



Voluntary vaccination dilemma with evolving psychological perceptions

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ABSTRACT

Voluntary vaccination is a universal control protocol for infectious diseases. Yet there exists a social dilemma between individual benefits and public health: non-vaccinators free ride via the herd immunity from adequate vaccinators who bear vaccination cost. This is due to the interplay between disease prevalence and individual vaccinating behavior. To complicate matters further, individual vaccinating behavior depends on the perceived vaccination cost rather than the actual one. The perception of vaccination cost is an individual trait, which varies from person to person, and evolves in response to the disease prevalence and vaccination coverage. To explore how evolving perception shapes individual vaccinating behavior and thus the vaccination dynamics, we provide a model combining epidemic dynamics with evolutionary game theory which captures the voluntary vaccination dilemma. In particular, individuals adjust their perception based on the inertia effect in psychology and then update their vaccinating behavior through imitating the behavior of a more successful peer. We find that i) vaccination is acceptable when the expected vaccination cost considering perception and actual vaccination cost is less than the maximum of the expected non-vaccination cost; ii) the *evolution* of perception is a “double-edged sword” for vaccination dynamics: it can improve vaccination coverage when most individuals perceive exaggerated vaccination cost, and it inhibits vaccination coverage in the other cases.

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1. Introduction

Vaccination is the most economical and effective public health intervention to control infectious diseases. Considering religious beliefs and civil liberties, voluntary vaccination policies are implemented in many countries. With voluntary vaccination, individuals voluntarily decide whether to vaccinate or not. Wherein minimizing costs is the guideline for individuals' decision-making. Both vaccination and non-vaccination can bring costs. A vaccinator will bear vaccination cost, which includes vaccine cost, time loss, possible side effects, and things like that. For non-vaccinators, their costs further depend on their healthy status. If a non-vaccinator gets away with being infected, he/she does not bear any loss. Whereas if a non-vaccinator is infected, he/she will bear infection cost, which includes suffering from illness, medical treatment fees,

loss in productivity, and so on. The probability of non-vaccinators being infected relates to the proportion of vaccinators in the population. Furthermore, non-vaccinators' expected cost and thus individuals' decision-making depend on the other individuals' behavior. Therefore, voluntary vaccination can be studied in the framework of game theory, which describes the situation where individuals' payoff depends on the strategies of others in the population (Feng et al., 2017; Li and Wang, 2015; Pacheco et al., 2009).

Previous studies have combined a game-theoretical model with an epidemic model to study voluntary vaccination (Bauch, 2005; Bauch and Earn, 2004; Bauch et al., 2003; Fu et al., 2010; Galvani et al., 2007; Wu et al., 2011; Zhang et al., 2010). They find that there is a social dilemma between individual benefits and public health in the coupled disease-behavior system. Specifically, the individual optimum level, at which individual cost minimizes, is less than the population optimum level, at which the cost of the whole population minimizes. In disease-behavior systems, individuals decide whether to vaccinate or not according to the costs of vaccination and infection. Typically, the actual costs of vaccination

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and infection are assumed to be known, and studies focus on how vaccination strategies (Bhattacharyya and Bauch, 2011; Poletti et al., 2009; Reluga, 2010), the update rules of strategies (Fu et al., 2010; Shim et al., 2012), and population structures (Bhattacharyya and Bauch, 2010; Chapman et al., 2012; Perisic and Bauch, 2009) influence vaccination dynamics. In fact, the actual costs are inaccessible for individuals. That's because an individual can not have connections with all the other individuals in the population, and it is hard to get the accurate information on vaccination and diseases from the connected ones.

Empirical studies have shown that individuals' decision-making depends on their perceived costs of vaccination and infection instead of the true costs (Bish et al., 2011; Coelho and Codeço, 2009; d'Onofrio et al., 2011; Reluga et al., 2006; Xia and Liu, 2014). Generally, perceived costs differ from the true ones. The discrepancy dramatically influences vaccination dynamics. For example, the measles-mumps-rubella (MMR) vaccine scare occurred in England and Wales in the 1990s (Jansen et al., 2003). At that time, people believed the false rumor that MMR vaccine caused autism. Their perceived vaccination costs were much greater than the true vaccination cost. And they refused to vaccinate their children. Then the vaccination coverage declined and measles outbreaks occurred. On the other hand, perceived costs may be lower than the true cost. Consider influenza vaccines having side effects. They may cause fever. An individual has taken influenza vaccines several times. Fortunately, the individual has never run a fever caused by the vaccines and never heard other vaccinated individuals suffered side effects. So, the individual may perceive influenza vaccines have no side effect, and his/her perceived vaccination cost is less than the true cost. How do perceived costs shape individual vaccinating behavior and thus the vaccination dynamics? To address this, we study the voluntary vaccination dynamics with perception. We assume all the individuals know the actual infection cost, and perceive vaccination cost. So, perception in this paper refers in particular to the perception on vaccination cost. Perception is an individual trait. It varies from person to person. There are two main reasons for this. One is individuals have various ways to obtain information, such as chat with friends, news media, and online social media. The other one is the circumstances around individuals are different (Fierro and Liccardo, 2013). Individuals getting false information on side effects of a vaccine perceive high vaccination cost. And individuals whose friends get away with the side effect of a vaccine perceive low vaccination cost (Anon, 2000; Yarwood et al., 2005). To complicate matters further, individual perception evolves along with disease prevalence and vaccination coverage. In previous studies of vaccination dynamics with evolving perceptions, perceptions have been assumed to evolve according to the curves assumed in advance (Bauch and Bhattacharyya, 2012; Nakamaru and Dieckmann, 2009). Moreover, Bayesian theory has been used to characterize perception update based on reported cases of disease and potentially adverse events from the vaccine (Coelho and Codeço, 2009; Xia and Liu, 2014). Here, based on the inertia effect in psychology (Huff et al., 1992; Tripsas and Gavetti, 2000), we propose a self-learning perception update rule, which depends on individuals' own perceived and actual payoffs. With this update rule, individuals prefer keeping their perceptions when they bear medium costs; otherwise, they adjust their perceptions.

To figure out the voluntary vaccination dynamics with evolving perceptions, a minimal model is proposed by us. The model focuses on vaccination dynamics over several epidemic seasons. In each epidemic season, the vaccination dilemma is described by a two-stage game: the first stage of vaccination campaign and the second stage of disease transmission (Fu et al., 2010). In the first stage, individuals update their strategy, consisting of the perception on vaccination cost and vaccinating behavior. As vaccinating behavior is driven by perception, individuals adjust

their perceptions first, and then update their vaccinating behavior (Doutor et al., 2016; Galvani et al., 2007; Xia and Liu, 2014). In the second stage, the disease spreads, and the epidemic model determines whether a non-vaccinator becomes infected or not. When the disease outbreak ends, the population goes into the next epidemic season. Our model captures the adaptiveness of the coupled disease-behavior system (Galvani et al., 2016): individuals adjust perceptions and vaccinating behaviors in response to the progress of disease and the others' vaccinating behaviors.

This paper tries to address two issues: i) what's the voluntary vaccination dynamics with perceptions on vaccination cost; ii) how the evolution of perception influences vaccination dynamics. For issue i), we study the case of fixed perception, where individual perception does not change over time, and the case of evolving perception, where perception changes in response to dynamic vaccination coverage and disease prevalence. Then, issue ii) is explored by comparing the vaccination dynamics for these two cases.

2. Model

Consider an infinite and well-mixed population, where voluntary vaccination is implemented. Our model focuses on vaccination dynamics over several epidemic seasons. Specifically, we focus on the vaccination dynamics for pediatric diseases (e.g. measles, mumps, rubella and pertussis), and the players of the vaccination game are parents (Bauch, 2005). Here, an epidemic season is defined as the duration between the ends of two successive outbreaks. And for every epidemic season, the voluntary vaccination dilemma is described by a two-stage game (see Fig. 1). Stage 1 is the vaccination campaign. At this stage, no one is infected, and individuals update their strategies. At stage 2, diseases spread, and individuals have no chance to adjust their strategies. We assume vaccines provide perfect immunity, and vaccinators cannot be infected. However, non-vaccinators take a risk of being infected.

Individual strategy is specified by two traits: the perception on vaccination cost, and the vaccinating behavior. Here, we assume all the individuals get the actual infection cost, which is set to be 1 for simplicity, but perceive vaccination cost. For an individual, the perception, which describes the relationship between actual vaccination cost and perceived vaccination cost, is either high or low. They are denoted by P_h and P_l , respectively. The former (latter) shows that the perceived vaccination cost is greater (less) than the actual one. Thus, compared to individuals with actual vaccination cost, individuals with high (low) perception have negative (positive) attitudes towards vaccination. Vaccination and Non-vaccination are two optional vaccinating behaviors. They are denoted by V and N , respectively. Therefore, the strategy set is $\{P_hV, P_lV, P_hN, P_lN\}$.

As the introduction of perception on vaccination cost, individuals have actual payoffs and perceived payoffs. For vaccinators, the actual payoff is $-r$, where r ($0 < r < 1$) denotes actual vaccination cost. The perceived payoff of individuals with P_hV is $-H_p r$ ($H_p > 1$ is the ratio of perceived vaccination cost to actual vaccination cost for vaccinators with high perception), and the perceived payoff of individuals with P_lV is $-L_p r$ ($0 < L_p \leq 1$ is the ratio of perceived vaccination cost to actual vaccination cost for vaccinators with low perception). For non-vaccinators, the actual payoffs further depend on their health status. If a non-vaccinator is healthy, the payoff is 0; otherwise, it is -1 . Because all the individuals know the actual infection cost, non-vaccinators' perceived payoff is the expected value of their actual payoffs. Thus, the perceived payoff for non-vaccinators is $-1 \cdot w(x_h + x_l) + 0 \cdot (1 - w(x_h + x_l)) = -w(x_h + x_l)$, where $w(x_h + x_l)$ denotes the probability of a non-vaccinator being infected when the fraction of vaccinators in populations is $x_h + x_l$. For the voluntary vaccination game with perception on vaccination cost, potential strategies, actual payoffs, and perceived payoffs are summarized in Table 1.

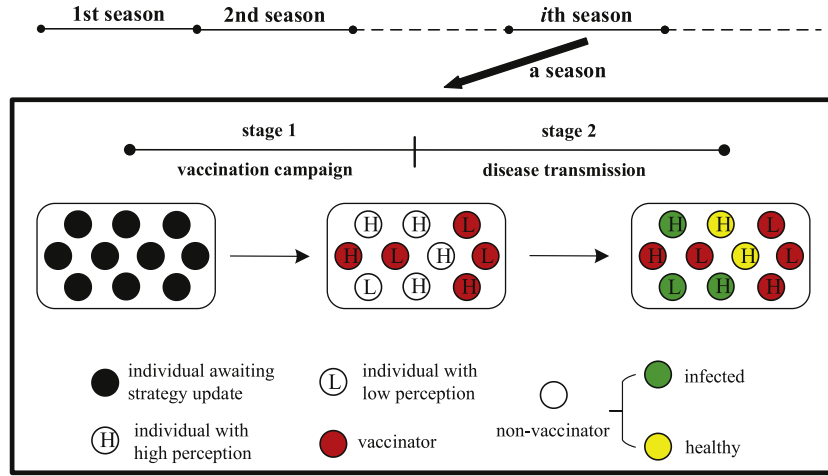


Fig. 1. The schematic of the model. The model focuses on vaccination dynamics over several epidemic seasons. Every epidemic season is described by a two-stage game. In the first stage of vaccination campaign, no one is infected, and individuals independently update their strategies comprised of perception on vaccination cost and vaccinating behavior. Vaccinators get perfect immunity, and non-vaccinators take a risk of being infected. In the second stage of disease transmission, diseases spread, and individuals have no chance to update their strategies. At the end of the second stage, whether each non-vaccinator becomes infected is found out.

Table 1

Potential strategies, the fractions of strategies, and the corresponding actual and perceived payoffs for the vaccination game. In the last column of the table, $H_p > 1$ is the ratio of perceived vaccination cost to actual vaccination cost for vaccinators with high perception, $0 < L_p \leq 1$ is the ratio of perceived vaccination cost to actual vaccination cost for vaccinators with low perception, and $w(x_h + x_l)$ denotes the probability of a non-vaccinator being infected when the fraction of vaccinators in populations is $x_h + x_l$.

Strategy	Fraction	Actual Payoff	Perceived Payoff
$P_h V$	x_h	$-r$	$-H_p r$
$P_l V$	x_l	$-r$	$-L_p r$
$P_h N$	y_h	infected: -1 healthy: 0	$-w(x_h + x_l)$
$P_l N$	y_l	infected: -1 healthy: 0	$-w(x_h + x_l)$

We notice that the probability of non-vaccinators being infected plays an important role in the voluntary vaccination dilemma. The probability influences non-vaccinators' payoffs and thus individuals' decision-making. In our model, there is not any infection in the first stage of vaccination campaign, and meanwhile there is no strategy update in the second stage of disease transmission. This assumption separates behavior dynamics and epidemic dynamics. Therefore, the probability of non-vaccinators being infected in the steady state of disease transmission serves as the probability of non-vaccinators being infected which individuals know in the stage of vaccination campaign. The probability can be obtained from epidemic models.

Here, the SIR model is used to model disease propagation in the second stage (Keeling and Eames, 2005). Individuals in the population are divided into three classes: susceptible individuals (S), who can catch the disease if exposed to infected individuals; infected individuals (I), who are infected and can infect others; recovered individuals (R), who are vaccinated or recovered from the disease and gain immunity against the disease. Here, the disease is not deadly, and all the classes of individuals have the same death rate. The fractions of susceptible, infected and recovered individuals are represented by S , I and R , respectively. The evolution of each class of individuals can be expressed by

$$\frac{dS}{dt} = \mu(1 - x_h - x_l) - \eta SI - \mu S, \quad (1)$$

$$\frac{dI}{dt} = \eta SI - \gamma I - \mu I, \quad (2)$$

$$\frac{dR}{dt} = \mu(x_h + x_l) + \gamma I - \mu R, \quad (3)$$

where, the mean birth rate μ equals the mean death rate μ to keep the population size constant, η is the mean disease transmission rate, and γ is the mean recovery rate. The basic reproductive ratio R_0 is the mean number of secondary infections caused by one infected individual in a completely susceptible population. We have $R_0 = \eta/(\mu + \gamma)$ (Anderson and May, 1991), and a large R_0 means strong infectivity. If $R_0 \leq 1$, the disease will not spread in populations. Here, we consider the case of $R_0 > 1$. When the fraction of vaccinators, $x_h + x_l$, exceeds a critical value, $1 - 1/R_0$, the herd immunity arises. At this time, the probability of a non-vaccinator being infected, $w(x_h + x_l)$, is 0, and populations evolve to the disease-free state $(S^*, I^*) = (1 - (x_h + x_l), 0)$. When $x_h + x_l < 1 - 1/R_0$, populations converge to $(S^*, I^*) = (1/R_0, \mu(R_0(1 - x_h - x_l) - 1)/\eta)$. A non-vaccinator either becomes infected or dies a natural death. When the epidemiological dynamics stabilizes, for non-vaccinators, the fraction of infected individuals is $\eta S^* I^*$, and that of natural death is μS^* in unit time. At this time, the probability of non-vaccinators being infected is $\eta S^* I^*/(\eta S^* I^* + \mu S^*) = 1 - 1/R_0(1 - x_h - x_l)$. Therefore, $w(x_h + x_l)$ is given by

$$w(x_h + x_l) = \begin{cases} 0, & \text{if } x_h + x_l \geq 1 - \frac{1}{R_0}; \\ 1 - \frac{1}{R_0(1 - x_h - x_l)}, & \text{if } 0 \leq x_h + x_l < 1 - \frac{1}{R_0}. \end{cases} \quad (4)$$

The probability, $w(x_h + x_l)$, is a decreasing function of the fraction of vaccinators. For simplicity, $w(x_h + x_l)$ is abbreviated to w in the following.

We study both of the fixed perception case and the evolving perception case. They are shown as follows.

2.1. Fixed perception model

Here, individual perception is fixed and does not change over time. In the stage of vaccination campaign, individuals adjust only vaccinating behavior. An arbitrary individual i randomly chooses an individual j as his/her role model. The probability that i imitates j 's behavior is given by the Fermi function

$$\frac{1}{1 + \exp^{-\beta(a_j - f_i)}}, \quad (5)$$

where, β is the intensity of selection, a_j and f_i denote individual j 's actual payoff and i 's perceived payoff in the last epidemic sea-

son, respectively. Otherwise, individual i persists in his/her behavior. Here, β measures the dependence of decision-making on the difference in payoffs. Large β , strong selection, means high dependence, and small β , weak selection, means low dependence. Recent experimental results suggest that the intensity with which humans adjust their strategies might be low (Wu et al., 2010; 2016; Zhang et al., 2015). Therefore, we focus on the situation of weak selection, $\beta \ll 1$, in the following.

Because individual perception does not evolve, the fraction of high perception, C , and that of low perception, $1 - C$, do not change over time. That is to say, $x_h + y_h = C$ and $x_l + y_l = 1 - C$ always hold. Thus, the dynamics of x_h and that of x_l are enough to describe the evolutionary dynamics of populations. The vaccination dynamics is expressed as (see Appendix A for details)

$$\begin{cases} \dot{x}_h = \frac{1}{2}(C - x_h)(x_h + x_l)\left(1 + \frac{\beta}{2}(w - r)\right) \\ \quad - \frac{1}{2}x_h(1 - x_h - x_l)\left(1 - \frac{\beta}{2}(w - H_p r)\right) \\ \dot{x}_l = \frac{1}{2}(1 - C - x_l)(x_h + x_l)\left(1 + \frac{\beta}{2}(w - r)\right) \\ \quad - \frac{1}{2}x_l(1 - x_h - x_l)\left(1 - \frac{\beta}{2}(w - L_p r)\right) \end{cases} \quad (6)$$

2.2. Evolving perception model

As individual vaccinating behavior is driven by perception, individuals update their perceptions first, and then they adjust their vaccinating behavior based on the updated perceptions. Our perception update rule is based on the inertia effect in psychology (Pitz, 1969). Here, the inertia effect has three meanings. First, infected non-vaccinators bearing the maximum cost are more likely to have low perception. Individuals with low perception have positive attitudes toward vaccination. After bearing the maximum cost, infected non-vaccinators seek vaccination to reduce their cost. Second, vaccinators bearing the medium costs prefer keeping their perceptions. Third, healthy non-vaccinators do not bear any loss, and are more likely to have high perception. Individuals with high perception have negative attitudes toward vaccination. Healthy non-vaccinators attempt to continue free riding. Therefore, the perception update rule can be expressed mathematically as follows. For any individual i , he/she updates the perception to be P_h with the probability given by

$$\frac{1}{1 + \exp[-\beta(a_i - \hat{f}_i)]}, \quad (7)$$

where, $0 < \beta \ll 1$ is the selection intensity, a_i and \hat{f}_i represent individual i 's actual payoff and perceived payoff in the last epidemic season, respectively. Otherwise, individual i adopts P_l . After the perception update, individuals adjust their vaccinating behavior. Individuals are more likely to imitate the behavior of a more successful peer, who has higher actual payoff. Specifically, individual i randomly chooses an individual j as the role model. The probability that individual i learns individual j 's vaccinating behavior is given by the Fermi function

$$\frac{1}{1 + \exp[-\beta(a_j - \hat{f}_i)]}, \quad (8)$$

where, a_j denotes the actual payoff of individual j in the last epidemic season, and \hat{f}_i denotes the perceived payoff of individual i with updated perception in the current season. Otherwise, individual i holds to his/her vaccinating behavior.

Because of $x_h + x_l + y_h + y_l = 1$, the dynamics of three strategies are enough to describe the dynamics of populations. The vaccination dynamics is expressed as (see Appendix B for details)

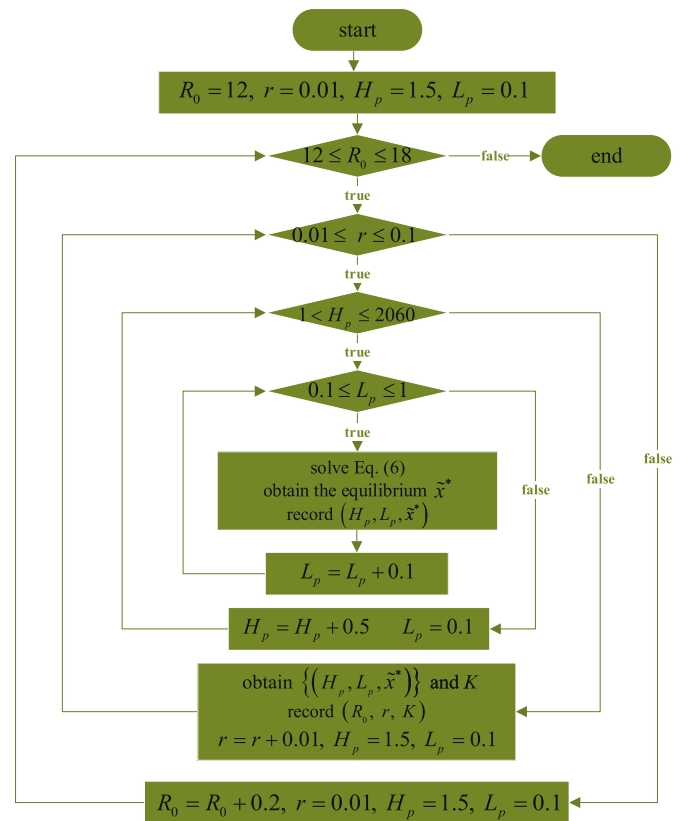


Fig. 2. The flow chart of figuring out the existence condition of the interior equilibrium for vaccination dynamics with fixed perception.

$$\begin{cases} \dot{x}_h = -x_h + \frac{2-\beta r}{4}(x_h + x_l) \\ \quad + \frac{\beta r}{8}K(1 + x_h + x_l) + \frac{\beta}{8}(x_h + x_l)(1 - x_h - x_l)T_h \\ \dot{x}_l = x_h - \frac{2-\beta r}{4}(x_h + x_l) - \frac{\beta r}{8}K(1 + x_h + x_l) \\ \quad + \frac{\beta}{8}(x_h + x_l)(1 - x_h - x_l)T_l \\ \dot{y}_h = -y_h + \frac{1}{2}(1 - x_h - x_l) + \frac{\beta r}{8}K(1 - x_h - x_l) \\ \quad - \frac{\beta}{8}(x_h + x_l)(1 - x_h - x_l)T_h \end{cases}, \quad (9)$$

where $K = H_p x_h + L_p x_l$, $T_h = 2w - H_p r$ and $T_l = 2w - 2r - L_p r$.

3. Results

3.1. Vaccination dynamics with fixed perception

As the complexity and nonlinearity of Eq. (6), we combine theoretical analysis with numerical calculations to study the dynamics. There are at least two equilibria: the pure vaccinator equilibrium $\tilde{e}_1 = (C, 1 - C)$ and the pure non-vaccinator equilibrium $\tilde{e}_2 = (0, 0)$. It is easy to obtain them analytically. In addition, there is an interior equilibrium \tilde{e}_3 , where vaccinators coexist with non-vaccinators. \tilde{e}_3 emerges under certain condition. Numerical calculations are used to obtain the existence condition and stability of \tilde{e}_3 . There are five parameters influencing the vaccination dynamics: the proportion of individuals with high perception C , basic reproduction ratio R_0 , actual vaccination cost r , the value of high perception H_p , and the value of low perception L_p . Three prototypical values of C are discussed here: $C = 0.1$, $C = 0.5$ and $C = 0.9$. They represent a few of, half of, and most of individuals with high perception, respectively. We consider $12 \leq R_0 \leq 18$, the typical R_0 values for measles (Anderson and May, 1982). The actual vaccination cost r takes value between 0.01 and 0.1. Here, the lower bound 0.01 and the upper bound 0.1 imply vaccination incurs cost and that the vaccination cost is much less than the infection cost, which is set

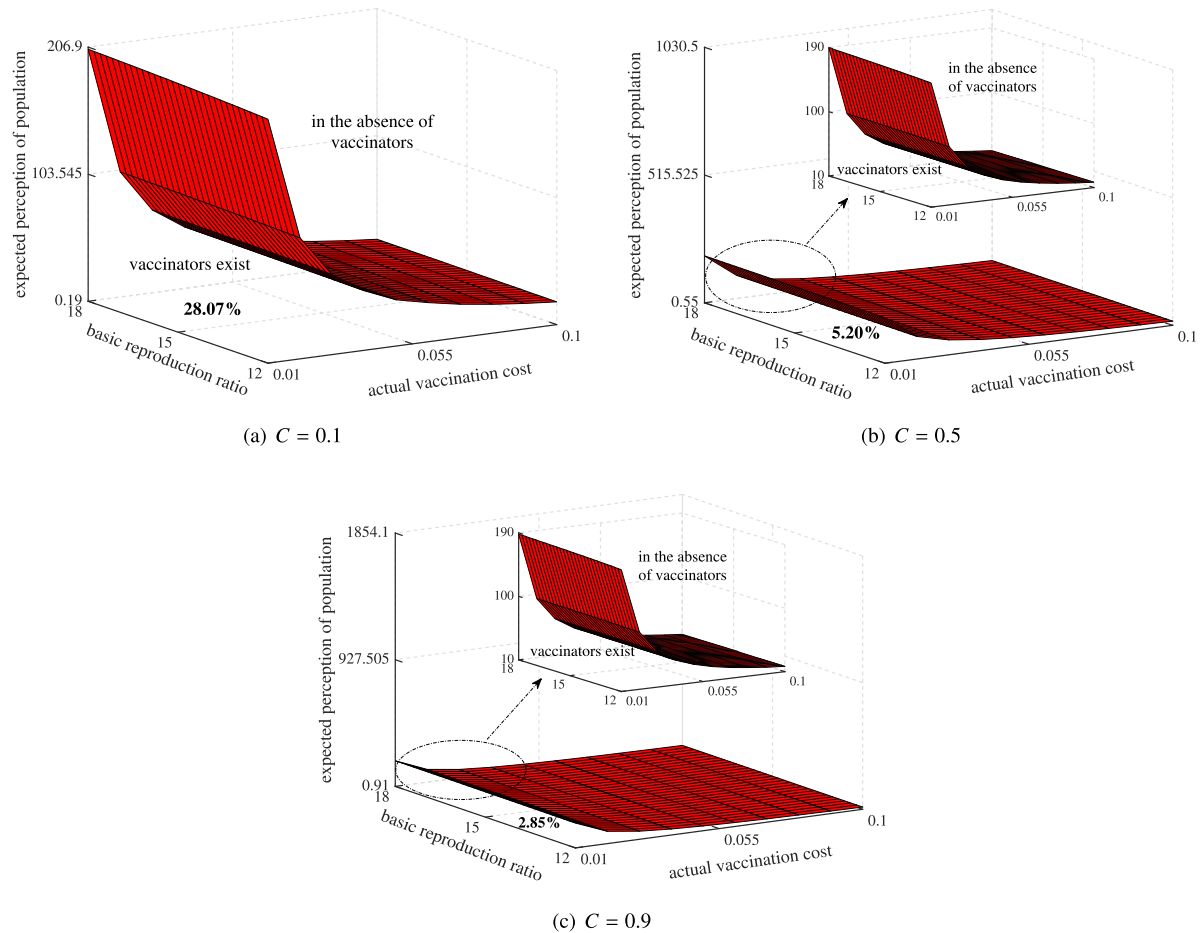


Fig. 3. The condition of vaccinators coexisting with non-vaccinators for fixed perception case. In each panel, the red surface is the critical surface. For parameters below the surface, the interior equilibrium \bar{e}_3 , where vaccinators coexist with non-vaccinators, exists. For parameters above the surface, \bar{e}_3 is absent, and the equilibrium is \bar{e}_2 where only non-vaccinators exist. Here, z-axis represents the expected perception of population which is expressed as $CH_p + (1 - C)L_p$. The percent in the bottom-left corner is the percentage of the volume below the critical surface. In panels (b) and (c), the inset magnifies the critical surface to make it clearly. Parameters: the intensity of selection $\beta = 0.01$; (a) the proportion of high perception $C = 0.1$; (b) $C = 0.5$; (c) $C = 0.9$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

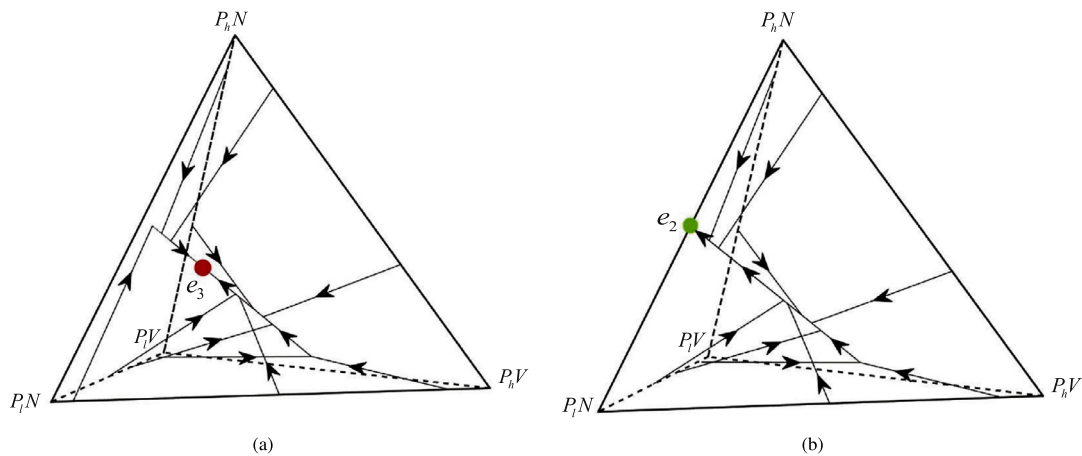


Fig. 4. Voluntary vaccination dynamics with evolving perception. The tetrahedrons represent the state space $\{(x_h, x_l, y_h, y_l) : x_h, x_l, y_h, y_l \geq 0, x_h + x_l + y_h + y_l = 1\}$ (Sasaki et al., 2012). The vertices P_hV , P_lV , P_hN and P_lN correspond to four homogeneous states where the population consists exclusively of vaccinators with high perception, vaccinators with low perception, non-vaccinators with high perception, and non-vaccinators with low perception, respectively. (a) When $(r + (H_p + L_p)r/2)/2 < 1 - 1/R_0$, populations with any mixing states initially evolve to the interior equilibrium e_3 . At e_3 , vaccinators coexist with non-vaccinators. (b) When $(r + (H_p + L_p)r/2)/2 > 1 - 1/R_0$, the interior equilibrium e_3 is absent, and populations with any initial states evolve to the pure non-vaccinator equilibrium e_2 . Parameters: the intensity of selection $\beta = 0.01$; (a) $R_0 = 13$, $r = 0.01$, $H_p = 352$, $L_p = 0.1$; (b) $R_0 = 15$, $r = 0.01$, $H_p = 450$, $L_p = 0.7$.

to be 1, respectively. For individuals with high (low) perception, the perceived vaccination cost is larger (less) than actual vaccination cost. Therefore, H_p (L_p) takes value in $(1, 2060]$ ($[0.1, 1]$). The increments for R_0 , r , H_p and L_p are 0.2, 0.01, 0.5 and 0.1, respectively. For every prototypical C , we try to figure out the existence condition and stability of the interior equilibrium for Eq. (6) as follows (also see Fig. 2).

Step 1.1 For any R_0 , r , H_p , and L_p , use MATLAB function 'solve' to find the equilibrium for Eq. (6). Moreover, use MATLAB function 'ode45' to verify the stability of the equilibrium. To avoid populations always evolve to the pure non-vaccinator equilibrium $\tilde{e}_2 = (0, 0)$, there are vaccinators at the initial state. Numerical calculations show that the stable equilibrium always exists, and it is unique. At the stable state, the vaccination coverage $\tilde{x}^* = \tilde{x}_h^* + \tilde{x}_l^*$ is either zero or positive. Here, $\tilde{x}^* = 0$ means the interior equilibrium \tilde{e}_3 is absent, and $\tilde{x}^* > 0$ means \tilde{e}_3 exists.

Step 1.2 Fix R_0 and r , and H_p and L_p take all possible values. For any pair of (H_p, L_p) , repeat **Step 1.1** to obtain \tilde{x}^* . Finally, we obtain $\{(H_p, L_p, \tilde{x}^*)\}$. Numerical calculations show that there is a boundary between $\tilde{x}^* = 0$ and $\tilde{x}^* > 0$. This boundary is expressed as $CH_p + (1 - C)L_p = K$, where K is constant. If $CH_p + (1 - C)L_p \geq K$, $\tilde{x}^* = 0$; otherwise, $\tilde{x}^* > 0$.

Step 1.3 R_0 and r take all possible values. For any pair of (R_0, r) , repeat **Step 1.2** to obtain K . Finally, we obtain $\{(R_0, r, K)\}$, which is represented as the critical surface in Fig. 3.

Fig. 3 shows \tilde{e}_3 emerges for parameters (the actual vaccination cost r , the basic reproduction ratio R_0 , and the expected perception of population $CH_p + (1 - C)L_p$) below the critical surface. When \tilde{e}_3 exists, populations evolve to and stabilize at \tilde{e}_3 . When \tilde{e}_3 is absent, \tilde{e}_2 is stable, and populations converge to \tilde{e}_2 . Here, \tilde{e}_1 is unstable. Therefore, vaccinators coexist with non-vaccinators only when parameters are below the critical surface. The volume below the critical surface shrinks with increasing C , increasing actual vaccination cost r , and decreasing basic reproduction ratio R_0 . These results coincide with the facts: individuals are willing to refuse vaccination when they perceive high vaccination cost, or vaccination causes large loss, or the disease is weakly infective. As mutation is not considered here, if a population consists exclusively of vaccinators or non-vaccinators at the initial state, individual vaccinating behavior will not evolve. Therefore, we consider the situation where vaccinators and non-vaccinators coexist at the initial state here.

3.2. Vaccination dynamics with evolving perception

Through the analysis of Eq. (9) (see Appendix C), we find that vaccinators can coexist with non-vaccinators. The condition of co-existence is

$$\frac{1}{2} \left(r + \frac{H_p + L_p}{2} r \right) < 1 - \frac{1}{R_0}. \quad (10)$$

From Eq. (10), individuals are willing to vaccinate when the expected vaccination cost is less than the maximum of the expected non-vaccination cost (see Fig. 4(a)). The left hand side of Eq. (10) is the expected vaccination cost. It consists of actual (objective) vaccination cost r and perceived (subjective) vaccination cost $(H_p + L_p)r/2$. The present work is based on weak selection $\beta \ll 1$. From the perception update rule (see Eq. (7)), individuals' payoffs have little influence on the evolution of perception. Therefore, individuals' perception is P_h or P_l with the same probability 1/2, and the expected value of perceived vaccination cost is $(H_p + L_p)r/2$. During the whole evolution process, actual cost and perceived cost play the same role. Therefore, the expected vaccination cost is $(r + (H_p + L_p)r/2)/2$. The right hand

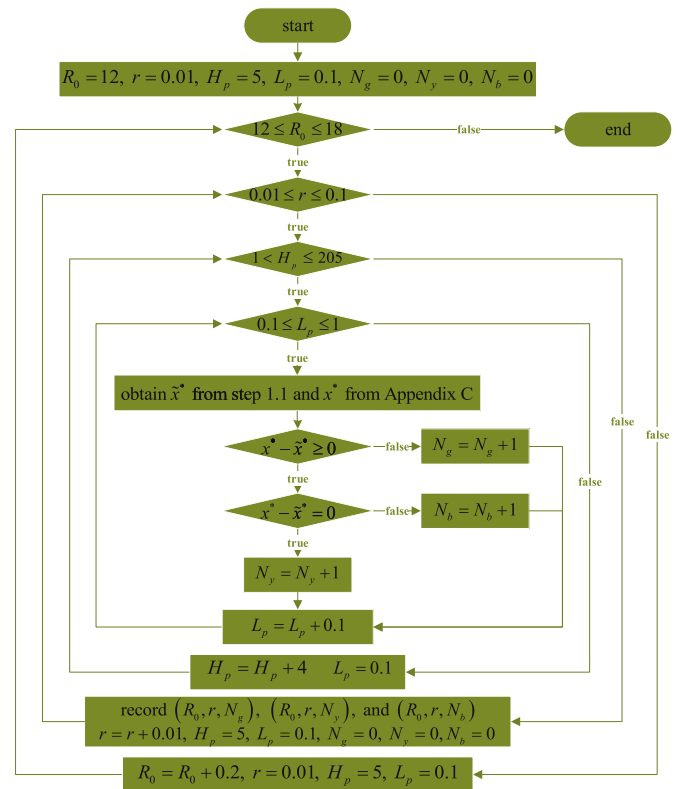


Fig. 5. The flow chart of figuring out the impact of the evolution of perception on vaccination dynamics.

side of Eq. (10) is the maximum of the expected non-vaccination cost. For non-vaccinators, the expected cost is $1 \cdot w + 0 \cdot (1 - w) = w = 1 - 1/(R_0(1 - x_h - x_l))$, where w denotes the probability of non-vaccinators being infected. Thus, the maximum of the expected non-vaccination cost is $1 - 1/R_0$. On other hand, when $(r + (H_p + L_p)r/2)/2 > 1 - 1/R_0$, populations evolve to the pure non-vaccinator equilibrium e_2 (see Appendix C). At this state, half of non-vaccinators have high perception and the other half have low perception (see Fig. 4(b)).

Notably, Eq. (10) is informative in the sense that it explicitly figures out that individual vaccinating behavior is affected not only by the actual costs of vaccination and infection but also by the psychological perception. This highlights the importance of perceptions. This simple and generalised condition could shed light on how vaccination behavior is influenced by psychological factors.

3.3. Impact of the evolution of perception on vaccination dynamics

The comparison between vaccination dynamics with evolving perception and that with fixed perception highlights the effect of the evolution of perception on vaccination dynamics. For three prototypical C ($C = 0.1$, $C = 0.5$ and $C = 0.9$), we explore how the evolution of perception influences vaccination dynamics as follows (also see Fig. 5).

Step 3.1 Define three variables N_b , N_y and N_g . Their initial values are 0.

Step 3.2 For any R_0 , r , H_p , and L_p , figure out the vaccination coverage of populations with fixed perception \tilde{x}^* (see Step 1.1) and that with evolving perception x^* (see Appendix C). Then, make a comparison between x^* and \tilde{x}^* with an accuracy of 15 decimal places. If $x^* > \tilde{x}^*$, add 1 to N_b . If $x^* = \tilde{x}^*$, add 1 to N_y . If $x^* < \tilde{x}^*$, add 1 to N_g .

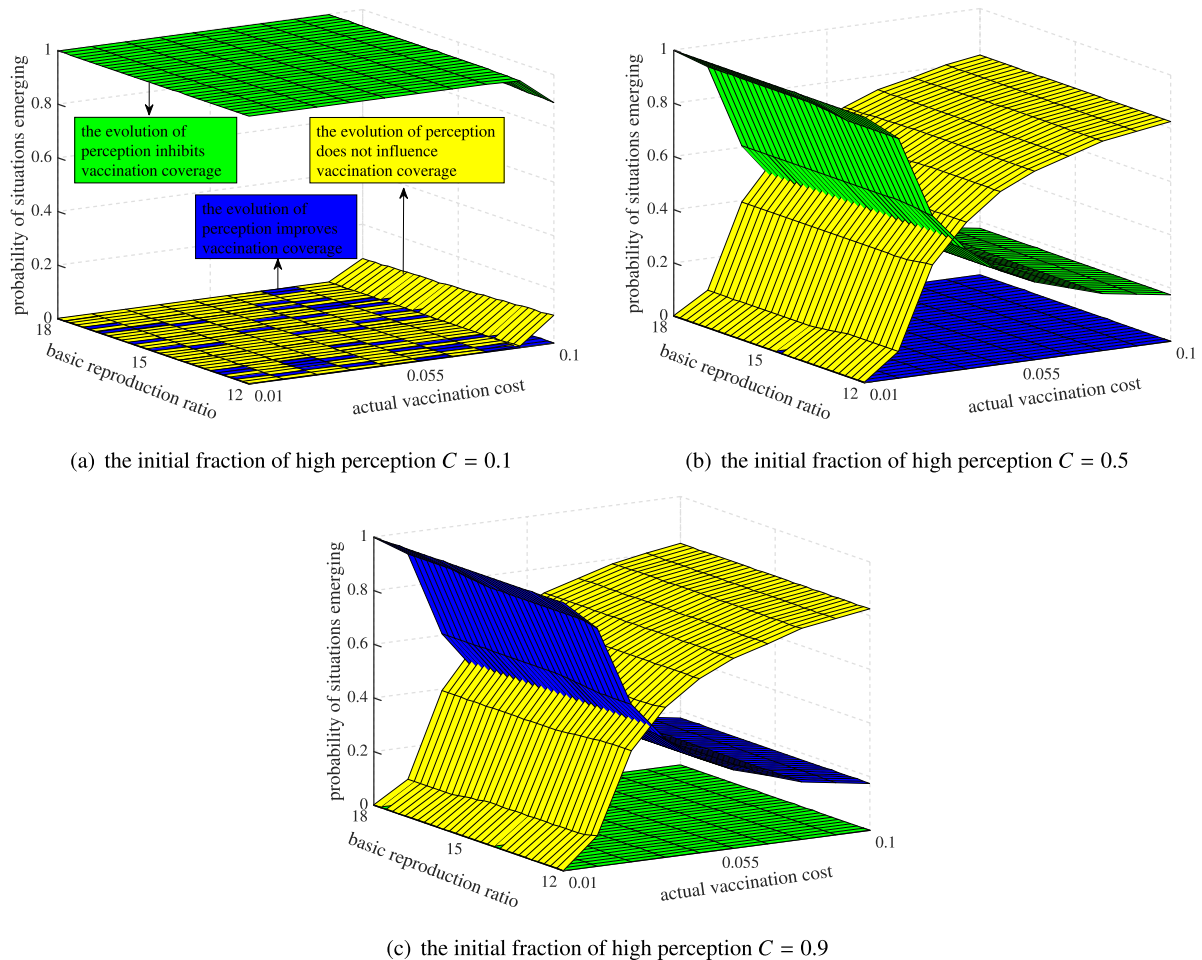


Fig. 6. The influence of the evolution of perception on vaccination dynamics. The evolution of perception improves, or does not influence, or inhibits vaccination coverage. The probabilities of these three situations emerging are shown as blue surfaces, yellow surfaces and green surfaces, respectively. These probabilities are functions of the actual vaccination cost, r , and the basic reproduction ratio, R_0 . Parameters: the intensity of selection $\beta = 0.01$; (a) the initial fraction of high perception $C = 0.1$; (b) $C = 0.5$; (c) $C = 0.9$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Step 3.3 Fix R_0 and r , and H_p and L_p take all possible values. For all the (H_p, L_p) , repeat **Step 3.2** to obtain N_b , N_y and N_g . Then, normalize N_b , N_y and N_g . Finally, obtain (R_0, r, N_b) , (R_0, r, N_y) and (R_0, r, N_g) .

Step 3.4 R_0 and r take all possible values. For any pair of (R_0, r) , repeat **Step 3.3**. Finally, obtain $\{(R_0, r, N_b)\}$, $\{(R_0, r, N_y)\}$ and $\{(R_0, r, N_g)\}$. They are represented as blue, yellow and green surfaces in Fig. 6, respectively.

The evolution of perception increases, or has no effect on, or inhibits vaccination coverage. Fig. 6 shows the evolution of perception inhibits vaccination coverage when most individuals perceive vaccination cost less than the actual vaccination cost, but that the evolution of perception can improve vaccination coverage when most individuals perceive vaccination cost greater than the actual vaccination cost. In this paper, perception refers in particular to individual perception on vaccination cost, and has nothing to do with non-vaccinators' payoffs. With our updating rule, perceptions do not influence the probability that non-vaccinators update themselves to be vaccinators, but have an effect on the probability of vaccinators becoming non-vaccinators. Vaccinators with high perception are more likely to update themselves to be non-vaccinators than vaccinators with low perception. Thus, if the evolution of perception leads to more individuals with low perception, there are more vaccinators insisting their behavior, and the vaccination coverage goes up. Here, the evolution leads the fre-

quency distribution of perceptions to be near $(1/2, 1/2)$. If populations stabilize at e_2 , it is obvious that the proportion of high perception and that of low perception are $1/2$. If a population is stable at the interior equilibrium e_3 , the frequency of high perception is $1/2 + \beta r((H_p - L_p)x_{h3}^* + (L_p - 1)f)/4$, and that of low perception is $1/2 - \beta r((H_p - L_p)x_{h3}^* + (L_p - 1)f)/4$ (see Appendix C). They are near $1/2$, because of weak selection $\beta \ll 1$. Therefore, when most individuals have low perception, such as the case of $C = 0.1$, the evolution of perception decreases the frequency of individuals with low perception from 0.9 to 0.5, and inhabits vaccination coverage (see Fig. 6(a)). On the other hand, when most individuals have high perception, such as the case of $C = 0.9$, the evolution of perception increases the frequency of individuals with low perception from 0.1 to 0.5, and improves vaccination coverage (see Fig. 6(c)).

4. Discussion

Individual vaccinating behavior is driven by the perceived costs of vaccination and infection instead of the actual costs. This paper particularly focuses on how the evolving perception on vaccination cost influences vaccinating behavior and thus vaccination dynamics over several epidemic seasons. Perception is an individual trait and evolves in response to dynamic vaccination coverage and disease prevalence. So, perception as well as vaccinating behavior is a component of individual strategy here. In the spirit of evolutionary game theory, a two-stage game is used to describe the voluntary

vaccination dilemma in each epidemic season. We study both the vaccination dynamics with fixed perception and that with evolving perception. For the case of evolving perception, individuals are willing to vaccinate when the expected vaccination cost, consisting of perception and actual vaccination cost, is less than the maximum of the expected non-vaccination cost. By comparing the vaccination dynamics for these two cases, we find the evolution of perception improves vaccination coverage for populations where most individuals overrate vaccination cost. But the evolution would inhibit vaccination coverage when most individuals underrate vaccination risk. Therefore, our model suggests that evolution of perception can improve and can also inhibit cooperation (vaccinators generate herd immunity, and so vaccination can be viewed as a cooperative behavior).

Self-learning and imitating others are two common ways for updating strategy in the framework of evolutionary game theory (Du et al., 2014; 2016; Nowak and Sigmund, 1993; Wu et al., 2008). Here, individuals first refresh their perceptions through self-learning, and then they adjust the vaccinating behavior via imitating others. The perception update rule is based on the inertia effect in psychology. The current perception of an individual depends on his/her experience, i.e., perceived and actual payoffs in the last epidemic season (see Eq. (7)). This update rule implies individual perception is not influenced by the others' perceptions directly and that perceptions do not spread among individuals. In reality, individual perception is not only self-dependent but also under the influences of peers. Perceptions could be contagious among people. The coupling between contagious disease and contagious perception can lead to novel vaccination dynamics, which do not occur when these two isolated from each other (Bauch and Galvani, 2013). Therefore, the vaccination dynamics with contagious perceptions deserves further investigation, although it is a real challenge to model the dissemination of invisible perceptions. After the update of perceptions, individuals adjust their vaccinating behavior through imitating a more successful peer based on their own perceived payoffs and the peer's actual payoff (see Eq. (8)). Here, individuals' perceived payoffs derive from their newly updated perceptions. This implies vaccinating behavior is driven by perception.

Our results show that the evolution of perception is a 'double-edged sword' for voluntary vaccination dynamics: it can improve vaccination coverage when most individuals overrate vaccination cost, but inhibits vaccination coverage when most individuals underrate vaccination cost. Weak selection $\beta \ll 1$ is a factor for this 'double-edged sword' effect. On the basis of weak selection, the payoff difference has little influence on the adjustment of perception. In one update step, an individual adopts high perception or low perception with the same probability 1/2. Then, at the stable state, almost half of individuals have high perception, and the other half have low perception. With our strategy update rule, vaccinators with low perception are less likely to update themselves to be non-vaccinators than vaccinators with high perception. So, if the evolution leads to more individuals with low perception, there are more vaccinators insisting their vaccinating behavior and vaccination coverage increases. For populations in which more than half of individuals have high (low) perception, the evolution of perception leads to the increase (decrease) of the frequency of low perception, and improves (inhibits) vaccination coverage. Here, we limit ourselves to weak selection for two reasons. First, recent experimental results suggest that the intensity with which humans adjust their strategies might be low. Humans do not simply accept any strategy that is performing better than their strategy (Traulsen et al., 2009). Second, weak selection enables theoretical stability analysis of the vaccination dynamics. However, the results for weak selection may not always be robust. Some important insights for weak selection case do not hold for strong selection. Therefore, it will be interest-

ing to study voluntary vaccination dynamics with strong selection through either numerical simulation or theoretical analysis.

Our study shows that populations stabilize at equilibria where the frequency of vaccinators is fixed. Bauch (2005) has also studied vaccination dynamics in the framework of evolutionary game theory. However, he found that the stable states can not only be equilibria but also be limit cycles where the frequency of vaccinators oscillates over time. This disagreement might stem from our assumption: in each epidemic season, no one is infected in the first stage of vaccination campaign, and meanwhile there is no strategy update in the second stage of disease transmission. This assumption separates vaccination campaign from disease transmission. Our study with this assumption focuses on the situation where vaccines are available only before diseases outbreaks. In reality, the recommended time to take vaccines is before diseases outbreaks, and the majority of vaccination efforts are before outbreaks. So, this assumption is reasonable to a certain degree. Nevertheless, the more realistic situation is that it is ok for individuals to vaccinate at any time point. Post-outbreak vaccination as well as pre-emptive vaccination is adopted by some people. This situation can be depicted by our model through removing the above assumption which separates vaccination campaign from disease transmission. The vaccination dynamics for this situation can exhibit richer dynamics, which may have limit cycles as the stable states.

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Appendix A. The derivation of vaccination dynamics with fixed perception

In the situation of fixed perception, individuals only update their vaccinating behavior in the stage of vaccination campaign. The update rule is a pairwise comparison process. In one update step, two individuals, a focal individual and a role model, are selected randomly from the population. The focal individual imitates the role model's vaccinating behavior with the probability given by Eq. (5); otherwise, the focal individual sticks to his/her vaccinating behavior. For large populations ($N \rightarrow \infty$), the update process is approximated as $\dot{x} = T_i^+ - T_i^-$ (Traulsen et al., 2005), where x denotes the frequency of individuals with a certain strategy, T_i^+ and T_i^- denote the probability that the number of individuals with this strategy increases from i to $i + 1$ and the probability that the number decreases from i to $i - 1$, respectively.

Let $x_h = m_h/N$, $x_l = m_l/N$, $y_h = n_h/N$ and $y_l = n_l/N$ (where, $N = m_h + m_l + n_h + n_l$) be the fraction of individuals with strategy P_hV , P_lV , P_hN and P_lN , respectively. The probability that the number of individuals with strategy P_hV increases from m_h to $m_h + 1$ is

$$T_{m_h}^+ = \frac{n_h}{N} \frac{m_h + m_l}{N} \frac{1}{1 + \exp^{-\beta(-r+w)}}, \quad (\text{A.1})$$

and the probability that the number of individuals with strategy P_hV decreases from m_h to $m_h - 1$ is

$$T_{m_h}^- = \frac{m_h}{N} \frac{n_h + n_l}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+H_p r)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+H_p r)}} \right). \quad (\text{A.2})$$

So, the dynamics of x_h is $\dot{x}_h = T_{m_h}^+ - T_{m_h}^-$. Furthermore, as weak selection ($\beta \ll 1$), the dynamics of x_h is expanded in a Taylor series at $\beta = 0$, and we obtain

$$\dot{x}_h = \frac{1}{2}(C - x_h)(x_h + x_l) \left(1 + \frac{\beta}{2}(w - r)\right) - \frac{1}{2}x_h(1 - x_h - x_l) \left(1 - \frac{\beta}{2}(w - H_p r)\right). \quad (\text{A.3})$$

Similarly, the probability that the number of individuals with strategy $P_l V$ increases from m_l to $m_l + 1$ is

$$T_{m_l}^+ = \frac{n_l}{N} \frac{m_h + m_l}{N} \frac{1}{1 + \exp^{-\beta(-r+w)}}, \quad (\text{A.4})$$

and the probability that the number of individuals with strategy $P_l V$ decreases from m_l to $m_l - 1$ is

$$T_{m_l}^- = \frac{m_l}{N} \frac{n_h + n_l}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+L_p r)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+L_p r)}} \right). \quad (\text{A.5})$$

Thus, we have

$$\dot{x}_l = \frac{1}{2}(1 - C - x_l)(x_h + x_l) \left(1 + \frac{\beta}{2}(w - r)\right) - \frac{1}{2}x_l(1 - x_h - x_l) \left(1 - \frac{\beta}{2}(w - L_p r)\right). \quad (\text{A.6})$$

Because individual perception does not change over time ($x_h + y_h = C$ and $x_l + y_l = 1 - C$ always hold), the dynamics of x_h and that of x_l are enough to express the vaccination dynamics of populations. We combine Eqs. (A.3) and (A.6) and obtain the vaccination dynamics with fixed perception (see Eq. (6)).

Appendix B. The derivation of vaccination dynamics with evolving perception

In the situation of evolving perception, individuals first update their perception, and then update their vaccinating behavior based on the updated perception. In one update step, one individual is chosen randomly to refresh his/her strategy. The individual updates his/her perception based on Eq. (7), which is a self-evaluation process. Then, the individual randomly chooses an individual as role model. The focal individual imitates the role model's vaccinating behavior with the probability given by Eq. (8), which is a pairwise comparison process. Based on the update rule, the number of individuals with strategy $P_h V$ increases from m_h to $m_h + 1$ in three cases.

Case 1 An individual with strategy $P_l V$ updates the strategy to be $P_h V$. The corresponding probability is

$$\frac{m_l}{N} \frac{1}{1 + \exp^{-\beta(-r+L_p r)}} \left(1 - \frac{n_l + n_h}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+H_p r)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+H_p r)}} \right) \right). \quad (\text{B.1})$$

Case 2 An individual with strategy $P_l N$ updates the strategy to be $P_h V$. The corresponding probability is

$$\frac{n_l}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+w)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+w)}} \right) \frac{m_l + m_h}{N} \frac{1}{1 + \exp^{-\beta(-r+w)}}. \quad (\text{B.2})$$

Case 3 An individual with strategy $P_h N$ updates the strategy to be $P_h V$. The corresponding probability is

$$\frac{n_h}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+w)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+w)}} \right) \frac{m_l + m_h}{N} \frac{1}{1 + \exp^{-\beta(-r+w)}}. \quad (\text{B.3})$$

Therefore, the probability that the number of individuals with $P_h V$ increases from m_h to $m_h + 1$, $T_{m_h}^+$, is the sum of Eqs. (B.1)–(B.3). Moreover, the number of individuals with strategy $P_h V$ decreases from m_h to $m_h - 1$ in three cases.

Case 1 An individual with strategy $P_h V$ updates the strategy to be $P_l V$. The corresponding probability is

$$\frac{m_h}{N} \left(1 - \frac{1}{1 + \exp^{-\beta(-r+H_p r)}} \right) \left(1 - \frac{n_l + n_h}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+L_p r)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+L_p r)}} \right) \right). \quad (\text{B.4})$$

Case 2 An individual with strategy $P_h V$ updates the strategy to be $P_h N$. The corresponding probability is

$$\frac{m_h}{N} \frac{1}{1 + \exp^{-\beta(-r+H_p r)}} \frac{n_h + n_l}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+H_p r)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+H_p r)}} \right). \quad (\text{B.5})$$

Case 3 An individual with strategy $P_h V$ updates the strategy to be $P_l N$. The corresponding probability is

$$\frac{m_h}{N} \left(1 - \frac{1}{1 + \exp^{-\beta(-r+H_p r)}} \right) \frac{n_h + n_l}{N} \left(w \frac{1}{1 + \exp^{-\beta(-1+L_p r)}} + (1 - w) \frac{1}{1 + \exp^{-\beta(0+L_p r)}} \right). \quad (\text{B.6})$$

The probability that the number of individuals with $P_h V$ decreases from m_h to $m_h - 1$, $T_{m_h}^-$, is the sum of Eqs. (B.4)–(B.6). For large populations ($N \rightarrow \infty$), the dynamics of x_h is expressed as $\dot{x}_h = T_{m_h}^+ - T_{m_h}^-$. As weak selection ($\beta \ll 1$), the dynamics of x_h is expanded in a Taylor series at $\beta = 0$, and we obtain

$$\dot{x}_h = -x_h + \frac{2 - \beta r}{4}(x_h + x_l) + \frac{\beta r}{8}(H_p x_h + L_p x_l)(1 + x_h + x_l) + \frac{\beta}{8}(x_h + x_l)(1 - x_h - x_l)(2w - H_p r). \quad (\text{B.7})$$

Similarly, we obtain the dynamics of $P_l V$ is

$$\dot{x}_l = x_h - \frac{2 - \beta r}{4}(x_h + x_l) - \frac{\beta r}{8}(H_p x_h + L_p x_l)(1 + x_h + x_l) + \frac{\beta}{8}(x_h + x_l)(1 - x_h - x_l)(2w - 2r - L_p r), \quad (\text{B.8})$$

and the dynamics of $P_h N$ is

$$\dot{y}_h = -y_h + \frac{1}{2}(1 - x_h - x_l) + \frac{\beta r}{8}(H_p x_h + L_p x_l)(1 - x_h - x_l) - \frac{\beta}{8}(x_h + x_l)(1 - x_h - x_l)(2w - H_p r). \quad (\text{B.9})$$

As $x_h + x_l + y_h + y_l = 1$ always holds, the vaccination dynamics of populations can be expressed by the combination of Eqs. (B.7)–(B.9) (see Eq. (9)).

Appendix C. Stability of vaccination dynamics with evolving perception

There are a pure vaccinator equilibrium $e_1 = ((2 + \beta r L_p - \beta r)/(4 + \beta r L_p - \beta r H_p), (2 - \beta r H_p + \beta r)/(4 + \beta r L_p - \beta r H_p), 0)$ and

a pure non-vaccinator equilibrium $e_2 = (0, 0, 1/2)$ for Eq. (9). In addition, when $(2 + H_p + L_p)r/4 < 1 - 1/R_0$ holds, there is an interior equilibrium $e_3 = (x_{h3}^*, f - x_{h3}^*, 1/2 + (\beta r(H_p - L_p)/4 - 1)x_{h3}^* + \beta r f(L_p - 1)/4)$, where $x_{h3}^* = (\beta r L_p(1 + f) + \beta r(1 - H_p/2 + L_p/2)(1 - f) - 2\beta r + 4)f/(8 - \beta r(H_p - L_p)(1 + f))$ and $f = 1 - 1/(R_0(1 - (2 + H_p + L_p)r/4))$.

To analyze the stability of Eq. (9), we linearize it in the vicinity of every equilibrium. The linearized system is given by

$$\begin{pmatrix} \dot{x}_h \\ \dot{x}_l \\ \dot{y}_h \end{pmatrix} = A|_{x_h=x_h^*, x_l=x_l^*, y_h=y_h^*} \begin{pmatrix} x_h \\ x_l \\ y_h \end{pmatrix}, \quad (C.1)$$

where

$$\begin{aligned} a_{11} &= -\frac{1}{2} - \frac{\beta r}{4} + \frac{\beta r}{8}K + \frac{\beta r}{8}H_p(1 + x_h + x_l) + \frac{\beta}{8}T_h(1 - 2x_h - 2x_l) \\ &\quad + \frac{\beta}{4}(x_h + x_l)(1 - x_h - x_l)\frac{\partial w}{\partial x_h}, \\ a_{12} &= \frac{1}{2} - \frac{\beta r}{4} + \frac{\beta r}{8}K + \frac{\beta r}{8}L_p(1 + x_h + x_l) + \frac{\beta}{8}T_h(1 - 2x_h - 2x_l) \\ &\quad + \frac{\beta}{4}(x_h + x_l)(1 - x_h - x_l)\frac{\partial w}{\partial x_l}, \\ a_{13} &= 0, \\ a_{21} &= \frac{1}{2} + \frac{\beta r}{4} - \frac{\beta r}{8}K - \frac{\beta r}{8}H_p(1 + x_h + x_l) + \frac{\beta}{8}T_l(1 - 2x_h - 2x_l) \\ &\quad + \frac{\beta}{4}(x_h + x_l)(1 - x_h - x_l)\frac{\partial w}{\partial x_h}, \\ a_{22} &= -\frac{1}{2} + \frac{\beta r}{4} - \frac{\beta r}{8}K - \frac{\beta r}{8}L_p(1 + x_h + x_l) + \frac{\beta}{8}T_l(1 - 2x_h - 2x_l) \\ &\quad + \frac{\beta}{4}(x_h + x_l)(1 - x_h - x_l)\frac{\partial w}{\partial x_l}, \\ a_{23} &= 0, \\ a_{31} &= -\frac{1}{2} - \frac{\beta r}{8}K + \frac{\beta r}{8}H_p(1 - x_h - x_l) - \frac{\beta}{8}T_h(1 - 2x_h - 2x_l) \\ &\quad - \frac{\beta}{4}(x_h + x_l)(1 - x_h - x_l)\frac{\partial w}{\partial x_h}, \\ a_{32} &= -\frac{1}{2} - \frac{\beta r}{8}K + \frac{\beta r}{8}L_p(1 - x_h - x_l) - \frac{\beta}{8}T_h(1 - 2x_h - 2x_l) \\ &\quad - \frac{\beta}{4}(x_h + x_l)(1 - x_h - x_l)\frac{\partial w}{\partial x_l}, \\ a_{33} &= -1, \\ K &= H_p x_h + L_p x_l, \\ T_h &= 2w - H_p r, \\ T_l &= 2w - 2r - L_p r. \end{aligned} \quad (C.2)$$

Near e_1 , the eigenvalues of matrix A are $\lambda_{11} = -1$, $\lambda_{12} = -1 + \beta r(H_p - L_p)/4$ and $\lambda_{13} = \beta r(2 + H_p + L_p)/8$. Therefore, the pure vaccinator equilibrium e_1 is unstable. In the vicinity of e_2 , the eigenvalues of matrix A are $\lambda_{21} = -1$, $\lambda_{22} = -1 + \beta r(H_p - L_p)/8$ and $\lambda_{23} = \beta(4 - 4/R_0 - 2r - H_p r - L_p r)/8$. If $(2 + H_p + L_p)r/4 > 1 - 1/R_0$, e_2 is stable. Whereas if $(2 + H_p + L_p)r/4 < 1 - 1/R_0$, e_2 is unstable. The eigenvalues of matrix A near e_3 are $\lambda_{31} = -1$, $\lambda_{32} = -1 + \beta r(H_p - L_p)(1 + f)/8$ and $\lambda_{33} = -\beta f/(2R_0(1 - f))$. Thus, the interior equilibrium e_3 is stable.

When $(2 + H_p + L_p)r/4 > 1 - 1/R_0$, populations evolve to e_2 , the vaccination coverage is $x^* = x_{h2}^* + x_{l2}^* = 0$, the frequency of high perception is $x_{h2}^* + y_{h2}^* = 1/2$, and that of low perception is $x_{l2}^* + y_{l2}^* = 1/2$. When $(2 + H_p + L_p)r/4 < 1 - 1/R_0$, populations evolve to e_3 , the vaccination coverage is $x^* = x_{h3}^* + x_{l3}^* = 1 - 1/(R_0(1 - (2 + H_p + L_p)r/4))$, the frequency of high perception is $x_{h3}^* + y_{h3}^* = 1/2 + \beta r((H_p - L_p)x_{h3}^* + (L_p - 1)f)/4$, and that of low perception is $x_{l3}^* + y_{l3}^* = 1/2 - \beta r((H_p - L_p)x_{h3}^* + (L_p - 1)f)/4$. The above results hold for the situation where vaccinators coexist with non-

vaccinators at the initial state. As this paper does not consider mutation, if a population consists exclusively of vaccinators or non-vaccinators at the initial state, individual vaccinating behavior will not evolve.

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