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Role of perception cost in tag-mediated cooperation

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ABSTRACT

Tag-mediated interaction has been known to be an effective means of promoting cooperation in theoretical models. However, most of the previous studies assume that the individuals do not incur any costs for their tag perception, although it is doubtful whether the cognitive effort for tag perception is empirically high. In this paper, we establish a spatial Prisoners dilemma model with tags to investigate the role of perception cost in tag-mediated cooperation. By introducing incomplete perception with perception cost, we find that partial perception can emerge and support cooperation under relatively low perception cost, but perception cost may inhibit the emergence of partial perception and thus is detrimental the evolution of cooperation. Moreover, the dynamics of cooperation level and perception intensity show interesting oscillatory patterns interacting with each other, which resemble those in other tag-based models. From the typical snapshots, we find that the high levels of cooperation can be explained by the clear boundaries between tag-mediated cooperative clusters. These boundaries can resist interactions between clusters and therefore prevent defectors from invading the whole population. Our work should be helpful in understanding the cognitive foundation of tag-mediated cooperation.

1. Introduction

Cooperation is a ubiquitous phenomenon in natural and social systems. However, cooperative individuals will reduce their fitness to contribute to the fitness of others, while defectors pay no costs but may benefit from the cooperators. Defectors are therefore favored by selection if no other mechanisms are at work. It is thus fascinating to understand why and how cooperation can emerge and be maintained among selfish individuals [1–6]. Among many theoretical approaches, evolutionary Prisoner's dilemma game (PDG) is a widely used metaphor and has proved to be helpful for understanding cooperative behavior between unrelated individuals. In a one-shot PDG, two players simultaneously choose one of two strategies: cooperation and defection. Although mutual cooperation leads to the Pareto optimal outcome, defection is always a better choice for a self-interested individual regardless of the other's choice, because a defective individual will gain a fitness advantage compared to an cooperative one. As a result, cooperators cannot prevail in a well-mixed population where no mechanisms are at work to specify how individuals interact and compete with others under natural selection.

To understand how cooperation can be favored in evolutionary systems, the previous studies have proposed five major mechanisms including kin selection [7], direct reciprocity [8], indirect reciprocity [9], spatial selection [10] and multilevel

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selection [11], all of which have proved to be effective in favoring the evolution of cooperation under a wide variety of conditions. A central problem in the investigations of these mechanisms is how assortment among individuals can emerge so that cooperators can interact more frequently with other cooperators but not defectors. As a remarkable example, in spatial PDG, cooperation can emerge and be maintained if cooperative clusters can be formed so cooperators have more payoffs than defectors due to the effect of spatial reciprocity (or network reciprocity)[2,10], which is still attracting greatest attention in the investigations of assortment mechanisms. It turns out that the spatial topologies have significant effects on the promotion of cooperation [10,12–20]. In addition to the static structures, it is demonstrated that dynamic and adaptive networks can promote cooperation in the context of strategy-structure coevolution [2,21–26]. Recently, more mechanisms, which cannot be simply classified as one of the classical mechanisms, are taken into account and have shed new light on the research of social dilemmas. It is found that payoff uncertainty or chaos caused by environmental factors may promote cooperation in spatial PDG [27,28]. The quality of information may have non-trivial effect on cooperative behaviour in a deceptive environment [29]. Herding instincts and crowd behaviour in humans and social animals may play an important role in social dilemmas if they lead to conformity [30], which is a widely discussed and studied subject in social sciences [31]. In addition, the risk of collective failure and risk-driven migration may solve the collective-risk social dilemma [32,33]. Generally speaking, these mechanisms are inspired by real world phenomenon, thus can help us to bridge the chasm between theoretical research and empirical research.

Tag-mediated cooperation, which dates back to Hamilton [7], can be seen as a special type of spatial reciprocity, which also facilitates assortment among individuals and thus supports the establishment of cooperation. The use of tags imposes an abstract topology on the individuals in the sense that an individual's "neighborhood" can be determined by tag similarity [34]. As a rudimentary version of tag-mediated mechanism, the so-called green beard effect offers a direct signal by which cooperators can recognize each other so they can selectively help each other but not defectors [7]. When a perceivable tag and the ability to recognize this tag and to help the individuals who own this tag can be encoded in a single gene or a cluster of genes, cooperation can emerge in the population. The resulting cooperation, however, is vulnerable to invasion of cheaters who also have green beard but defect. If the tag and cooperative behavior are encoded separately, the cheaters will be the winner. Interestingly, there are some real world evidences supporting the idea of green beard effect, as discovered in animals [35,36]. However, the relation between genotype and phenotype is so complicated that the cooperative behavior in most social animals such as humans cannot be explained solely by green beard effect.

Although green beard effect is not a universal solution for the evolution of cooperation, it has generated a growing body of research, either empirical or theoretical, showing that phenotypic tags play an important role in the evolution of cooperation [34,37–56]. In the theoretical research, tag-based models can be classified into two major approaches: the conditional cooperation approach and the selective interaction approach. In the former one, an individual has perception of dissimilarity according to the combination of observed tags and its own tolerance [34]. If the distance between an individual and its partner is less than the tolerance level, it will cooperate with the partner, otherwise it defects. In this approach, either in well-mixed population or in spatial structured population, individuals are not allowed to select their partners and change their social ties autonomously. In the latter approach, various partner search methods can be implemented. For example, individuals may search the population for only the identical partners on the basis of tag perception [44]. Alternatively, a higher tolerance level, as a parameter, may be applied to the perception of dissimilarity so that not only identical individuals but also similar individuals with short distance can interact with each other [52]. It is also possible to investigate what is the optimal tolerance level for promoting cooperation and whether this optimal level can evolve in the context of endogenous tolerance [57]. It is worth noting that individuals' strategies, either unconditional or stochastic, are encoded as an independent trait separated from the tolerance levels, which is another important difference between these two approaches.

In most previous literatures, tag perception is assumed to be complete and perfect, in the sense that all tags in the tag space are distinguishable and there is no error when an individual performs tag perception. To investigate the cognitive aspect of tag-based models, Ref. [51] introduced a version of imperfect perception limited by some environmental constraint, which assumes that individuals may err in the perception of partner's tag. Specifically, with probability $\rho \in [0, 1]$, an individual can perfectly identify the tag of its partner; with probability $1 - \rho$, an individual cannot identify the tag of its partner and only perceive this tag as a randomly assigned one. Both exogenous perception and evolving endogenous perception are considered in Ref. [51]. In the former case, $\rho \in [0, 1]$ is an endogenous parameter assigned to all of the individuals. In the latter case, each individual has an inheritable ρ which is also subject to mutation and selection. It has been demonstrated that partial perception (non-zero value of ρ) may evolve to a level that leads to an optimal level of cooperation, which is coincident with the level found in the exogenous version. In spite of the fruitful findings, this model omitted the possibility that tag perception is cognitively costly and imposes a cost on the individuals. In this situation, even partial perception may not evolve, because the individuals with high perception intensity are at a fitness disadvantage. It is interesting to investigate what happens if perception cost is explicitly introduced into tag-based models. For the model in Ref. [51], we may be curious about the results of a modified model with increasing perception cost on perception level (for example, we may consider a linear cost function $c = k\rho$, where k measures the difficulty of tag perception as one of individuals' cognitive abilities, and c represents the perception cost incurred by an individual).

To understand the relationship between perception cost and the evolution of tag-mediated cooperation, here we propose a tag-based model with incomplete tag perception and perception cost, by which individuals may incur fitness losses if they try to differentiate similar others from dissimilar others. By the term "incomplete" we mean that the tags in the whole tag space are only partly distinguishable. As a result, even individuals with dissimilar tags can be perceived as similar in the tag-mediated interactions. In addition, we assume that the ability to distinguish tags is an independent trait which is also subject to evolution so that individuals are allowed to have low or high perception intensity, but the higher the perception intensity, the higher the cost imposed on an individual. An interesting question is how the incompleteness of tag perception and perception cost affect the evolution of tag-mediated cooperation. Namely, can partial tag perception emerge through selection and mutation and thus promote cooperation? Does the existence of perception cost inhibit the emergence of tag-mediated cooperation? In the rest of this paper, we will first describe our model and then present the findings in detail.

2. Methods

We consider an evolutionary Prisoner's dilemma game (PDG) consisting of N spatially separated agents who occupy a $L \times L$ square lattice with periodic boundary conditions [10,14]. Each agent inhabits a single cell on the lattice and may play the on-shot PDG with its four direct neighbors in the von Neumann neighborhood. We assume $N = L^2$ so the lattice is fully occupied and the agents have no chance to move away from their initial cells. In the one-shot PDG, each player chooses either cooperation (C) or defection (D) as its strategy. The PDG is characterized by the payoff matrix where R ("reward") is the payoff for mutual cooperation, P ("punishment") is the payoff for mutual defection, and T ("temptation") is the payoff for unilateral defection, which leads to the payoff S ("sucker") for the cooperative agent. The inequalities $T > R > P > S$ and $2R > T + S$ ensure that the payoff structure satisfies the conditions for the classical PDG. Although there are many alternative scaling methods for the PDG and it is hard to design a universal scaling method especially in the context of heterogeneous interaction structure [58,59], the simple re-scaled payoff matrix: $T = b > 1,\ R = 1,$ and $P = S = 0$ is adopted in our model. The resulting game is given by the matrix below:

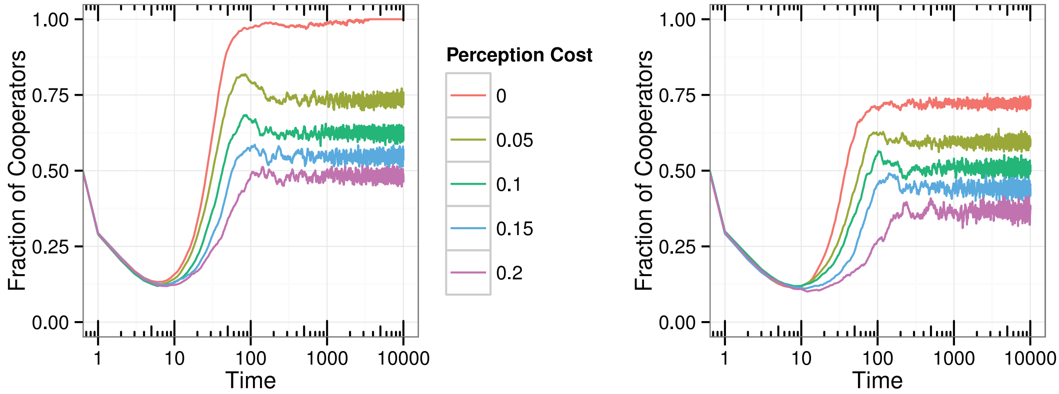
$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 1 & 0 \\ b & 0 \end{pmatrix} \end{array}$$

Initially, the agents are randomly located on the lattice and are assigned a strategy (C or D) with equivalent probability.

Besides the strategy trait, each agent i has an inheritable multidimensional tag represented by a bit sequence $t_i \in 0,\ 1^n$. The reason we use a discrete representation rather than a continuous representation [34,48] of tags is that discrete values are theoretically easy to be identified so they do not cause the perception problems such as how much memory and computational power are needed to process these values. These problems may be empirically crucial in biological applications. Unlike the previous tag-based models with selective interaction approach [44,45,52], our model assumes the dissimilarity of the tags cannot directly determine whether the interaction between two agents will happen. There is an additional trait (perception) for each agent i to decide which of the tag bits are perceivable and then determine the interaction partners in the neighborhood. This trait is also represented by a bit sequence with the same length as tag: $p_i \in 0,\ 1^n$. Each bit in this sequence determines whether the corresponding tag bit, i.e. the tag bit with the same index, is perceivable for the focal agent. If the bit value is 1, the corresponding tag bits of the focal agent and of the possible partners all can be perceived by the focal agent, otherwise they are not perceivable. Only the perceivable tag bits will determine whether the focal agent interact with another agent. We assume that the agents have totally intolerant preference towards dissimilar others. Specifically, if any tag bits with the same index are perceived as dissimilar by the focal agent or the possible partner, they cannot interact with each other (i.e., they do not play the PDG). Only when the perceivable tag bits have no difference between the two agents, will the agents interact with each other. For example, if $t_i = \langle 0111 \rangle,\ t_j = \langle 0101 \rangle,\ p_i = \langle 0110 \rangle$, and $p_j = \langle 0000 \rangle$, then agents i and j do not interact with each other to play the PDG. This is because the 2nd and 3rd bits in the tags can be perceived by agent i and they have difference between the two agents (the 3rd bit for agent i is 1, but the bit for agent j is 0), though agent j does not consider the tags to be dissimilar. For another example, if $t_i = \langle 1000 \rangle,\ t_j = \langle 0110 \rangle,\ p_i = \langle 0001 \rangle$, and $p_j = \langle 0000 \rangle$, then agents i and j engage in the interaction to play the PDG. This is because only the 4th bit in the tags can be perceived by agent i and agents i and j both have the value 0 at this tag bit, though the first 3 bits are all different between the two agents. By this definition, the agents have more chances to discriminate between similar others and dissimilar others if they have more perceivable tag bits.

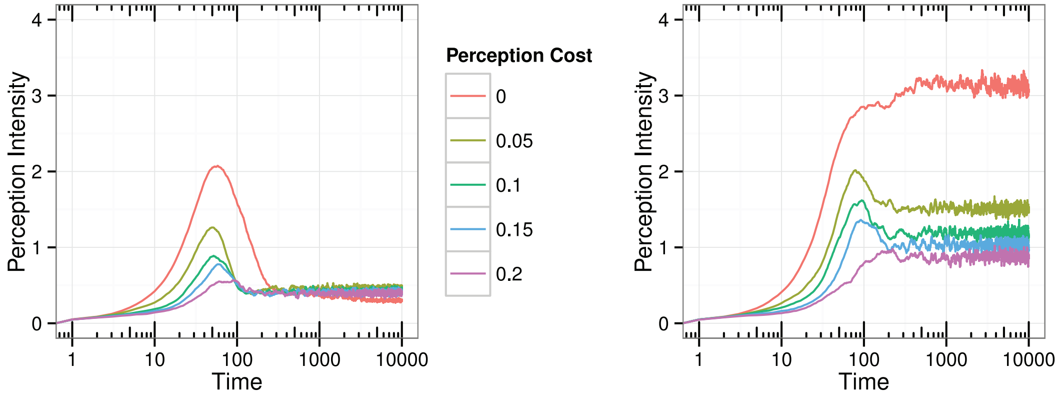
In the initiation step, the tags are also assigned randomly from the uniform distribution. For the perception trait, we assume that the agents do not have perception ability so p_i is set to $\langle 000\ldots0 \rangle$ for each agent i. However, this trait is subject to evolution both through selection and through mutation so it can have more possible values, as described soon below. Additionally, a key assumption of our model is that the perception will impose a cost on each agent. For simplicity, we assume that for each time step, each perceivable tag bit will impose a cost of c on the focal agent i. Thus the total cost will be kc, where k is the occurrence of value 1 in p_i.

The agents are updated asynchronously in a random sequential order via the Monte Carlo simulation procedure. The selected agent i and its neighbors perceive the dissimilarity between the focal agent and each of the neighbors to decide the interaction partners, then agent i obtain the total payoff U_i by playing the corresponding PDGs with its partners and subtracting the perception cost defined above. Next, agent i chooses one of its neighbors at random. The chosen agent j also obtain the total payoff U_j in the same way as agent i. Finally, agent i will try to update all of its traits from agent j with the



(a) $m_s = 0$ (b) $m_s = 0.01$

Fig. 1. Fraction of cooperators as a function of time step for different strategy mutation rates. Both enduring (END) period and expanding (EXP) period are illustrated in all of the cases. It is clear that perception cost affects the final levels of cooperation. Each data point is averaged over 20 different realizations. Other parameter: $m_t = 0.01$, $m_p = 0.05$, $b = 1.4$, $N = 10$, $L = 60$, K=0.1.



(a) $m_s = 0$ (b) $m_s = 0.01$

Fig. 2. Perception intensity as a function of time step for different strategy mutation rates. Without strategy mutation (the left panel), the perception intensity decreases to low levels once high levels of cooperation have been established, while the perception intensity can be maintained at high levels with strategy mutation (the right panel). In addition, the effect of varying perception cost is more significant if strategy mutation is in effect. Each data point is averaged over 20 different realizations. Other parameter: $m_t = 0.01$, $m_p = 0.05$, $b = 1.4$, $N = 10$, $L = 60$, K=0.1.

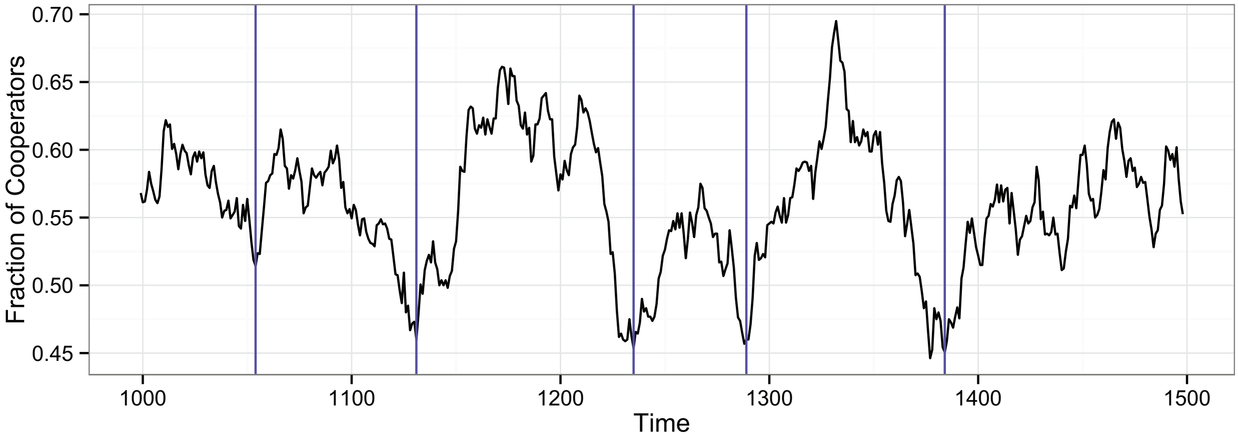
following Fermi-like rule:

$$Prob(X_i \leftarrow X_j) = \frac{1}{1+e^{\frac{U_i-U_j}{K}}}$$

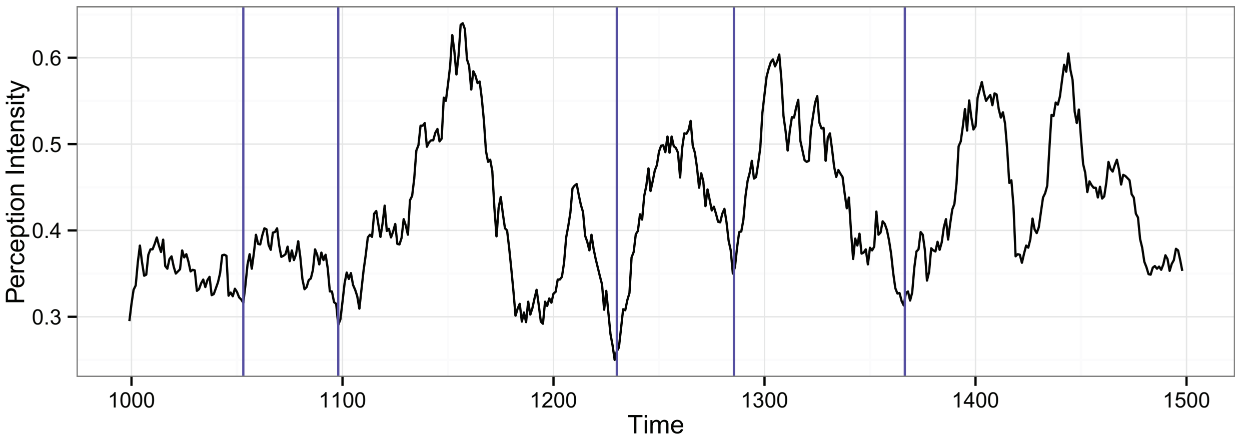
where X represents all of the traits (strategy, tag and perception) owned by the agents and K represents the selection noise or the reverse of selection strength.

In addition to the learning mechanism described above, we take into account mutations. When an agent is selected to update, there are some probabilities for all of its traits to mutate. The mutation procedure of each trait is defined independently as follows. When the strategy trait mutates (with probability m_s), it will be assigned at random with equivalent probability. Each bit in the tag sequence has a probability m_t to mutate independently. When it mutates, it will also be assigned at random in the same way as the initiation step. Thus it is possible that multiple bits in the tag trait mutates simultaneously. For the perception trait, we assume that at most one of the bits can mutates. With probability m_p, a bit in the sequence p_i is randomly picked and will be assigned as value 0 or 1 with equivalent probability.

In summary, we have provided a description of an evolutionary PDG model with both tags and the corresponding perception of these tags. This model can be seen as a simple artificial world where the agents have incomplete knowledge of their phenotypical traits so that they have chances to treat others discriminately. Unlike most previous tag-based models, our model relaxes the assumption that the agents have complete and perfect information about others' traits. As mentioned in the Introduction, Ref. [51] considered perception noise and found that partial perception can coevolve with tag-mediated cooperation, but it omitted the possibility that low noise level of perception may impose costs on the agents. With a different definition of partial perception, our model explicitly takes account of the cognitive cost for the possible perception, which is a more empirically plausible assumption for the explanation of the evolution of cooperation. It is also possible



(a) Evolutionary dynamics of cooperation level



(b) Evolutionary dynamics of perception intensity

Fig. 3. Comparison of typical evolutionary dynamics of f_c and $\bar{p}$. The cooperation level and the perception intensity oscillate and interact with each other. Parameter: $c = 0.15,\ m_p = 0.05,\ m_t = 0.01,\ m_s = 0,\ b = 1.4,\ N = 10,\ L = 60,$ K=0.1.

to introduce incomplete and imperfect perception simultaneously. By imperfect perception we mean that even if an agent decides to observe the tags and differentiate between them, it may err with some probability. In this paper, however, we only deal with incomplete perception and only consider the cost incurred via high completeness (or high perception intensity). We may consider the combination of incomplete and imperfect perception in a future paper. Another difference between our model and the model in Ref. [51] is that we adopt the selective interaction approach instead of the conditional cooperation approach.

The goal of this paper is to answer the following questions:

1. Can high levels of cooperation emerge in the simulation of our model?
2. Can partial or complete perception of tags coevolve with the evolution of cooperation?
3. What is the role of perception of tags in supporting the emergence and maintenance of cooperation?
4. Does high cost of perception undermine cooperation and the emergence of partial perception?

To answer these questions formally, we will record the following two quantities for characterizing the evolutionary population:

1. The fraction of cooperators, which characterizes the cooperation level in the whole population.
2. The average number of perceivable tag bits of the agents, $\bar{p}$, which characterizes the perception intensity in the tag-mediated interactions.

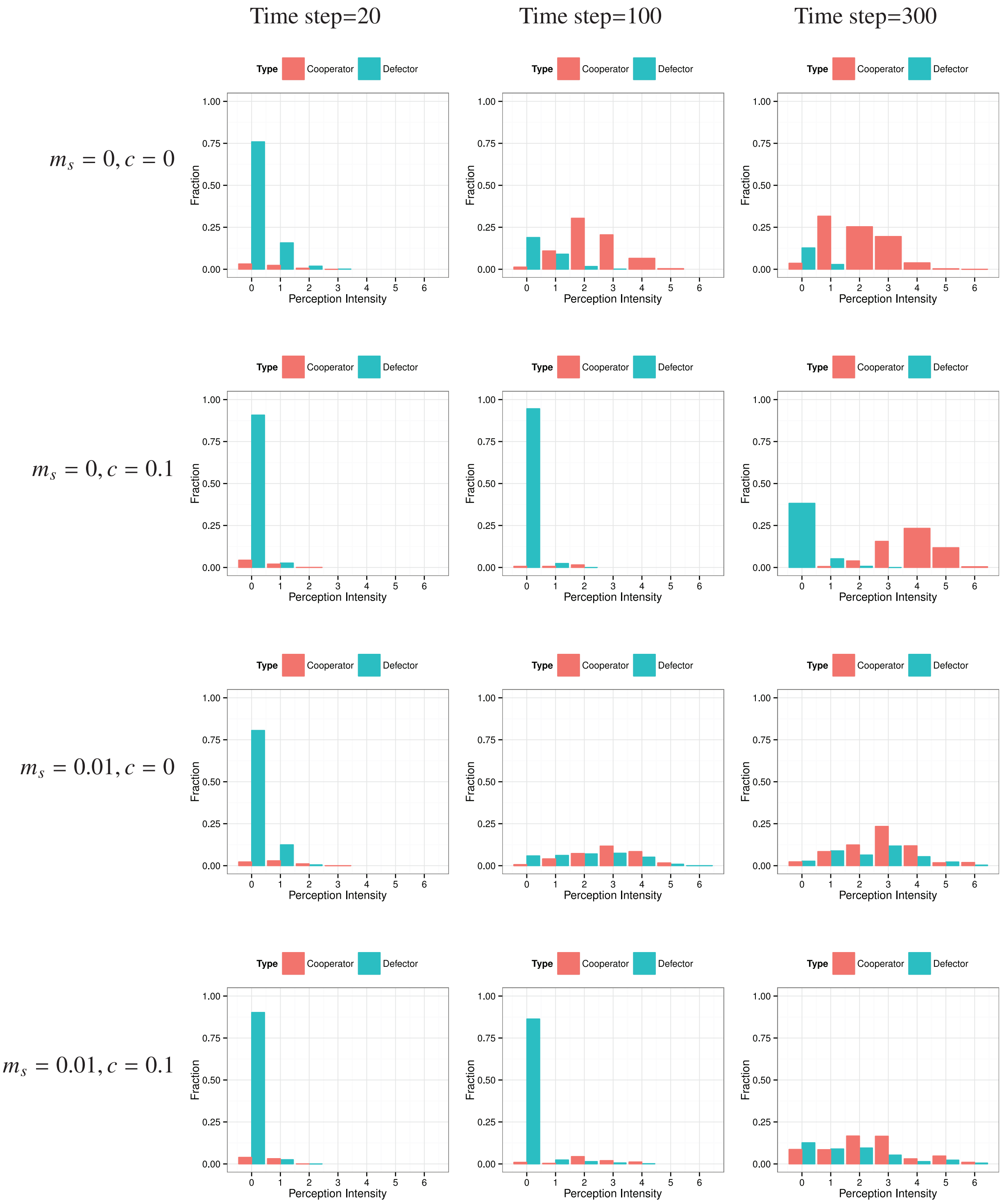


Fig. 4. Distributions of cooperators and defectors with different perception intensities at different time steps for different conditions. The perception intensities greater than 6 are omitted for a better view of the distributions. It is clear that cooperators and defectors have significantly different distributions, which demonstrates the mechanism behind the emergence of tag-mediated cooperation. Moreover, perception cost may create a two-sided distribution in the population. Other parameters: $b = 1.4$, $m_t = 0.01$, $m_p = 0.01$, $N = 10$, $L = 60$, K=0.1.

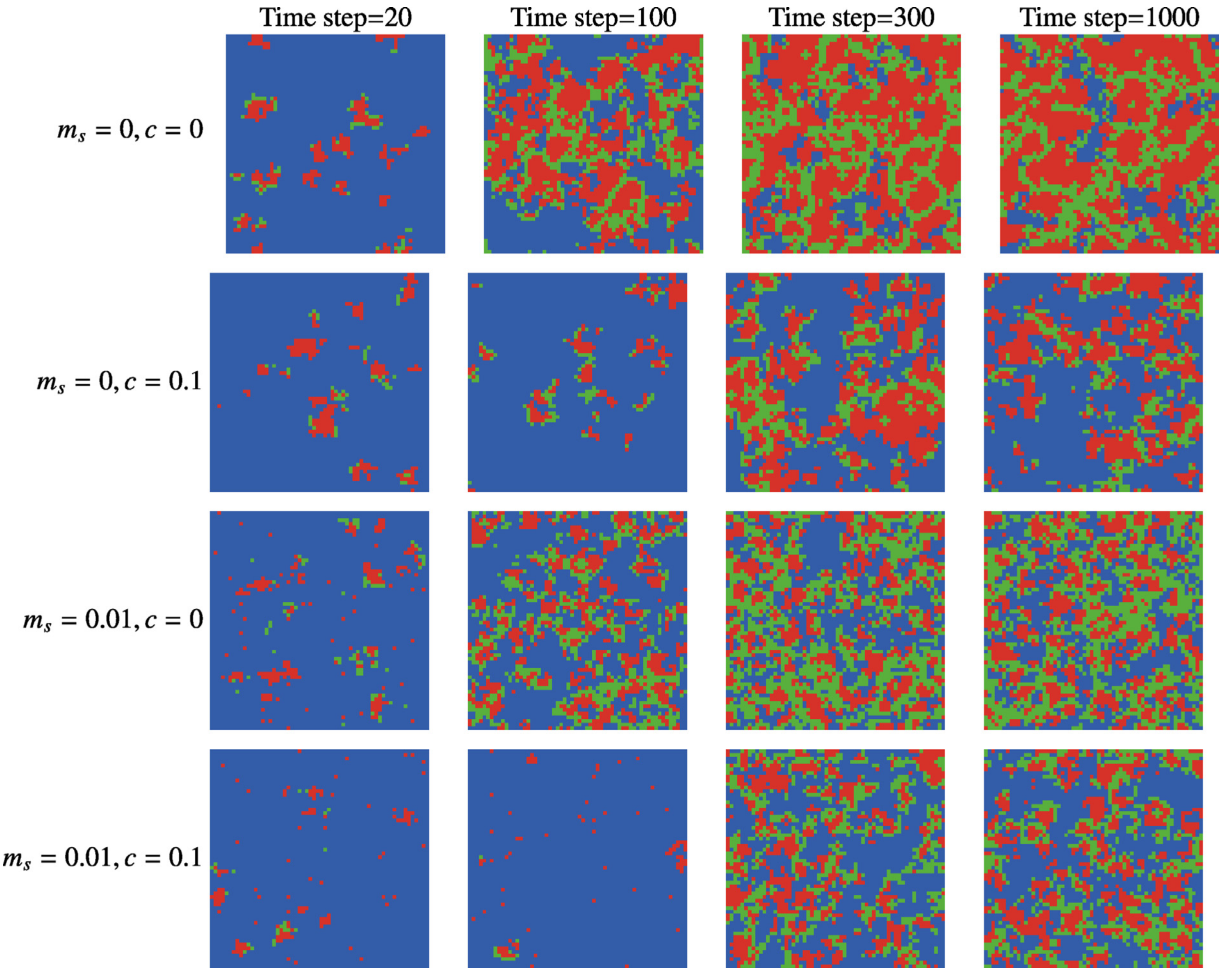
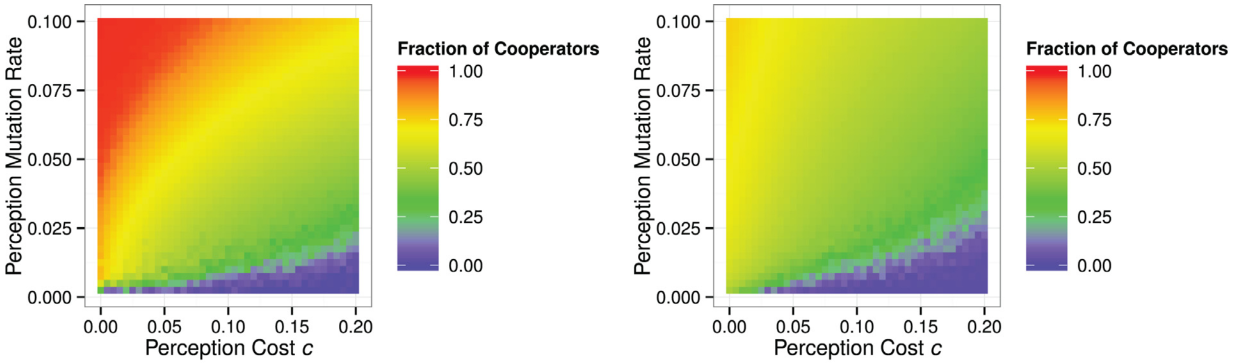


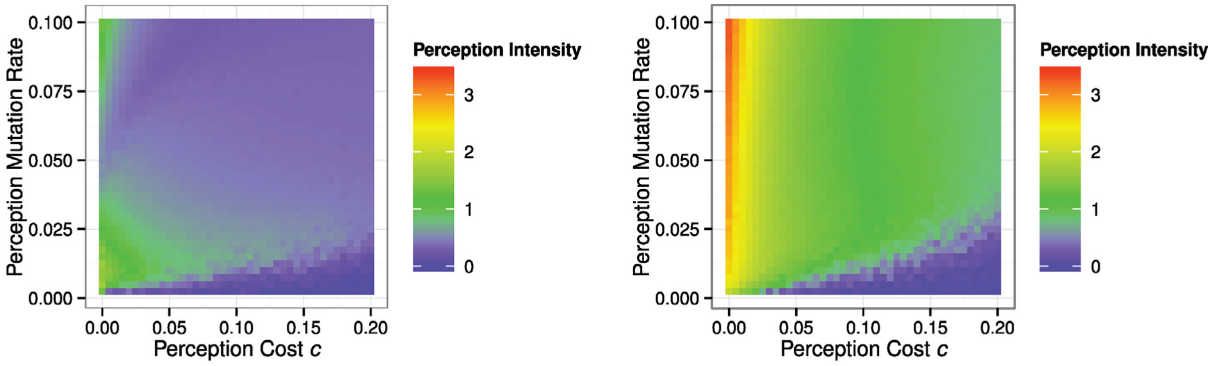
Fig. 5. Typical spatial snapshots at different time steps for different conditions. Cooperators with full interaction are represented by red patches. Cooperators with interacting partners less than 4 are represented by green patches. Defectors are represented by blue patches. The clear boundaries between clusters, represent by the green patches, contribute to the resistance against the invasion of defectors. Other parameters: $b = 1.4$, $m_t = 0.01$, $m_p = 0.01$, $N = 10$, $L = 60$, K=0.1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



(a) $m_s = 0$

(b) $m_s = 0.01$

Fig. 6. Fraction of cooperators as a function of perception cost c and perception mutation rate m_p for different strategy mutation rates. Cooperation can be enhanced by increasing perception mutation rate or reducing perception cost. Other parameter: $m_t = 0.01$, $b = 1.4$, $N = 10$, $L = 60$, K=0.1. As in all following figures, results are averaged over 30 independent realizations for each set of parameter values.



(a) $m_s = 0$ (b) $m_s = 0.01$

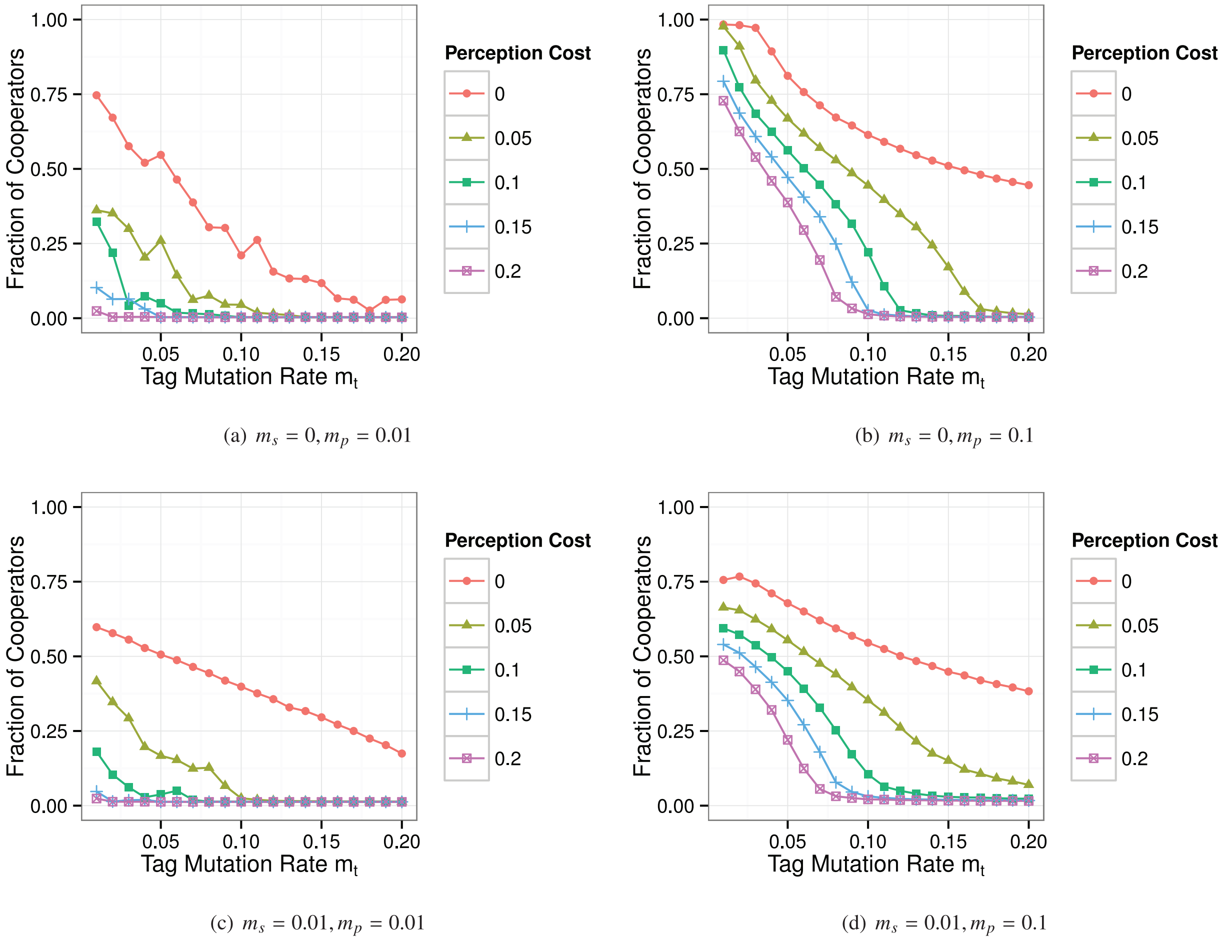
Fig. 7. Perception intensity as a function of perception cost c and perception mutation rate m_p for different strategy mutation rates. The levels of perception intensity are relatively low if there is no strategy mutation. If there is strategy mutation, the cooperation level and the perception intensity are highly correlated with each other (see the right panel here and the right panel in Fig. 6). Other parameter: $m_t = 0.01$, $b = 1.4$, $N = 10$, $L = 60$, K=0.1.

3. Results

We first examine the evolutionary dynamics with some typical simulation setups and investigate how perception cost affects the evolutionary characteristics of the system. The evolutionary paths of cooperation level and perception intensity under different perception costs are shown in Figs. 1 and 2. We find a demonstrable enduring (END) period and an expanding (EXP) period in the evolutionary process over time, which is widely observed in the previous studies [12,60–63], regardless of whether there is strategy mutation. The former represents the early stages where cooperators are soon invaded by defectors and the latter represents the takeoff stages where cooperators have an effective expansion with an ameliorated environment. The initial takeoff of cooperation can be explain by the emergence of partial perception, as shown in Fig. 2. We see that the perception intensity always has a takeoff started at the beginning of evolution. After the establishment of partial perception, the agents can partly differentiate between similar and dissimilar others and selectively interact with others. Therefore, cooperators with similar tags can form clusters and resist the invasion of defectors. The emergence of partial perception itself can be explained as follows. For defectors, it is best to have no perception because they cannot be exploited in their interactions. For cooperators, it may be beneficial to add some perceivable tag bits so they can differentiate similar others from dissimilar others, because the selective interaction lowers the probability that a cooperator is exploited by a defective partner. Moreover, cooperators with high perception intensity do not lose the benefits of full interaction within a cluster because all of their neighbors are similar as perceived.

The paths of perception intensity have a significant difference between the case with strategy mutation and the case without strategy mutation. If there is no strategy mutation (Fig. 2(a)), the perception intensity will decrease to low levels once high levels of cooperation have been established. This is because the agents can benefit from high interaction intensity and high perception intensity can lower the interaction intensity. Furthermore, a cooperative cluster is not likely to encounter a defector within the cluster so the lowered perception intensity is enough to prevent defectors from corroding the population. If strategy mutation is in effect (Fig. 2(b)), the perception intensity can be maintained at some high levels. The high levels of perception intensity are beneficial for cooperators because the clusters with similar tags can be maintained at a small size with high perception intensity. By the clear boundaries between different clusters, it is difficult for mutant defectors to invade the whole population.

Now we focus on the effect of perception cost. First, the paths of f_c show an obvious difference after expanding period between the costly perception cases and the no cost cases. Typically, there is a small decrease after f_c attains the maximum level when perception cost is in effect, while f_c can end with expanding period when there is no perception cost. After the small decrease, cooperators still survive, and the cooperation levels depend on the magnitude of cost, though there remain significant oscillations. It is clear that the final levels of cooperation are reduced by the increase of perception cost especially when there is no strategy mutation. In fact, we have found that even a very small perception cost (for example, $c = 0.01$) can lead to the unattainability of full cooperation. The levels of perception intensity are also be reduced by the increase of perception cost, except for the case without strategy mutation and perception cost (Fig. 2(a)). In this case, we see that the perception intensity finally reach the levels even lower than those with perception cost. This is because once full cooperation or approximate full cooperation has been established, the benefits of cooperative interactions create the advantage of low perception intensity. In addition, the introduction of perception cost significantly reduces the perception intensity when strategy mutation is in effect (Fig. 2(b)). The paths of $\bar{p}$ will diverge after the establishment of cooperation. Without perception cost, $\bar{p}$ will continue to increase and finally reach high levels. In contrast, $\bar{p}$ will have a decrease if perception imposes costs on the agents.



(a) $m_s = 0, m_p = 0.01$

(b) $m_s = 0, m_p = 0.1$

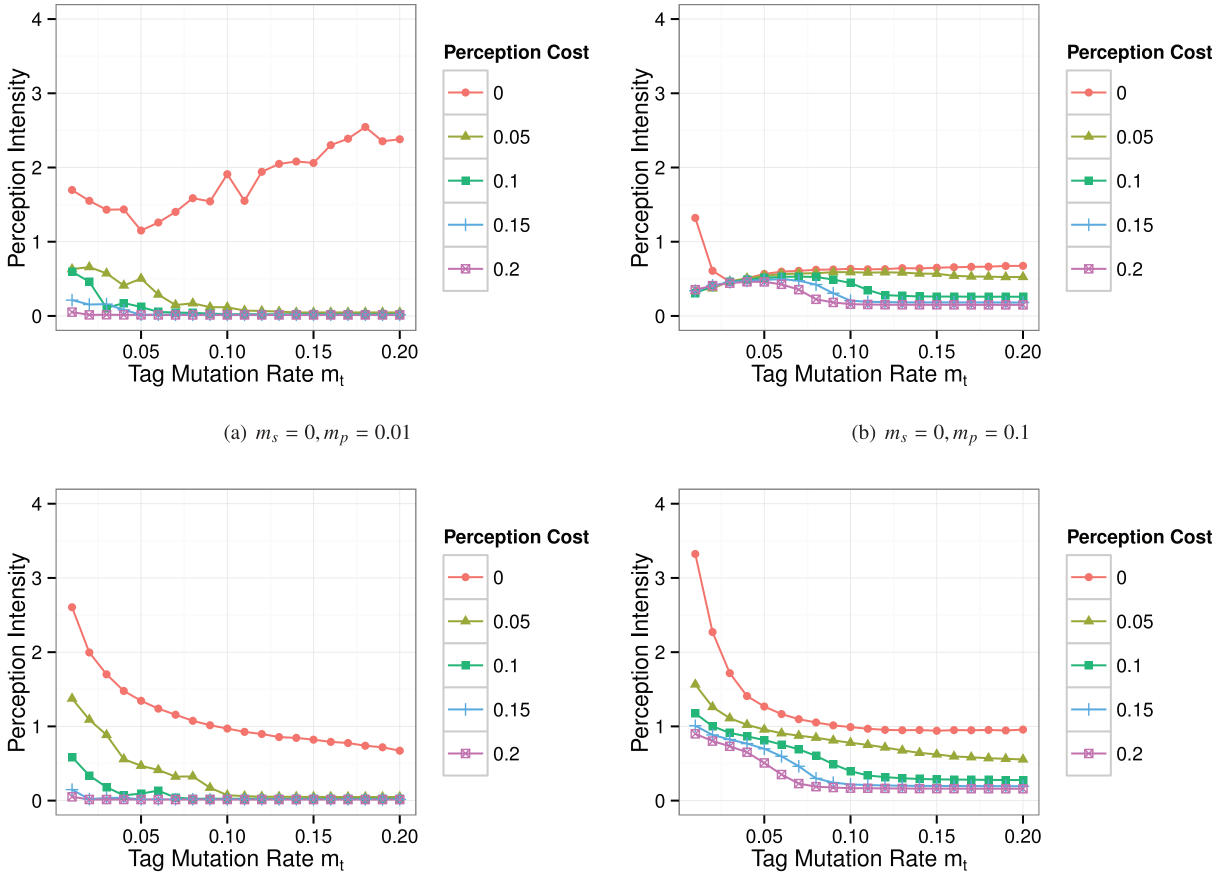
(c) $m_s = 0.01, m_p = 0.01$

(d) $m_s = 0.01, m_p = 0.1$

Fig. 8. Fraction of cooperators as a function of tag mutation rate m_t for different perception costs. Raising tag flexibility has detrimental effect on the evolution of cooperation. Other parameter: $b = 1.4$, $N = 10$, $L = 60$, K=0.1.

As mentioned above, there are significant oscillations in the paths of both f_c and $\bar{p}$. For a better understanding of these oscillations, we provide a microscopic view of the evolutionary dynamics by showing a segment of the paths in Fig. 3. Instead of averaged paths, here the paths are plotted from a single simulation run with typical parameter values. Even without strategy mutation, the fraction of cooperation can constantly oscillate within some range, and it is also true for the perception intensity. An important observation is that a takeoff of $\bar{p}$ is often followed by a takeoff of f_c, indicating that the increased levels of perception intensity are the cause of the increased levels of cooperation. The increased levels of cooperation will lead to the disadvantage of high perception intensity, thus cause the decline of perception intensity ahead of the decline of cooperation levels. The oscillatory pattern here is similar to those in some previous studies (for example, Ref. [34] found “tides of tolerance [64]”, which resembles tides of perception here. A major difference is that our model have two independent variables by definition but they oscillate and correlate with each other in the evolutionary process; however, Ref. [34] only consider one variable (tolerance) which represents the conditional strategies), indicating that the constant oscillations may be a common characteristic in tag-based systems.

The above discussion only consider the average values (over the whole population) of perception intensity, thus may omit some important information which can further our understanding of the system. Now we explore how the distribution of perception intensity evolves. Fig. 4 depicts the evolution of perception intensity by showing the distributions of perception intensity both for cooperators and for defectors at different time steps. First, we compare the conditions without strategy mutation (where $m_s = 0$). If there is no perception cost, a large number of cooperators with high perception intensity can emerge quickly, accompanied by some defectors with low perception intensity. If there is perception cost, defectors with 0 perception intensity will persist well along with cooperators who have high perception intensity. Moreover, the distribution in this case is two-sided, i.e. individuals with high perception intensity and individuals with low perception intensity coexist, while the perception intensities are homogenized when there is no perception cost. Next, we compare the conditions with strategy mutation. We find less difference between the cases. Because of strategy mutation, there are always some defectors with high perception intensity inherited from cooperators, resulting in a dynamical equilibrium of perception intensity.



(a) $m_s = 0, m_p = 0.01$ (b) $m_s = 0, m_p = 0.1$

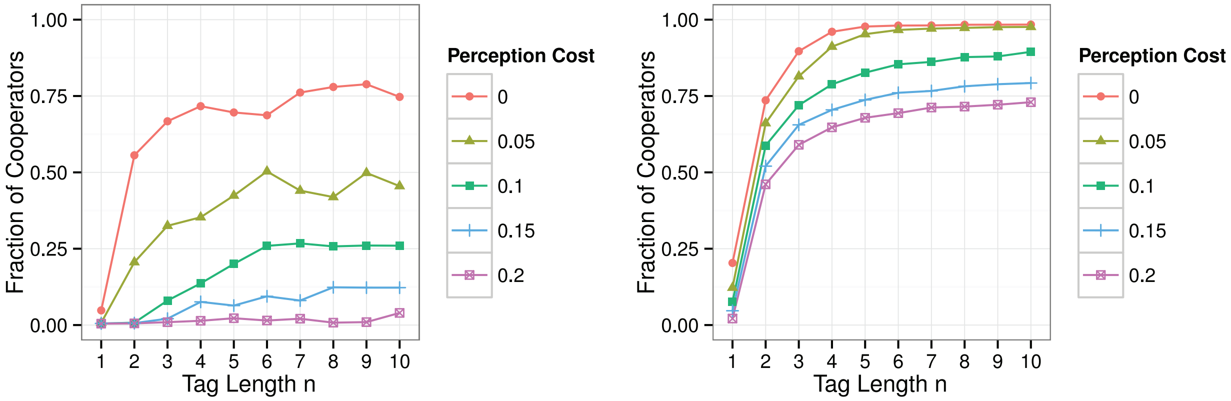
(c) $m_s = 0.01, m_p = 0.01$ (d) $m_s = 0.01, m_p = 0.1$

Fig. 9. Perception intensity as a function of tag mutation rate m_t for different perception costs. With strategy mutation, the perception intensity decreases as the tag mutation rate is increased. However, the effect of varying tag flexibility will be complicated when there is no strategy mutation. Other parameter: $b = 1.4,\ N = 10,\ L = 60,\ \text{K}{=}0.1$.

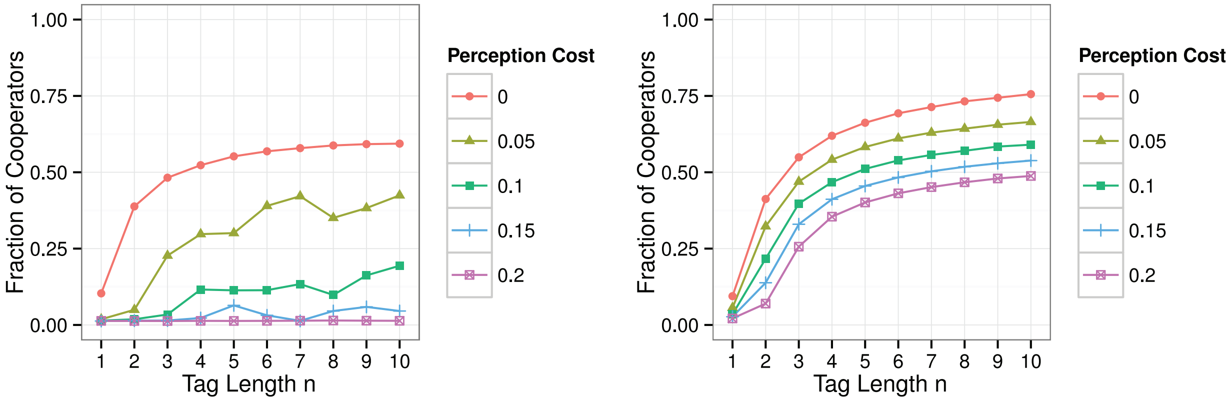
Perception cost leads to stronger selection pressure against high perception intensity, thus reduces the perception intensities of defectors more effectively. High perception intensities, however, are more important for cooperators, so we see more difference between the distribution for cooperators and the distribution for defectors if perception cost is in effect.

As demonstrated in the previous studies [34,52,65], cluster or group formation is important in tag-based models even with well-mixed population. Now we focus on the spatial patterns of the tag-based system and examine whether tag-mediated cooperative clusters can emerge and serve as a means of supporting global cooperation. In Fig. 5, it is clear that cooperative clusters with similar tags can emerge in all of the cases. It can also be seen that there are clear boundaries between different tag clusters, which prevent interactions between different clusters. Due to these boundaries, even when defectors can invade a cooperative cluster, they cannot expand their territory and will soon be replaced by surrounding cooperators. Without mutant defectors and perception cost ($m_s = 0$ and $c = 0$), some large clusters with clear boundaries can be formed and can hardly be invaded even with relatively low perception intensity. If, however, perception cost is added ($c = 0.1$), it will be harder for the cooperative clusters to maintain clear boundaries. As a result, defectors have more chances to invade the clusters. When strategy mutation is in effect ($m_s = 0.01$), we see that there are more clusters with small size and more boundary cooperators. This is because high perception intensity in cooperators is favored by selection under the threat of mutant defectors.

As discussed above, perception cost play an important role in the evolution of tag-mediated cooperation, but we have not yet consider the effects of other parameters such as tag mutation rate (m_t) and perception mutation rate (m_p) and the interactions between perception cost and these parameters. In Figs. 6 and 7, we provide an extensive sensitivity analysis on the effects of m_p and c on f_c and $\bar{p}$. Fig. 6 shows that f_c can be increased as c is decreased or as m_p is increased and high levels of cooperation appear at the left-top in the panels, whether there is strategy mutation or not. High perception mutation rate can expand the region of c that supports cooperation. This is because high perception mutation rate allows a rapid takeoff at the beginning and the fast adjustment of perception intensity, though it may also lead to more noise in the



(a) $m_s = 0, m_p = 0.01$ (b) $m_s = 0, m_p = 0.1$

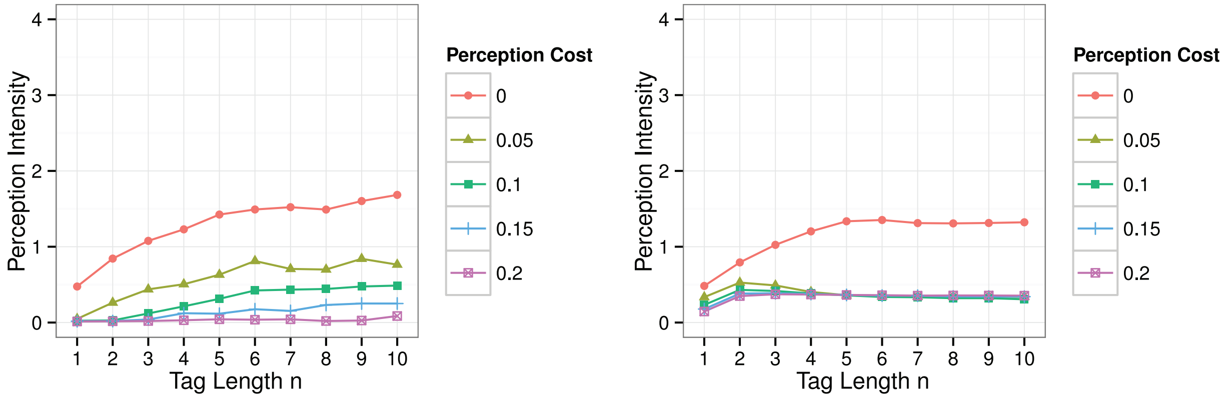


(c) $m_s = 0.01, m_p = 0.01$ (d) $m_s = 0.01, m_p = 0.1$

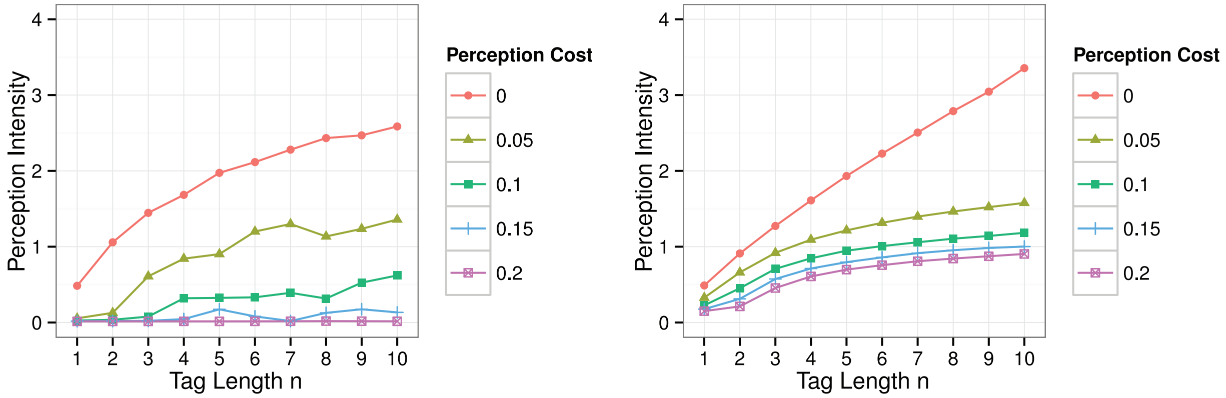
Fig. 10. Fraction of cooperators as a function of tag length n for different perception costs. Large tag space is beneficial to the evolution of cooperation, which is consistent with the previous studies. Other parameter: $m_t = 0.01$, $b = 1.4$, $L = 60$, K=0.1.

evolutionary dynamics. Fig. 7(a) shows that $\bar{p}$ is less than 1 at almost all the parameter points. Interestingly, there are two separated regions that support high perception intensity, one of which is at the left-top and the other is at the left-bottom. The former is coincident with the region of high cooperation levels but the latter is not. When perception mutation rate is low, it is hard for the population to achieve full or approximate full cooperation so the advantage of high perception intensity is maintained over time. As perception mutation rate is increased, there will be a rapid takeoff of cooperation, which reduces the advantage of high perception intensity. The region of high $\bar{p}$ is therefore reduced by the increase of m_p. If there is strategy mutation (Figs. 6(b) and 7(b)), the cooperation level and the perception intensity are highly correlated with each other. We see that the region of high levels of cooperation is accompanied by high levels of perception intensity. This observation confirms the importance of partial perception for promoting tag-mediated cooperation especially under the threat of mutant defectors.

Figs. 8 and 9 show the effects of m_t on f_c and $\bar{p}$. We see that f_c will be decreased as m_t is increased, which contradicts the findings in some previous studies [45,57]. It is found in Ref. [45] that “change your tags fast” is beneficial for supporting cooperation and it is found in Ref. [57] that cooperation can be promoted most effectively if tag mutation rate is moderate. These contradictory findings warn us about the danger of applying these theoretical models to the analysis of real world phenomenons. We think the effect of tag mutation rate on tag-mediated cooperation is still an open question and needs further research. The effect of m_t on $\bar{p}$ is simple with strategy mutation (Fig. 9(c) and (d)): as m_t is increased, $\bar{p}$ will be decreased. The effect, in contrast, will be more complicated when there is no strategy mutation (Fig. 9(a) and (b)). When there is no perception cost, $\bar{p}$ first decreases and then increases as m_t is increased. Once high levels of cooperation can be achieved, low perception intensity will be favored if tag mutation rate is high, because high tag mutation rate can cause low interaction intensity and reduce the benefits from cooperative interactions. As tag mutation rate is increased further, high levels of cooperation and constant interacting partners can hardly be maintained so the strength of perception mutation can play a significant role in the evolution of perception. Meanwhile, the strength of perception mutation can be reduced significantly by the introduction of perception cost.



(a) $m_s = 0, m_p = 0.01$ (b) $m_s = 0, m_p = 0.1$



(c) $m_s = 0.01, m_p = 0.01$ (d) $m_s = 0.01, m_p = 0.1$

Fig. 11. Perception intensity as a function of tag length n for different perception costs. In most cases, enlarging tag space obviously raises the perception intensity, but the effect is less significant if perception cost is introduced. Other parameter: $m_t = 0.01$, $b = 1.4$, $L = 60$, K=0.1.

It is predictable that a large tag space is necessary for supporting high levels of cooperation [44,66]. It is instructive to explore what tag length can ensure the emergence of cooperation. Figs. 10 and 11 show the effects of n on f_c and $\bar{p}$. We see that f_c has a drastic increase as n is increased from 1 to a moderate value and it will be increased slightly as n is increased further. This observation is consistent with the previous studies which also suggest that large tag space is beneficial for supporting cooperation [44,66]. In most of the cases, $\bar{p}$ is increased as n is increased. However, when there is no strategy mutation and the perception mutation rate is high (Fig. 11(b)), the perception intensity will converge to a low level. This is because there is no need to maintain high perception intensity so long as high levels of cooperation can be achieved and maintained. In other cases, as n is increased, higher perception intensity can be achieved by both selection and mutation and is thus helpful for resisting the invasion of defectors.

Finally, we have confirmed that our results are robust with respect to different types of payoff matrix (D_g-D_r scaling, benefit/cost ratio), to different updating fashions (synchronous, asynchronous), and to different initial fraction of cooperators. Namely, the qualitative results do not change much under a wide range of variations to our model.

4. Conclusion

To investigate whether the cognitive ability to perceive tags can emerge and serve as a means of partner selection in the evolution of cooperation, a question which dates back to Ref. [52], we have studied a model which consists of incomplete perception of tags, tag-based partner selection and spatial PDG. Taking into account the cognitive perspective, we considered both costless perception and costly perception to analyse the role of perception cost. The simulation results show that partial perception can emerge even when tag perception imposes some costs on the agents. It is also shown that high perception cost has detrimental effect on both the evolution of cooperation and the emergence of tag perception. In the microscopic view, cooperation and perception intensity show complex interaction patterns similar to those found in other tag-based models with different mechanisms, thus can deepen our understanding of tag-mediated cooperation as a whole.

Furthermore, we found that cooperative clusters or groups with clear boundaries can be formed through the help of tag perception, which can explain why mutant defectors can hardly invade the whole population.

In the analysis of evolutionary dynamics, we found that the emergence of partial perception may create boundary agents who have relatively low degrees of activity. As demonstrated in some previous studies, the real activity patterns, which is allowed by the so-called "game exit option" [67], may affect cooperation via the enhancement of network reciprocity. For instance, the agents may interact with their neighbors in a random fashion with heterogeneous activity, resulting in cascading failures and the recoveries of cooperation especially on scale-free network [68]. A more realistic scenario is where the agents select their partners stochastically based on payoffs of their neighbors [69,70]. This scenario is empirically meaningful because in a real society a human tends to select some favorable friends from all the acquaintances. An important finding is that the reduced "effective degree" may explain how network reciprocity works in the evolution of cooperation [69]. In the simulations of our model, we can also observe the time evolution of real effective degree which can be predicted from the average perception intensity. Cooperators can frequently avoid interactions with others by regarding more agents as out-group members if they have high perception intensity, thus prevent the absorption by all-defectors-state in END period. An important difference between our model and the previous partner selection models is that the system always have full interaction state at the initiation step due to the assumption that the agents have no initial perception ability. However, the low activity level or effective degree can emerge as a result and then support the establishment and maintenance of cooperation. This observation demonstrates that selective interaction is not only beneficial to the evolution of cooperation but also can be favored by natural selection, thus justifies the use of selective interaction in various models especially in biology.

It is worth noting that high perception cost may impede the evolution of cooperation in tag-based models. If the cognitive abilities such as tag perception are empirically costly in real world, the question of whether cooperation can be supported by tag mechanism will remain unsolved. On the one hand, the real costs incurred by the individuals who use their cognitive abilities need to be examined. Indeed, numerous experimental studies with human subjects have demonstrated that in-group biases can be enabled by our brain in a fast and automatic fashion with relatively low cognitive cost [71–73], suggesting that the cognitive foundation of in-group biased behavior may have its evolutionary roots [43,56]. On the other hand, even if the empirical data have shown that tag-mediated cooperation can benefits from the low cognitive cost, there is still an unanswered question: why and how the cognitive abilities, especially in humans, to distinguish between "us" and "them" without high mental effort emerge in biological evolution [74,75]. It is an important direction of further research to deeply investigate the cognitive foundation of tag-mediated cooperation.

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