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Perception without self-matching in conditional tag based cooperation

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HIGHLIGHTS

- We consider a tag based model for the evolution of cooperation in a population.
- Individuals play the prisoner's dilemma game with neighbors on a square lattice.
- Strategies are contingent on a partner's tag, without self-matching.
- When individuals start with an inability to perceive tags partial perception evolves.
- Cooperation rates are higher than in the usual spatial prisoner's dilemma game.

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ABSTRACT

We consider a model for the evolution of cooperation in a population where individuals may have one of a number of different heritable and distinguishable markers or tags. Individuals interact with each of their neighbors on a square lattice by either cooperating by donating some benefit at a cost to themselves or defecting by doing nothing. The decision to cooperate or defect is contingent on each individual's perception of its interacting partner's tag. Unlike in other tag-based models individuals do not compare their own tag to that of their interaction partner. That is, there is no *self-matching*. When perception is perfect the cooperation rate is substantially higher than in the usual spatial prisoner's dilemma game when the cost of cooperation is high. The enhancement in cooperation is positively correlated with the number of different tags. The more diverse a population is the more cooperative it becomes. When individuals start with an inability to perceive tags the population evolves to a state where individuals gain at least partial perception. With some reproduction mechanisms perfect perception evolves, but with others the ability to perceive tags is imperfect. We find that perception of tags evolves to lower levels when the cost of cooperation is higher.

1. Introduction

One of the fascinating questions in evolutionary biology, which dates back to Darwin (1859), is how cooperation can emerge in a competitive environment where the struggle for survival and natural selection would seem to favor selfish behavior. Since cooperation between individuals is widespread in nature (Smith and Szathmáry, 1997), from micro-organisms which exhibit complex social behavior (West et al., 2006; Crespi, 2001) to social animals which form cooperative groups (Clutton-Brock et al., 2000; Sharp et al., 2005), an explanation for its emergences is needed. Among many theoretical approaches to this problem, evolutionary game theory (Maynard Smith, 1974), in particular the prisoner's dilemma game, has proved to be fertile ground for research. One version of this game involves interacting individuals choosing one of two strategies: cooperate by donating a benefit to the other player at some cost to itself, or defect by offering nothing. An individual who defects will gain a fitness advantage compared to one who cooperates, but a group of cooperators who benefit from mutual cooperation is better off than a group of defectors who gain nothing.

This observation points to a mechanism by which cooperative behavior can evolve. If cooperative individuals preferentially interact with others who also cooperate with them they may gain a fitness benefit from the interaction. One way that this can happen is if the population has some spatial structure or viscosity. The usual approach is to restrict individuals to particular locations on a spatial grid (Nowak and May, 1992; Nowak et al., 1994; Szabó and Tőke, 1998; Schweitzer et al., 2002; Langer et al., 2008). Alternatively individuals may preferentially interact in certain isolated groups or demes, with limited migration between them, as in Wright's island model (Wright, 1943; Taylor, 1992; Lehmann et al., 2006; Rousset and Billiard, 2000). In a population with spatial structure individuals reproduce in their local neighborhood, and therefore are more

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likely on average to have genes in common with their interacting partners. An individual who carries a gene for cooperation will preferentially donate benefits to other individuals who share that gene, and in turn receive benefits from those individuals. In this way the gene for cooperation can be sustained provided neighbors are sufficiently related. The exact condition for the maintenance of cooperation depends on a number of factors, including the nature of the population structure, how costs and benefits relate to fitness, and the reproduction mechanism. In general, cooperative behavior can survive and even grow provided initial clusters of cooperating individuals can form and the cost of cooperating is sufficiently low compared with the benefit given (Langer et al., 2008). However, spatial structure alone may not be sufficient to sustain cooperation when the cost to benefit ratio is high. Indeed, for some update schemes, such as asynchronous birth–death schemes (Huberman and Glance, 1993; Ohtsuki and Nowak, 2006, 2008), spatial structure does not lead to the evolution of cooperation.

A more direct mechanism by which cooperating individuals may preferentially direct donations of a benefit to related individuals who cooperate with them is through kin recognition. Kin can be recognized through familiarity based on environmental or learned cues, or through pattern matching based on some inherited trait. If individuals display a heritable marker or tag, such as a scent, color or some other phenotype, which interacting partners can recognize, individuals who preferentially cooperate with partners who share their own marker can gain an indirect benefit from that interaction, since those individuals are likely to be kin who also share the gene for cooperation.

A thought experiment by Hamilton (1964), which illustrates how this mechanism can work even when individuals are not genealogical kin, has come to be called the *green beard* effect (Dawkins, 1976). If a gene for some distinguishable trait or tag (such as a green beard) also codes for a strategy of cooperating with others who share that tag then cooperation can be sustained. Indeed, in the green beard effect cooperation will occur between any individuals who share the green beard gene, even if they are not genealogical kin. While a single gene or closely linked genes coding for tag, tag recognition and a cooperative response might seem too happen stance to be a likely biological model, there is some evidence in support of this idea. For example, the social amoeba, *Dictyostelium discoideum*, which forms cooperative fruiting bodies, has been shown to preferentially direct benefits to carriers of the *csA* gene. Both the recognition and altruism behaviors derive directly from cell adhesion protein encoded by em csA (Queller et al., 2003).

More generally genetic kin recognition refers a situation where individuals recognize and preferentially cooperate with other individuals based on some phenotype similarity, where the gene for recognizing and cooperating with related individuals and the gene for displaying the tag are different. Dawkins dubbed this as the *armpit effect* (Dawkins, 1982). There is some question about whether genetic kin recognition can be sustained in nature due to what is sometimes referred to as Crozier's paradox (Crozier, 1986). If a successful genetic cue for cooperation leads to fixation and loss of diversity then this would open the way to exploitation by individuals who share the tag, but do not cooperate. Thus the success of genetic kin recognition as a route to cooperation is sensitive to the maintenance of diversity in tags through mutation or some other mechanism (Rousset and Roze, 2007; Jansen and Van Baalen, 2006; Gardner and West, 2007).

Several theoretical models for the evolution of cooperation involving heritable markers or tags have been proposed to explore this question (Riolo et al., 2001; Sigmund and Nowak, 2001; Traulsen and Schuster, 2003; Axelrod et al., 2004; Jansen and Van Baalen, 2006; Hammond and Axelrod, 2006a; Crozier, 1986; Rousset and Roze, 2007). The mechanism by which tags are introduced varies, but the common thread is that individuals adopt strategies that are contingent on the tag of their opponent. Both the tag and the strategy are inherited and are subject to mutation, although they need not evolve together. Riolo et al. (2001) and Sigmund and Nowak (2001) discuss a model in which well-mixed individuals cooperate with those who have a tag that is within a particular tolerance level of their own, and defect otherwise. The tags in this instance are continuous. The system can evolve to a state with a relatively high level of cooperation, were most individuals share similar tags, but have a relatively low tolerance level. However the dynamics are quite unstable, leading to “tides of tolerance”. Highly intolerant mutant strategies typically invade more tolerant and cooperative ones, which results in a drop in the cooperation rate. Eventually mutations give rise to more tolerant individuals with a different tag—resulting in a return to cooperative behavior, and the cycle continues. Traulsen and Schuster (2003), proposed a discrete version of this model, in which there are 2 tags and 2 levels of tolerance. This model is amenable to analysis using replicator dynamics and leads to a similar dynamical situation. Roberts and Sherratt (2002) pointed out that in these models interacting individuals who share identical tags unconditionally cooperate, as in the green beard effect, so it is not surprising that cooperation evolves. When they made a modification that allows individuals the option of not cooperating with those who have identical tags the results was a loss of cooperative behavior. However, it has since been shown that if the mutation rate for tags is greater than the mutation rate for strategies, cooperative behavior can predominate, even if like-individuals are not assumed to cooperate with each other Traulsen and Nowak (2007).

Another approach has been to study these and more general tag models for the case where individuals are not uniformly mixed, but are constrained by some viscosity or spatial structure (Jansen and Van Baalen, 2006; Hammond and Axelrod, 2006a; Crozier, 1986; Rousset and Roze, 2007). While cooperation can evolve in the spatial prisoner's dilemma without tags provided the cost of cooperation is low compared to the benefit and the update scheme is favorable, the inclusion of conditional cooperation based on heritable tags can enhance the rate of cooperation and may allow it to evolve where it would not otherwise do so. In the model introduced by Jansen and Van Baalen (2006), individuals can adopt a strategy of either cooperating or defecting against those who share their tag and defecting against those with a different tag. The dynamics is relatively stable and cooperative provided the tag and strategy are not always inherited together. One interesting feature is the positive correlation between number of tags and the level of cooperation. Hammond and Axelrod (2006a) allowed for the additional conditional strategy that individuals could optionally cooperate with those who had a dissimilar tag. Although such behavior rarely evolved, they showed that the cooperation rate is sustained at levels above what is normally expected in the spatial prisoner's dilemma even when the cost of cooperation is high.

Thus a common outcome in tag models with spatial structure or viscosity is that cooperation is enhanced by the presence of heritable tags in a population—with the nice result that tag diversity yields a higher cooperation rate. However, while individuals cooperate within groups of the same tag, they almost invariably defect against those with different tags. We refer to cooperation with liked-tagged individuals as *loyalty* and cooperation with dissimilar others as *hospitality*. Individuals who are loyal but in-hospitable are said to exhibit *ethnocentrism* (Hammond and Axelrod, 2006b) or *nepotism*, and this is the typical way that cooperation manifests itself in these models. Thus defection between individuals is now replaced by defection between groups of otherwise cooperative individuals. While this may seem unfortunate from a social perspective, the overall rate of cooperation is