Comment by Delton et al. is on following page.

LETTER

Flexible strategies, forgiveness, and the evolution of generosity in one-shot encounters

By using agent-based simulations, Delton and colleagues (1) suggested in PNAS that cooperation by humans in one-shot interactions could have evolved as a byproduct of selection for reciprocity when it is uncertain if interactions will be repeated. We believe their work should be commended both for the novelty of the hypothesis proposed and the explicit cognitive framework in which the model is posed, providing new insight into an important interdisciplinary problem. However, as a result of the authors' focus on decision-making in the first round of interaction, the possibility of subsequent strategy updating is ignored and, as a result, only a small region of the possible strategy space is examined. We believe it is these constraints that have determined the outcome of cooperation in one-shot interactions, which are probably not as general as the authors claim.

The main limitation of the model is that individuals must decide on their strategy for all subsequent rounds during the first round of interaction, choosing between tit-for-tat (or grim) and always defect. The authors stated that decision-making with imperfect knowledge leads to errors (1), yet players were not allowed to correct their mistakes. If we follow the logic of Delton et al. (1) and assume that a reciprocal cooperative strategy is optimal when interactions are repeated, then a player finding him- or herself in a second interaction should always assume a reciprocal cooperative strategy, correcting for any error in the first interaction. If correction of errors becomes possible, then selection for forgiveness of errors should be expected, thereby reducing the cost of an early mistake (2). It is well known that more forgiving strategies (such as more forgiving versions of tit-for-tat and Pavlov) are favored over tit-for-tat when errors occur (2–5). As forgiveness of errors occurs more frequently, each single interaction has less importance in the long-term payoff from the game, eroding the effect that Delton et al. reported (1).

An interesting question directly resulting from the approach of Delton et al. (1) is: What kinds of strategies should evolve when the probability of repeated interaction is a function of the number of previous interactions? We would suggest that the inability of tit-for-tat and grim to forgive an opponent's errors would make them unlikely candidates. To assert the generality of the mechanism proposed, a much broader investigation of the strategy space would be required. The importance of first-interaction decisions for long-term cooperation is certainly influenced by the strategic composition of the population (i.e., the type of society). Allowing individuals' strategies to freely evolve would allow for the determination of the societal compositions that can favor cooperation in one-shot interactions. We propose that one-shot cooperation would be more likely to evolve in an unforgiving Machiavellian society, as Delton et al. (1) have shown. Ironically, a more forgiving society would undermine the importance of generosity, leading to a conflict between these beneficent traits.

ACKNOWLEDGMENTS. We thank Andrew L. Jackson for helpful discussion.

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Author contributions: L.M. and C.J.T. wrote the paper.

The authors declare no conflict of interest.

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LETTER

Reply to McNally and Tanner: Generosity evolves when cooperative decisions must be made under uncertainty

We thank McNally and Tanner (1) for their considered critique of our article (2). Our article addressed the puzzle of why humans, in one-shot interactions, often choose to incur costs to allocate benefits to others, with no possibility of recouping these losses (i.e., "irrational" generosity) (2). This empirical pattern challenges standard models of economic and evolutionary rationality, and has prompted the development of ever-more-cumbersome explanations (e.g., group selection, gene–culture coevolution, cultural group selection)—models fragilely dependent on many hard-to-verify assumptions. In our article, we demonstrated that the well-documented selective regime of direct reciprocity produces agents willing to cooperate in apparently one-shot encounters, when the cognitive problem of discriminating one-shot from repeated encounters under uncertainty has been incorporated into the analysis (as, realistically, it must be). This is a parsimonious solution to the puzzle that flows naturally out of well-understood selection pressures.

McNally and Tanner (1) voice the reasonable concern that our results may not generalize widely because we did not model hesitant or forgiving strategies. A hesitantly cooperative strategy initially defects but may cooperate if the interaction continues. A forgiving cooperative strategy will switch to cooperation if its partner ceases defection. In contrast, the cooperative strategies we modeled cooperate initially, and the defecting strategy defects forever. The crux of their concern is that the magnitude of the effects we observed might be reduced had we instead made the defection strategy hesitantly cooperative. We concur that the fitness differential between initial cooperation and defection might be smaller in such a model. Importantly, however, the direction of selection would be the same, just with reduced strength. Hence, the effects would not be eliminated and the generality of our results would be unchanged.

Indeed, the joint space of possible strategies and parameters is vast. So, to derive conclusions that were as general and transparent as possible, we selected cooperative strategies that are well understood and directly relevant to our question. Hesitant strategies, in contrast, introduce aspects of cooperation beyond the empirical issue we were addressing: the human propensity to be generous with a novel partner on the first move in a situation that appears to be one-shot. In such situations, a hesitant strategy—unlike humans—would not be generous on the first move and could thus not plausibly model the actual behavior we sought to understand. All strategies explored in game theory, including tit for tat, hesitant, and forgiving strategies, are far too simple to capture human cooperative psychology, but we think our results nonetheless generalize to all fundamentally cooperative strategies because uncertainty is a reliable feature of realistic ecologies. Although their details differ, these cooperative strategies are designed to extract the benefits of cooperation by selectively cooperating with other cooperative strategies and avoiding noncooperative strategies. Because uncertainty exists in the detection of one-shots (or last moves, or games with definite expected lengths), when cooperation yields gains in trade, selection should generally favor generosity. Forgiving, hesitant, or not, a psychology that is generous in the absence of anticipated payoffs is anything but Machiavellian.

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Author contributions: A.W.D., M.M.K., L.C., and J.T. wrote the paper.

The authors declare no conflict of interest.

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