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Dear editors,

Please find attached a copy of our manuscript submitted to *Proceedings of the National Academy of Sciences of the United States of America*, entitled "Learning to cooperate: The evolution of social rewards in repeated interactions".

In this article, we demonstrate, using a mathematical model, that natural selection can favor learners that have positive preference for cooperation in the iterated prisoner's dilemma. This result provides a theoretical explanation of apparently other-regarding preferences expressed by humans and animals in laboratory settings. The psychological motives behind human and animal cooperation are a matter of current inquiry (Raihani NJ and Bshary R, 2015, Front. Behav. Neurosci., 9) and our paper provides an important new step in understanding what is evolutionarily possible in this regard, by integrating learning and the evolution of preferences in a unifying theoretical framework.

In our model, individuals interact repeatedly with social partners and learn to cooperate or defect according to the rewards they perceive from their actions. The rewards an individual perceives from his social behaviors represent his preferences for the outcomes of the interaction, and consitute the evolving trait. This modeling choice is the key novelty of our article with respect to previous attempts to model the evolution of cooperation in the field of social evolution. Our idea relies on the well-accepted notion in neurobiology that rewards are subjective and need not reflect the real fitness effects of behavior (Schultz, W., 2015, Physiological Reviews, 95(3), 853–951).

Our model shows that cooperation in repeated interactions can be supported by other-regarding preferences when the benefit from receiving cooperation is much larger than the cost of cooperating. We also show that several types of individuals, with different reward functions may co-exist at an evolutionary equilibrium, in agreement with recent empirical results (Burton-Chellew et. al., 2016, PNAS, 113(5), 1291–1296). Indeed, one of our evolutionarily successful reward functions produces behavior that is similar to individuals who reciprocates the opponent's behavior, whereby being able to learn either cooperation or defection depending on the opponent's behavior; this behavior is possible when individuals have positive preference for the opponent's cooperating but have negative preference for unilateral cooperation on their side. A second successful type is the one who only prefers to defect and hence can only learn to defect. These two types are amongst the behavioral types that have been identified in the aforementioned behavioral experiment.

By modeling at the same time the learning dynamics and the evolution of rewards at the core of learning processes, our results provide a more integrated modeling of behavior in species with a learning ability. This approach has allowed us to provide an evolutionary rationale for the diversity of behavioral types found in humans, and show the promise of such an approach to refine our understanding of the the psychological motives underlying social behavior.

Sincerely,
Slimane Dridi, on behalf of all authors.