



SUBJECT AREAS:

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# Meeting now suggests we will meet again: Implications for debates on the evolution of cooperation

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21 November 2012Accepted  
16 April 2013Published  
29 April 2013Correspondence and  
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Humans are often generous, even towards strangers encountered by chance and even in the absence of any explicit information suggesting they will meet again. Because game theoretic analyses typically conclude that a psychology designed for direct reciprocity should defect in such situations, many have concluded that alternative explanations for human generosity—explanations beyond direct reciprocity—are necessary. However, human cooperation evolved within a material and informational ecology: Simply adding consideration of one minimal ecological relationship to the analysis of reciprocity brings theory and observation closer together, indicating that ecology-free analyses of cooperation can be fragile. Using simulations, we show that the autocorrelation of an individual's location over time means that even a chance encounter with an individual predicts an increased probability of a future encounter with that same individual. We discuss how a psychology designed for such an ecology may be expected to often cooperate even in apparently one-shot situations.

Cooperation in humans is ubiquitous, richly variable in form, and complex in organization. We cooperate in an enormous range of endeavors with both kin and non-kin, exchange a wide range of goods and activities, and even cooperate in large, flexible groups of overlapping membership. These facts have led to an intense debate over whether human cooperation emerges from the same selective dynamics that are widely believed to have produced cooperation in most other species<sup>1–3</sup> (e.g., kin selection, reciprocation), or whether qualitatively different selective dynamics are needed to explain human sociality<sup>4–6</sup>.

Much of the motivation for abandoning traditional explanations has centered on the empirical results of experimental economic games, played both among undergraduates in developed nations and among members of small-scale populations<sup>7–13</sup>. By design, these games are often anonymous and one-shot: Players never learn who their co-players are and play the game just once. Although there would appear to be no way to benefit from cooperative strategies in such one-shot games, many players nonetheless choose to be generous—e.g., by cooperating in a one-shot prisoners' dilemma or allocating money to a co-player when the player could have kept it all<sup>4,6,14–16</sup>. These findings have, in part, led many researchers to conclude that higher-order forms of selection are necessary to explain human cooperation, such as cultural or genetic group selection or gene–culture coevolution<sup>5,17–23</sup>. These researchers typically make the critical assumption that the design of these experiments rule out traditional explanations for cooperation: Proponents of this view maintain that theories invoking reciprocity<sup>2,24–27</sup> cannot explain such results because the interactions are stipulated to never repeat; that theories invoking reputation<sup>28</sup> cannot explain the results because anonymity precludes anyone learning of a player's behavior; and that theories invoking kin selection<sup>3,29</sup> cannot explain the results, because interactants are not genetic kin. With these explanations apparently ruled out, it seems logical to conclude that some other evolutionary dynamic must be at work.

However, this line of argument suffers from a serious flaw: direct reciprocity and kin selection are general models of selection pressures, not theories of the phenotypic designs that these selection pressures construct independent of circumstances. The ways that selection pressures impact the design of organisms' minds and bodies necessarily depends on the material and informational structure of the environments in which a particular species evolved and is therefore designed to operate within. To generate a model of an organism's phenotypic design, general theories of selection must be combined with data on the idiosyncratic material and informational structure of a species' environment.

For example, for kin selection models to work<sup>3</sup>, organisms must cause assistance to be delivered to genetic relatives, suggesting that evolved systems of kin detection should accompany systems of kin assistance. Indeed,



many species, such as humans, have cognitive mechanisms for identifying probable genetic relatives for use in regulating cooperative and mating behavior<sup>30–32</sup>. However, while kin selection applies broadly, kin detection mechanisms are selected only when material and informational ecologies have a particular form. Other ecologies, and hence other psychologies, are possible. Consider a hypothetical species of wasp where females lay their eggs inside figs. Females mate only once and only lay eggs in figs untouched by other females. In this case, a newborn wasp will meet only full siblings; it does not need any psychological mechanisms that allow it to distinguish kin from non-kin within the fig. This hypothetical wasp's perinatal environment has a structure that does not require kin detection mechanisms—even if kin selection were an active selective dynamic<sup>33</sup>. Selection will set a default level of altruism inside the fig, without the wasp needing to possess kin detection mechanisms.

It is similarly necessary to consider the ancestral material and informational ecology to predict how selective dynamics would have shaped the human cooperative architecture. Given the social and natural ecology that humans actually evolved in, would theories like direct reciprocity suffice to create a psychology that cooperates to some extent in games that seem one-shot, or would higher-order selection in fact be necessary?

As has been discussed by other authors<sup>10</sup>, multiple features of the ecology faced by ancestral humans suggest that selection for direct reciprocity might create psychologies willing to cooperate even in (likely rare) anonymous and one-shot conditions. One important feature is that social interactions in the real world (both ancestral and present day) involve a high degree of uncertainty. First, there is uncertainty over relative valuation, as valuations in both present and ancestral real world environments are often implicit and heterogeneous across individuals. For example, one party may misestimate the value another party places upon a resource with drastic strategic consequences: If I underestimate the value of a resource to you, I may take it and unintentionally incur your wrath<sup>34</sup>. Although the stakes in experimental games are often explicit with clear monetary values attached, the relative value between individuals can still be ambiguous; a player in need may place a greater internal valuation on a given stake than others do. Second, there is uncertainty over the spread of reputation. In experimental games, experimenters often go to great lengths to (i) ensure that subjects' behavior will be kept confidential, and (ii) communicate this fact to subjects<sup>35</sup>. In contrast, in the real world, both now and ancestrally, situations hardly, if ever, contain such certainty—there is always a chance of being observed by agents whose presence is undetected. Indeed, even highly controlled experimental games may have residual uncertainty: Although assurances from an experimenter might be strong predictors of anonymity, other cues, such as knowledge that other players are community members, point in the opposite direction<sup>36</sup>. Third, there is uncertainty over a relationship's time horizon. In experimental games, situations are often structured so as to occur only once before the experiment is concluded, and in concert with the anonymity this fact should preclude any future consequences from game behavior. In contrast, in the real world the future of nearly every interaction is uncertain and, because of this, analytic and simulation results show that selection favors decision rules that are generous even in apparently one-shot encounters<sup>1</sup>.

Although many features of ancestral human ecology, in concert with selection pressures for direct reciprocity, might create psychologies willing to cooperate in anonymous and one-shot conditions, here we focus on a single, simple feature: encountering someone now probabilistically predicts encountering that person again. Indeed, the only event that uniquely precludes the possibility of future interactions is the death of one of the interactants. Aside from this case, the probability of future encounter may be decidedly greater than zero.

Why might encounter probabilistically predict re-encounter? The world is a complex causal system, and whatever causal forces went

into encountering a particular individual, to the extent that these forces persist over time, they are more likely than chance to cause re-encounter<sup>37</sup>. For example, the world is large relative to an individual's ability to navigate within it, especially under ancestral conditions without modern transportation technology. Thus, an individual's location will be autocorrelated over time. That two individuals are in the same place at the same time—conditions necessary for encounter—suggests that they have a higher than baseline chance of a future encounter based merely on the autocorrelation of location.

A large literature explores the effects of spatiality (or viscosity) on the evolutionary dynamics of cooperative strategies. Viscosity, for example, in the dispersal of offspring can lead to designs for cooperation gaining a larger share of the benefits of cooperation than in other environments (but at the same time can lead to greater competition among kin for access to local resources)<sup>38–40</sup>. As in the wasp example, viscosity may also relax selection on kin detection leading to less discriminant cooperation, but can also expose patches of cooperators to roving exploiters<sup>41</sup>. Yet, one facet of a spatially viscous ecology that has gone relatively unexplored is the impact of spatial viscosity on re-encounter rates. In other words, while viscosity limits the dispersal of genes in a spatial environment, raising genetic assortment, it also limits the dispersal of agents in a social environment, potentially raising re-encounter rates.

When environments are structured such that encounter predicts re-encounter, natural selection might favor phenotypic designs that act as if conspecifics encountered now will be re-encountered. To the extent that the human mind is designed to act as if it expected repeated interactions, humans will be more cooperative in apparently one-shot or short-term interactions than a retrospective or omniscient analysis would predict. Game theoretic analyses show that if an interaction is one-shot or has a clear, finite endpoint then the payoff-maximizing behavior is to defect. But real minds necessarily have access to only limited and imperfect information—it is impossible to know for certain whether an interaction will be one-shot or will repeat indefinitely into the future. Thus, although some cues in a current interaction might suggest it is one-shot (e.g., the interactants are strangers), if encountering someone now predicts encountering them again, selection might create cooperative psychologies that expect this correlation. Such an expectation will lead to greater default levels of cooperation. Moreover, the strength of this expectation—and thus default levels of cooperation—should increase in proportion to the strength of the correlation between encountering someone now and encountering them again.

It is critical to note that such expectations are not necessarily conscious or articulable; instead, they might be implicit in the design of the mechanisms that generate cooperative decisions. This is analogous to human color constancy mechanisms: The visual system expects a certain spectrum of wavelengths as produced by long-enduring celestial and terrestrial light sources. This expectation is, of course, not conscious or articulable. Moreover, it can be fooled by anomalous, modern experiences, such as artificial lighting in a night-time parking lot giving rise to the illusion that a yellow car is blue<sup>42</sup>. Analytic and simulation studies of the evolution of reciprocity show that selection can build extremely strong implicit expectations of repeat encounters. Such expectations can cause high levels of cooperation even in situations where agents have explicit, articulable beliefs that an interaction is one-shot<sup>1</sup>. In other words, people might have reportable beliefs that an interaction is one-shot but, because of the expectations embodied in their evolved cooperative psychology, they cooperate nonetheless.

Our goal here is to use simulations to explore how the spatial structure of ancestral ecologies affects whether people will re-encounter each other. While human life is intricately complex, in these simulations we include only the most basic of assumptions—that the world has spatial extent, that agents can move within it, that agents encounter each other when they are nearby—so that our



results are as generalizable as possible. It is impossible to believe the world of our ancestors lacked these minimal features. We conducted a series of 8,250 simulations to determine whether—under these minimal assumptions—encountering someone now predicts encountering them in the future. We also test the degree to which this relationship is dependent upon quantitative features of the social ecology. (Simulations were written in Java by author M.M.K., and checked for errors by author A.W.D. Source code is available upon request to author M.M.K.) In these simulations a population of agents was allowed to randomly navigate a simulated world; throughout, the simulation recorded which other agents they encountered along the way.

## Results

**Simulation details.** To parameterize our simulated environment, we consulted the average living conditions of traditionally living populations reported by Marlowe<sup>43</sup>. Marlowe reports the averages of two samples: the average population density across all surveyed groups was .25 persons/km<sup>2</sup> with an average local group area of approximately 1600 km<sup>2</sup>; for the subset warm climate non-equestrian sample—thought by Marlowe to better represent ancestral conditions—the average population density was .31 persons/km<sup>2</sup> with an average local group area of approximately 500 km<sup>2</sup>. To approximate this range of conditions, we simulated populations of 125, 250 and 500 agents. Assuming the 1600 km<sup>2</sup> living area of the full sample, this yields a population density ranging from .08–.31 persons/km<sup>2</sup>, enclosing the mean of the full sample (.25); assuming the 500 km<sup>2</sup> living area of the ancestrally representative sample, this yields a population density ranging from .25–1.0 persons/km<sup>2</sup>, enclosing the mean of the ancestrally representative sample (.31). As illustrated by Table 1, population size contributed to approximately 0.00% of the variance in re-encounter rate, suggesting that differences in population density within even a range this large are relatively unimportant.

In each simulation run  $n \in \{125, 250, 500\}$  agents were each randomly assigned a location within a two-dimensional space with sides 1 arbitrary unit long. How this space maps onto real area depends on assumptions that cannot be known with certainty. As described in the previous paragraph, this space could be viewed as 1600 km<sup>2</sup> or 500 km<sup>2</sup>; either way the population densities within this space represent reasonable values for small-scale societies. To test for the existence of edge-effects, this space was sampled twice: once with hard edges which constrained agents' movements (agents' movements perpendicular to an encountered edge were truncated at the edge), and once without edges such that space wrapped seamlessly from top-to-bottom and left-to-right. On each of 500 time steps these agents moved by drawing a random distance from a normal distribution with mean of 0 and a standard deviation  $d \in \{.01, .02, .03, .04, .05\}$ , and a random angle  $\theta \sim U(0, 360)$ . If the distance drawn was negative, the agent moved in the direction opposite to the drawn angle. Assuming the population density of Marlowe's<sup>43</sup> full sample, these walking distance parameter values represent an average

movement between 0.17 km (for  $n = 125$  &  $d = .01$ ) and 1.78 km (for  $n = 500$  &  $d = .05$ ) every time step (and movements larger than 0.44 km and 4.47 km, respectively, 4.6% of the time). These movements could be thought of as frequent, periodic foraging trips, or other less frequent transitions; as illustrated by Fig 1, the rates of encounter and re-encounter are extremely stable over all but the final time steps in a simulation run. This suggests that our choice of 500 time steps had little impact on the qualitative effects in our simulation. Indeed, a greater number of time steps would have only strengthened our effect, increasing the likelihood that a person encountered now will be encountered later. Moreover, a much smaller number of time steps would be unrealistic: On almost any interpretation of what a time step represents, several hundred over the course of a forager's lifespan would be likely. Finally, the number of time steps per run was chosen to give an adequate sampling without introducing the computational burden of simulating longer, yet informationally redundant runs, allowing easier direct replicability by other researchers.

At each time step, for each agent, the program evaluated if another agent was within a defined meeting radius  $r \in \{.005, .01, .015, .02, .025\}$ ; if so, the program recorded that the two agents met during this time step. Assuming the average ecology of Marlowe's<sup>43</sup> sample, these meeting radius parameter values represent a range between 0.11 km (for  $n = 125$  &  $r = .005$ ) and 1.12 km (for  $n = 500$  &  $r = .025$ ) wherein agents would be considered encountered.

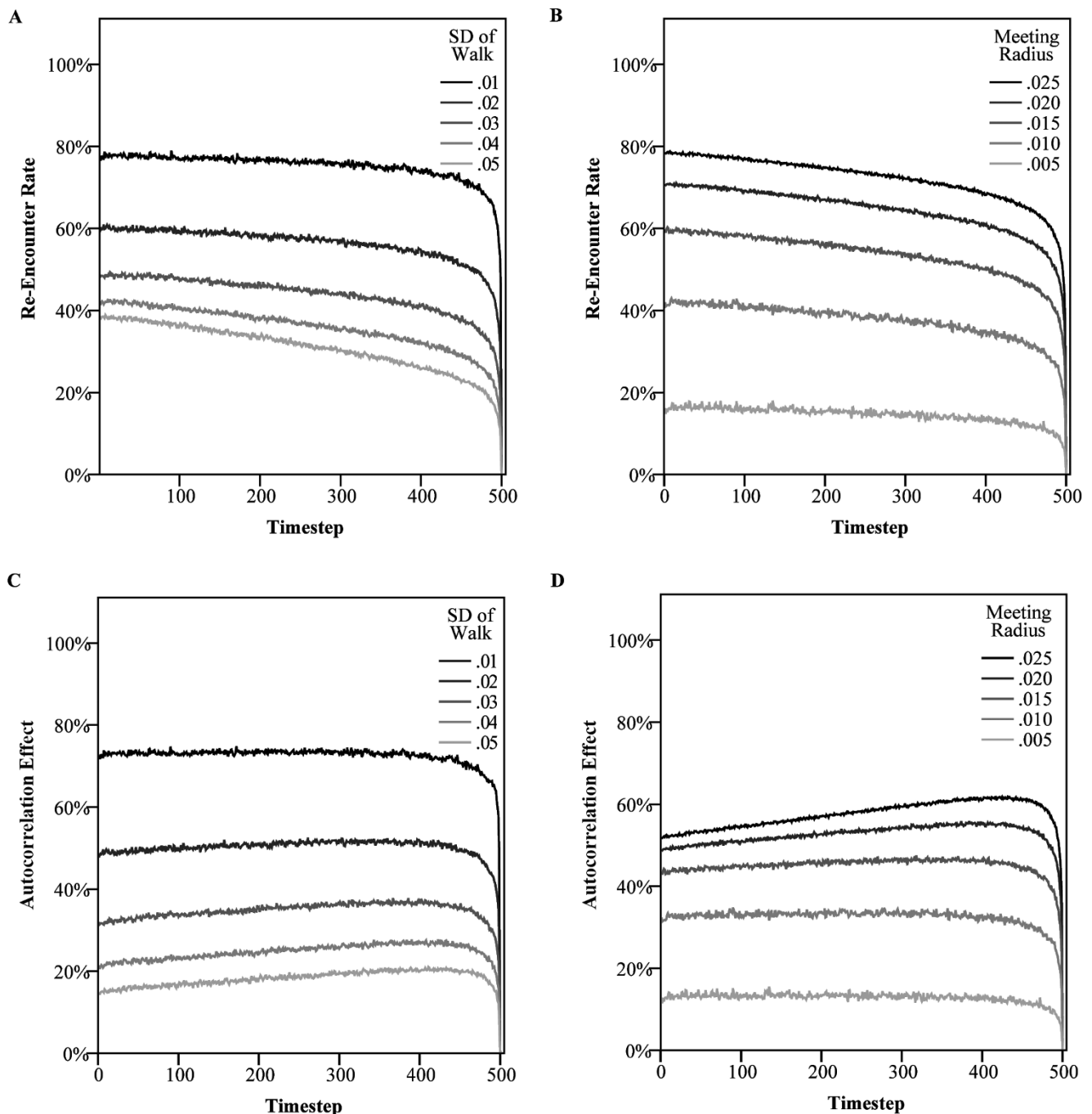
After a run was completed, we computed for each time step: (1) The average re-encounter rate: For each agent, we computed the proportion of other agents encountered during that time step who were re-encountered in the future; these values were then averaged across agents. (2) The average encounter base rate: For each agent, we computed the proportion of all other agents (regardless of whether they met this time step) who were encountered in any future time step; these values were then averaged across agents. The re-encounter rate is a conditional probability: Given that two agents are meeting in this time step, it is the probability they will meet in a future time step. The encounter base rate quantifies, irrespective of any additional information during this time step, the probability that two agents will meet in a future time step. The difference of these two values gives the "autocorrelation effect": the marginal increase in the probability of future encounter given present encounter in a spatial world. Randomness—-independent of any effects of spatiality—can cause agents to encounter each other in the future. Computing the autocorrelation effect allows us to quantify how spatiality affects re-encounter rates.

The strength of the autocorrelation effect depends on the extent to which spatiality affects agents' social interactions; this is manipulated across simulations by the walking distance and meeting radius parameters. Increasing walking distance should lead to a smaller autocorrelation effect. To see this, consider what happens if the walking distance approaches infinity. If so, then the probability of two agents meeting now is unaffected by where they were located previously; this would imply that a person is just as likely to encounter someone

**Table 1 | GLM of Re-Encounter Rate**

| Source                | SS       | df   | MS    | F          | p     | $\eta^2$    |
|-----------------------|----------|------|-------|------------|-------|-------------|
| Model                 | 2279.15  | 150  | 15.19 | 201163.67  | <.001 |             |
| Walking Distance      | 188.61   | 4    | 47.15 | 624284.26  | <.001 | 0.083       |
| Meeting Radius        | 316.18   | 4    | 79.04 | 1046505.98 | <.001 | 0.139       |
| Population Size       | 1.06     | 2    | 0.53  | 7037.91    | <.001 | 0.000       |
| Edges State           | 4.61     | 1    | 4.61  | 61058.46   | <.001 | 0.002       |
| All 2- & 3- way inxns | —        | —    | —     | —          | —     | <.007 total |
| Error                 | 278.39   | 7350 | 0.00  |            |       |             |
| Total                 | 23069.90 | 7500 |       |            |       |             |

Note. "Edges State" refers to whether a given simulation had hard edges that stopped movement or whether edges wrapped around. "Inxns" = interactions.



**Figure 1** | (A) Average re-encounter rate over lifetime graphed by standard deviation of walking distance & averaged over meeting radius. (B) Average re-encounter rate over lifetime graphed by meeting radius & averaged over standard deviation of walking distance. Meeting someone now predicts meeting them again: Average re-encounter rates are high for all cases but the smallest meeting radius and at the very ends of organisms' lives. (C) Average autocorrelation effect (re-encounter rate less the encounter base rate) over lifetime graphed by standard deviation of walking distance & averaged over meeting radius. (D) Average autocorrelation effect (re-encounter rate less the encounter base rate) over lifetime graphed by meeting radius & averaged over standard deviation of walking distance. Meeting someone now predicts meeting them again, over and above the base rate of meeting them in the future: Effects are high at all but the largest walking distances and smallest meeting radii and at the very ends of organisms' lives.

living kilometers away as they are to encounter their next-door neighbor. Although there will be re-encounters in this case—you might randomly meet your neighbor or the distant person again—spatiality per se would have no effect on the rates of re-encounter.

Decreasing meeting radius should also lead to a smaller autocorrelation effect. Consider what happens as the meeting radius approaches zero: It will be almost impossible to ever meet anyone, pushing re-encounter rates and base rates of encounter to zero; when

both rates take the same value (viz., zero), there is no autocorrelation effect. At the limit of infinitely small meeting radius people would not meet or interact with others standing next to them. (We only studied values for meeting radius that were relatively small compared to the total size of the population's range. If the meeting radius was large, encompassing most of the range, we would also expect no autocorrelation effect. In this case, however, both re-encounter rate and encounter based rates would be very high. This would occur because





Table 2 | GLM of the Autocorrelation Effect

| Source                | SS      | df   | MS    | F         | p     | $\eta^2$    |
|-----------------------|---------|------|-------|-----------|-------|-------------|
| Model                 | 1705.42 | 150  | 11.37 | 142267.57 | <.001 |             |
| Walking Distance      | 283.02  | 4    | 70.75 | 885355.44 | <.001 | 0.166       |
| Meeting Radius        | 191.59  | 4    | 47.90 | 599342.07 | <.001 | 0.112       |
| Population Size       | 1.06    | 2    | 0.53  | 6643.21   | <.001 | 0.001       |
| Edges State           | 7.32    | 1    | 7.32  | 91596.45  | <.001 | 0.004       |
| All 2- & 3- way inxns | —       | —    | —     | —         | —     | <.014 total |
| Error                 | 0.59    | 7350 | 0     |           |       |             |
| Total                 | 1706.01 | 7500 |       |           |       |             |

Note. "Edges State" refers to whether a given simulation had hard edges that stopped movement or whether edges wrapped around. "Inxns" = interactions.

all agents would constantly be encountering every other agent. Thus, over a very broad range the relationship between meeting radius and the autocorrelation effect would be an inverse U-shape.)

Fifty runs were completed at each combination of  $n$ ,  $d$ ,  $r$  and edges state yielding 7500 runs. These aggregated re-encounter rates and their margins over baseline (the autocorrelation effect) were analyzed in a general linear model (GLM) framework to produce estimates of effect size (Tabs. 1 and 2). An additional 50 runs were completed at each combination of  $n$  &  $r$  such that each agent's location was completely random in the current time step relative to its location in the previous time step (totaling 750 additional simulation runs). This models the null case of a world without autocorrelation of location over time and was accomplished by setting  $d = 1$  (effectively,  $d$  approached infinity in these runs).

**Findings.** Our analysis makes two related claims. First, given even the most minimal assumptions, encountering someone now should predict encountering them again. This is measured by re-encounter rate. Selection can use the quantitative level of this rate to set default levels of cooperation. Second, the re-encounter rate should be partially a function of how spatiality affects social encounters. This is measured as the autocorrelation effect (the re-encounter rate minus the base rate of encounter).

Were individuals encountered in the present likely to be encountered again in the future? Yes, re-encounter rates were sizeable: As depicted in Fig. 1, across the range of both walking distance (Fig. 1a) and meeting radius (Fig. 1b) agents encountered on a given time step were often re-encountered. For instance, at the median walking distance ( $d = .03$ ), encountering someone now meant there was approximately a 50% chance of meeting them again within the arbitrary time frame. Similarly, at the median meeting radius ( $r = .015$ ), encountering someone now meant there was approximately a 60% chance of meeting them again. As such, and given an ecology where cooperation yielded gains in trade, an agent could profit from a design expressing the default expectation that those she encountered may be encountered again and were potentially profitable cooperation partners. Holding parameters constant, re-encounter rate was highly stable across much of an agent's life, only falling off around the final few time steps. Considering the GLM estimates for re-encounter rate, shorter distances walked lead to higher re-encounter rates, and walking distance accounted for 8.3% of all variance in re-encounter rates (Table 1). Larger meeting radii lead to higher re-encounter rates, and meeting radius accounted for 13.9% of all variance in re-encounter rates.

Although raw re-encounter rates are the ecological value that should be used by selection in designing cooperative psychology, our analysis predicts that re-encounter rates will be affected by how spatiality affects sociality. Was the spatiality of social interactions important in setting raw re-encounter rates? Yes, this can be seen in autocorrelation effects. As depicted in Figs. 1c,d and Fig. 2, the marginal increase in future encounter was substantial. For instance, at the median walking distance ( $d = .03$ ), the

autocorrelation effect increased the probability of future encounter given present encounter by a margin of over 30%. Similarly, at the median meeting radius ( $r = .015$ ), the autocorrelation effect increased the probability of future encounter given present encounter by a margin of over 40%.

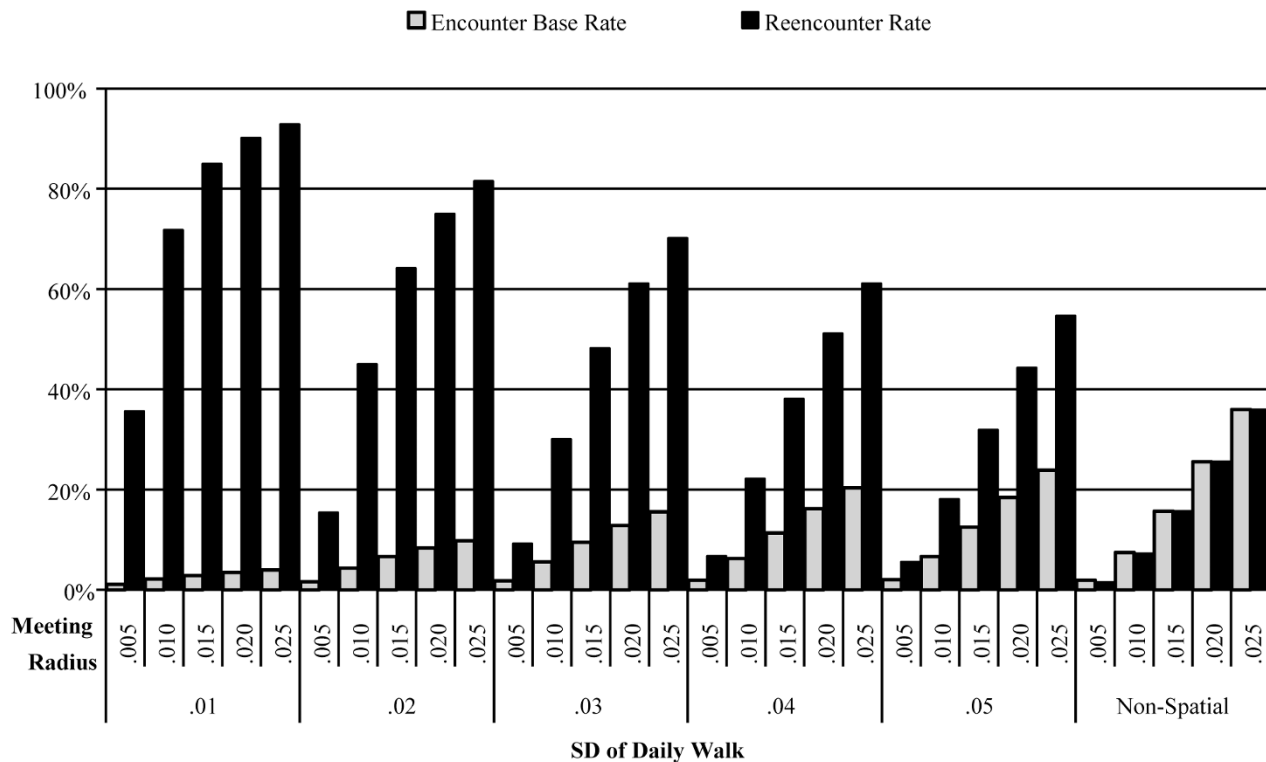
To illustrate the effect of spatiality and autocorrelation on determining re-encounter rates, Fig. 2 graphs the base rates of encounter and the re-encounter rates separately. This figure reveals the generally large differences between these two measures, and therefore the generally large effect of autocorrelation in location on re-encounter rate. As expected, this autocorrelation effect diminished as walking distance increased, eventually being eliminated once agents walked so far that the locations were no longer autocorrelated ( $d = 1$ , non-spatial baseline); see right-most columns in Fig. 2. Note that when locations were no longer autocorrelated raw re-encounter rates were still sometimes sizeable. Nonetheless, they were no different than encounter base rates, showing that autocorrelation was not the cause of these high re-encounter rates. Walking distance accounted for 16.6% of the variance in the autocorrelation effect (Table 2).

Also as expected, within each walking distance lower values of the meeting radius led to a smaller autocorrelation effect; see Fig. 2. Although we did not conduct simulations analogous to the walking distance case where autocorrelation is entirely removed, reflection can illustrate this for meeting radius. Imagine that meeting radius is reduced to zero. Agents never meet any other agents, necessarily eliminating the differences between re-encounter rates and encounter base rates, as both are zero. Meeting radius accounted for 11.2% of the variance in the autocorrelation effect (Table 2).

There was also a small recency effect observed most in large walking distances and large meeting radii, which can be seen in the upward trending slopes before the end of life declines in Figs 1c & 1d. The autocorrelation effect reached a maximum for recent time steps and dissipated as the encounter faded back into the past. Finally, we note that there was little effect of whether edges stopped movement or whether edges wrapped seamlessly (see Tables 1 and 2).

## Discussion

The simulation presented here rests on extremely plausible, extremely minimal assumptions: If the world has spatial extent, is large relative to agents' ability to navigate in it, and an agent's time horizon extends beyond the immediate present, then merely encountering an agent once predicts a higher chance of encountering them again. These minimal assumptions were almost certainly true throughout human evolution. This suggests that natural selection will have calibrated our cooperative psychology in light of these realities. It is exceedingly simple for natural selection to exploit this environmental regularity to improve the performance of the cooperative architecture: in the absence of other information suggesting whether there will or will not be future interactions with an interaction partner, have a default expectation that re-encounter was the ancestral average<sup>1</sup>. These results obtain even when no organismal or environmental structure otherwise correlates agents' movements.



**Figure 2 | Lifetime average re-encounter rate and encounter base rate for the parameter space.** The larger the social world is relative to the organism's ability to navigate within it, the more re-encounter rate exceeds the encounter base rate and thus the greater the effect of autocorrelation. In a non-spatial world—or a world an organism can circumnavigate daily—the effect of autocorrelation on re-encounter disappears.

Yet in reality, both organism and environmental structure would strongly have correlated agents' movements, thus greatly amplifying the degree to which an encounter predicted re-encounter compared to the minimal case where agents are moving randomly. That is, unconnected foragers would have shared many of the same goals in the same local environment (e.g., different individuals frequently visited the same sources of food, water, shelter, refuge, mates). Any such structure, such as a common attractant like a stable resource patch or repellent like a stable environmental hazard, by systematically causing agents to cluster at or disperse from a particular location, would serve to increase the rate of re-encounter.

For a species like humans where individuals possess specialized knowledge and skills such that the gains in trade from cooperation are often large, these results imply that—in order to cultivate such valuable relationships—the mind should be designed to assume by default that the probability of a repeat interaction with a newly encountered stranger is far greater than zero. Note that this reasoning does not predict that a default cooperative psychology should be common among species; we may share a spatial ecology with other species on the planet, but it is this ecological fact in concert with the possibility of large benefits through cooperation that can select for such a psychology. Delton et al.<sup>1</sup> find that, under reasonable parameterization, cooperation in uncertain one-shot circumstances evolves only when the *average* gains in trade from cooperation are larger than two or three times the cost. While this is a low hurdle for particular instances of cooperation, it is hard to see how this could characterize the interactions of non-human animals on average throughout their lives.

Although we argue that re-encounter rate creates psychologies that (probably implicitly) assume or act as if interactions will be repeated, we are not arguing that this implies humans should always cooperate or be generous. In making any cooperative decision, the mind should integrate a number of situational cues along with any default assumptions. Some cues may make cooperation more likely:

For instance, in laboratory samples of economic games, subjects in the experiments are often of similar age, attending the same school if not the same classes; in anthropological samples, subjects are often all members of the same face-to-face communities. In contrast, other cues may make cooperation less likely, such as a past history of aggressive interaction.

To be clear, these simulations suggest that selection acting on the human cooperative architecture might have had two different, related effects on its design. First, the evolutionary long-run degree to which one encounter predicted repeat encounters would have made the architecture's default probability of cooperating higher than previously appreciated. Second, the architecture might have been selected to include detection systems to monitor within-lifespan local parameters that provide cues to the degree to which one encounter predicts another. This would suggest that greater autocorrelation in location (less travel) should increase cooperativeness.

More importantly, this work is simply a modest illustration of how theories of cooperation (and any other psychological adaptation) need to be fleshed out by taking explicit account of the local material and informational ecologies. That such a minor factor as location autocorrelation can potentially shift best-bet reciprocity responses suggests that when all relevant features of the world are taken into account, an efficient reciprocity-exchange architecture might look very different than how it is usually conceived.

Beyond evidence that humans often cooperate in one-shot and anonymous interactions, stable cross-cultural differences in cooperative behaviors have also been advanced to support cultural group selection and gene-culture co-evolutionary theories of human cooperation<sup>6,44</sup>. These proposals argue, not implausibly, that differential rates of cooperative behaviors across societies are due to these societies having different cultural norms and institutions. But although viable, a cultural explanation is not the only possible explanation. An alternative explanation would be that the same universal evolved cooperative architecture is designed to be calibrated by the detection



of local magnitudes of ecological factors that affected the payoffs of cooperative relationships ancestrally. For example, stable differences in the numbers of social partners and kin present in the vicinity are plausible input parameters to facultative mechanisms for cooperativeness and generosity—factors that themselves might be partial functions of the degree of autocorrelation in location. That is, what are commonly interpreted as “cultural differences” may turn out to be outputs produced by ecological and demographic inputs to our evolved psychology. In support of this view, recent research suggests that variance comparable to that found between cultures can also be found among communities of a single culture—communities that share the same norms and institutions<sup>7</sup>. If different locations in the same culture present the same variability as different cultures do, this implies that noncultural factors could be responsible for between culture variability as well.

Mathematical and simulation work also provides alternative explanations for cross-cultural differences, explanations that do not rely on higher-order levels of selection. Delton et al.<sup>1</sup> show that cooperation, even in apparent one-shot encounters, increases as the gains in trade from cooperation increase. Although humans, compared to other species, have flourished by finding and exploiting possible gains in trade, modern societies have unlocked enormous gains in trade not possible in small-scale, face-to-face societies. On this view, it is not surprising that behaviors like cooperation and generosity are observed at higher rates in societies with (e.g.) more market integration<sup>44</sup>. To be clear, what is at issue is not whether humans have developed novel institutions and cultural practices that make modern life possible. What is at issue is why human cooperation and generosity exist and vary as they do. We suggest that human cooperation and generosity are not an accident of birth, a lucky draw in a lottery of cultural milieus. Instead, they are facultative elements in a universal human nature.

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## Acknowledgments

This research was made possible by an NIH Director’s Pioneer Award to L.C., NSF grant #0951597 to L.C. and J.T., and a grant from the John Templeton Foundation. The opinions expressed in this publication are those of the authors and do not necessarily reflect the views of the John Templeton Foundation.

## Author contributions

M.M.K. and A.W.D. developed and analyzed the simulations. All authors contributed to theoretical development, discussion, and writing of the paper.

## Additional information

**Competing financial interests:** The authors declare no competing financial interests.



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**How to cite this article:** Krasnow, M.M., Delton, A.W., Tooby, J. & Cosmides, L. Meeting now suggests we will meet again: Implications for debates on the evolution of cooperation. *Sci. Rep.* 3, 1747; DOI:10.1038/srep01747 (2013).