∞ instead of receiving Π_D^∞ in the future, with probability p:

$$\Pi_D < \Pi_C \Leftrightarrow c < p \times \frac{\Pi_C^\infty - \Pi_D^\infty}{1+\delta}.$$

And, by replacing Π_C^∞ and Π_D^∞ by their values, we deduce the logical equivalence:

$$\Pi_D < \Pi_C \Leftrightarrow \delta < p \times \left[(1-\sigma)\left(\frac{r}{c} - 1\right) - \sigma\frac{r}{c}\right].$$

Under condition (3.1), the Signaller therefore always stands to strictly lose from deviation from CTT. If her discount rate δ is smaller than $\hat{\delta}$, she strictly gains on average from cooperating her whole life instead of defecting her whole life; if conversely, $\delta > \hat{\delta}$, she strictly benefits from defecting. Note that CTT does not prescribe behaviour for the Signaller when her discount rate is precisely equal to the threshold. Here, we neglect this possibility, based on the fact that the population distribution of discount rates is continuous (we come back to this in the electronic supplementary material).

(b) Chooser equilibrium pay-offs

We show that in equilibrium, Choosers stand to strictly lose from deviation from CTT when equation (3.2) is verified. Let us first consider a Chooser faced with information $\mathcal{T}$. If the Chooser rejects the Signaller, she gains nothing; if she accepts, she gains b if the Signaller plays C and loses h if the Signaller plays D. Her expected benefit is then equal to: $\mathbf{P}(C|\mathcal{T}) \times b + \mathbf{P}(D|\mathcal{T}) \times (-h) = \mathbf{P}(C|\mathcal{T})(b+h) - h$. Accepting given $\mathcal{T}$ is therefore strictly beneficial iff:

$$\mathbf{P}(C|\mathcal{T}) > \frac{h}{b+h}.$$

Let $\tau = \mathbf{P}(C) = \mathbf{P}(\delta < \hat{\delta})$ be the equilibrium probability that the Signaller is trustworthy. Following Bayes' rule, $\mathbf{P}(C|\mathcal{T}) = \mathbf{P}(\mathcal{T}|C)/\mathbf{P}(\mathcal{T}) \times \tau$. The above inequality can be rewritten as:

$$\frac{1-\sigma}{\tau(1-\sigma)+(1-\tau)\sigma} \times \tau > \frac{h}{b+h}.$$

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This is equivalent to:

$$\tau > \frac{\sigma h}{\sigma h + (1 - \sigma) b}. \tag{5.1}$$

Let us now consider a Chooser faced with information $\mathcal{E}$. An analogous calculation shows that rejecting given $\mathcal{E}$ is strictly beneficial iff:

$$\mathbf{P}(C|\mathcal{E}) < \frac{h}{b + h}$$

Using Bayes' rule, we find: $\mathbf{P}(C|\mathcal{E}) = \mathbf{P}(\mathcal{E}|C)/\mathbf{P}(\mathcal{E}) \times \tau = \sigma/(\tau\sigma + (1 - \tau)(1 - \sigma)) \times \tau$. By replacing in the above inequality, we deduce that rejection given $\mathcal{E}$ is strictly beneficial iff:

$$\tau < 1 - \frac{\sigma b}{\sigma b + (1 - \sigma) h}. \tag{5.2}$$

Combining equations (5.1) and (5.2), and using $\tau = \mathbf{P}(\delta < \hat{\delta})$, we deduce equation (3.2). Under that condition, Choosers therefore stand to strictly lose from deviation from CTT. We deduce that CTT is an ESS under the conditions set by equations (3.1) and (3.2): any mutant is strictly counter-selected. We show in the electronic supplementary material that we in fact have an equivalence; CTT is an ESS if and only if both equations are verified.

Data accessibility. The data are provided in electronic supplementary material [106].

Authors' contributions. J.L.-P.: conceptualization, investigation, methodology, validation, writing—original draft, writing—review and editing; J.-B.A.: conceptualization, methodology, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This study was supported by the EUR FrontCog grant no. ANR-17-EURE-0017 and funding from the EURIP Graduate School for Interdisciplinary Research.

Acknowledgements. We thank an anonymous reviewer, Pat Barclay, Léo Fitouchi and Moshe Hoffman for their insightful feedback, and Clara Lie for her graphic prowess.

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