Social Imitation Dynamics of Vaccination Driven by Vaccine Effectiveness and Beliefs

Ran Zhuo

Senior Honors Thesis Submitted to the Department of Mathematics, Dartmouth College

Feng Fu, Advisor

Abstract

The invention of vaccine has significantly reduced the levels of morbidity and mortality from infectious diseases. However, the success of vaccines is often impaired by the free-rider problem: while vaccinated individuals incur the cost of vaccination, unvaccinated individuals are protected from the disease given that population immunity is in effect. This provides self-interested individuals an incentive to forgo vaccination. An emerging literature has investigated the epidemiology of individuals facing the free-rider problem given the choice of voluntary vaccination. Such studies properly apply the framework of game theory to describe how individuals react when facing the vaccination dilemma. In this paper, we extend previous work in imitation dynamics of vaccine uptake by accounting for imperfect vaccines, whose effects on individuals' vaccination behavior on spatial populations have not been fully answered. We combine vaccination dynamics with an epidemiological model, in particular the SIR model. We then further extend our model to account for varying perceived vaccination costs during the decision-making for vaccination. The results from this paper show incomplete information together with ineffective vaccines in a population of imitators further aggravate the problem of suboptimal level of vaccination if the initial vaccination rate is low. A bi-stability phenomenon is observed: two separate equilibrium vaccination rates exist for high initial vaccination and low initial vaccination. When initial vaccination rate is high, vaccination rate moves to a high equilibrium. When initial vaccination rate is low, vaccination rate moves to a low equilibrium. The effect is observed when the population is homogeneous in terms of beliefs of vaccination effectiveness or heterogeneous with fixed beliefs or spreading beliefs. Our results provide support for intensifying vaccination campaigns to overcome vaccine hesitancy and to boost initial vaccination rate.

Introduction

The invention of vaccine has significantly reduced the levels of morbidity and mortality from infectious diseases [1]. However, achieving widespread population immunity by voluntary vaccination poses a major public health challenge [2]. It often concerns public health administration that voluntary vaccination cannot lead to sufficiently high herd immunity for disease eradication due to the free rider problem [3–6]: while vaccinated individuals incur the cost of vaccination, unvaccinated individuals are protected from the disease given that population immunity is in effect. This provides self-interested individuals an incentive to escape vaccination, free-riding on those who vaccinate. The free rider problem is further aggravated by the rise of vaccination refusal [7–9] due to increasing concerns about vaccine safety and a low level of concern about the risk of many vaccine-preventable diseases [8]. For example, the common belief that the measles-mumps-rubella (MMR) vaccine causes autism and irritable bowel syndrome caused a severe decline in MMR vaccine uptake in Britain, which was well below the target herd immunity level of 95% [1, 10–12]. In 2003, polio was on the verge of global eradication when vaccine scares in northern Nigeria caused an international resurgence of the disease [13, 14]. Vaccine scares or other forms of free-riding, which may result in low vaccination levels and severe consequences, could become more common as we approach eradication goals for many vaccine-preventable diseases [10, 13, 15], and therefore require studies dedicated to analyzing their mechanism and effects.

An emerging literature [1, 6, 10, 15, 17–20] has investigated the epidemiology of individuals facing the free rider problem given the choice of voluntary vaccination. Such studies properly apply the framework of game theory to describe how individuals react when facing the vaccination dilemma [21–31]. Many studies incorporate complex network theory to account for contact patterns of populations [2, 10, 11, 33–36], as traditional mathematical methods mainly based on ordinary differential equations have been proven to be inadequate to reflect the vaccination dynamics in structured populations [11] and interests in understanding and controlling the spreading of diseases in complex networks [16, 32, 50, 59] are growing. In particular, our previous work [10] uses an evolutionary game-theoretic approach to explore the roles of individual imitation behavior [37, 38] and population structure in vaccination. An individual's vaccination decisions are often influenced by opinions of his social neighbors. Individuals have incomplete information and tend to reply on salient anecdotes from friends and media in order to form opinions of disease risks and prevention [10, 39–41]. Each person can encounter different anecdotal evidence, depending on her social network [19, 42]. We realistically model this aspect of social learning in spatial populations, which shapes individuals' decision-making about vaccination, and find that the coverage of vaccination is sensitively dependent on the effectiveness of vaccination.

Here, we extend previous work by accounting for imperfect vaccines, whose effects on individuals' vaccination behavior in spatial populations have not been fully answered. Previous literature usually assumes that the vaccinated individuals gain perfect immunity against the disease [10, 15, 17], which is not true, for example, in the cases of measles [43] and malaria [44]. Moreover, individuals' perceptions of vaccine effectiveness vary. This perceived efficacy of vaccination, influenced by psychological effects, plays a determinant role since individuals adjust their strategic behavior based on perceptions of the vaccination efficacy and cost rather than the actual ones [2, 6, 18]. Therefore, imperfect vaccine and individuals' varying perceptions of vaccination effectiveness and cost, should be taken into account in the game theoretical analysis of the vaccination behavior [2,45–47]. Motivated by the issues discussed above, we propose a model that incorporates imperfect vaccines into the interaction between disease and vaccination in structured populations. We combine vaccination dynamics with an epidemiological model, in particular the SIR model, to track populations of susceptible, infected and recovered individuals over time, within each season of epidemic [2]. Individuals make vaccination decisions during a vaccination campaign, before each epidemic season. Whether each susceptible individual becomes infected at some point during the season is then determined by the epidemiological model. Vaccinated individuals have reduced chance of being infected. At the end of the season, individuals revise their vaccination decision for the next season based on their payoffs, taken into account of their health outcomes and cost incurred. We then further extend our model to account for varying perceived vaccination costs during the decision-making for vaccination. Our model is most appropriate for describing flu-like diseases, for which vaccines are usually available prior to the seasonal epidemic and are only effective for the strain of pathogen of that particular season [48].

Materials and Methods

In view of the periodic outbreak of infections such as influenza and imperfect vaccines, we use an evolutionary game-theoretical approach to study the seasonal vaccination game. A feedback loop exists between the vaccination decisions of individuals and their health outcomes. The disease incidence feeds on vaccination behavior: high level of vaccine coverage can decrease disease incidence to very low levels, reducing the perceived risk of infection and hence the need to get vaccinated, in turn, the drop in vaccine coverage allows the number of individuals who are susceptible to infection to accumulate [49]. When the percentage of susceptible individuals exceeds a tipping point, an outbreak of infectious disease can occur [49]. A surge in disease incidence can convince individuals to start being vaccinated again [13].

The vaccination game has two stages: a vaccination campaign at the beginning of the season, followed by the disease epidemic [10,11,17,51,52]. The proposed model is illustrated in Fig 1. As shown in Fig 1, during the vaccination campaign, each individual decides whether or not to get vaccinated based on anecdotal evidence to estimate costs and benefits of vaccination. A vaccinated individual pays a cost $C_v > 0$ while an unvaccinated individual pays nothing. This cost includes the time spent in taking the vaccination as well as the perceived risks of vaccination, long-term health impacts, and other intangibles. During the epidemic season, the epidemic is initiated by a number I_0 of individuals and then spreads in the square lattice with Moore neighborhood according to susceptible-infected-recovered (SIR) dynamics, with per day per infected neighbor transmission rate β and per day recovery rate γ. Let vaccination effectiveness be E, then the vaccinated population has a reduced transmission rate of $\beta(1-E)$. The epidemic continues until there are no more newly infected individuals (which occurs in under 200 days for all cases simulated). The SIR epidemiological process in the epidemic season is simulated by the Gillespie algorithm [10, 35]. Once the epidemic ends, individuals can revise their vaccination decisions for the next season. The infection bears a cost $C_I > 0$, which includes expenses and time for health care as well as an elevated chance of mortality. Without loss of generality, we set $C_I = 1$ and $0 \leq C_v \leq 1$.

When the epidemic season ends, individuals adjust their strategies by imitation where successful individual's strategy is more likely to be followed [53, 54]. An individual's imitation behavior is based on the current payoff difference between herself and a randomly selected neighbor. If the strategy of the selected neighbor has a higher payoff than his own strategy in the past epidemic season, then the individual imitates his neighbor's strategy with a higher probability. Here we use the Fermi function to determine the probability of imitation [55–57, 57, 58] to account for potential stochasticity in the decision process. Individual i randomly selects one neighbor j from her immediate neighborhood, then the probability that individual i adopts individual j's strategy is given by [37, 55, 56]:

$$W(S_i \leftarrow S_j) = \frac{1}{1 + exp(-K(P(j,t) - P(i,t)))}, \tag{1}$$

where S_i means the vaccination choice for individual i: vaccination or non-vaccination. $P(i,t)$ denotes the current payoff of individual i at season t. For i's payoff, we have:

$P(i,t) = -C_v$ if i is vaccinated and is not infected;

$P(i,t) = -C_v - 1$ if i is vaccinated and is infected;

$P(i,t) = -1$ if i is not vaccinated and is infected;

$P(i,t) = 0$ if i is not vaccinated and is not infected.

K is the selection intensity indicating how strongly individuals are responsive to payoff difference. It has been suggested that the selection intensity for human imitation is rather weak [38, 54]. Here we adopt $K = 0.1$, which is widely used in many previous work [37, 55]. This updating dynamic diverges from a fully rational model. Individuals adjust their strategies retrospectively, in response only to the observed payoff outcomes and not the expected payoffs of strategies. In a population with low vaccination uptake, many non-vaccinators fall ill, but if individual i happens to choose one of the few successful free riders as a role model, then he will be more likely to imitate the free rider's strategy [10].

The initial state consists of a fraction V_0 of vaccinated individuals, randomly distributed throughout the population. Each two-stage iteration (vaccination strategy updating followed by an epidemic process) updates the proportion of each strategy. The equilibrium results are obtained by averaging over the last 500 iterations from a total of 10000 iterations, and each data point presented in this paper results from an average of over 45 realizations, for which the system does not reach the absorbing state within first

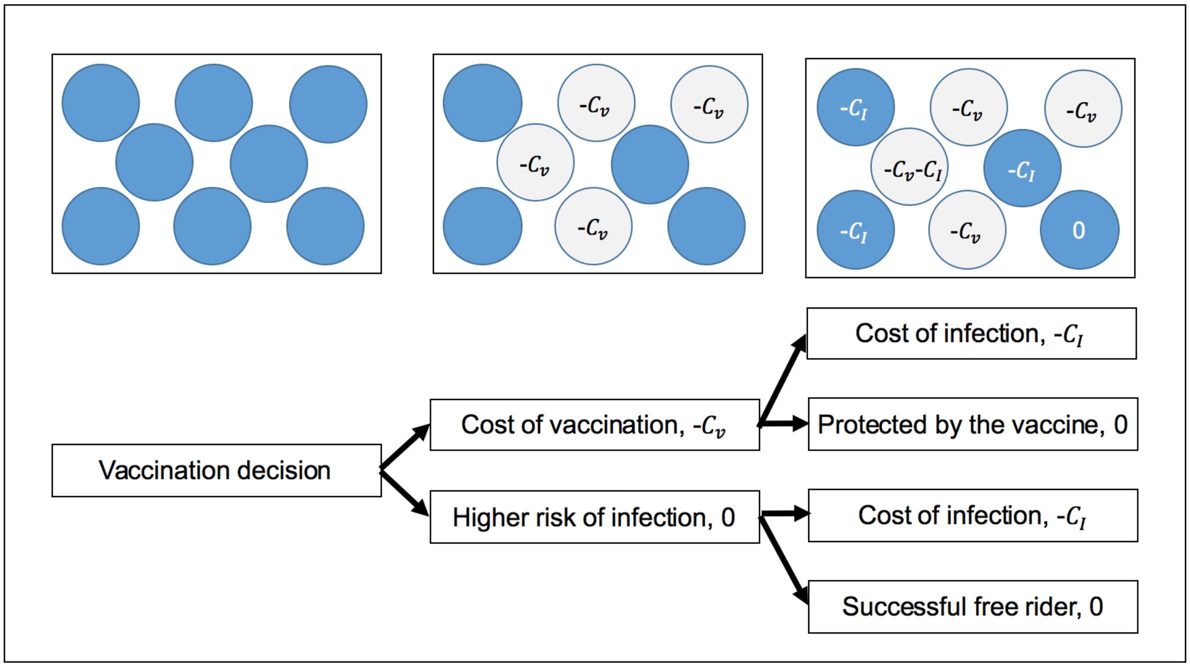


Fig 1. Schematic diagram of our model. We model the vaccination dilemma as a two-stage game. At stage 1 (vaccination choice), a proportion $V - 0$ of the population decides to vaccinate. Vaccination costs C_v and provides imperfect protection from the disease. At stage 2 (health outcome), we use the SIR model to simulate the epidemiological process. Each individual faces the risk of infection, which varies with the individual's vaccination status and the number of infected neighbors he has. The cost of infection is C_I. Those unvaccinated individuals who remain healthy are free-riders off the vaccination efforts of others, and they are indirectly protected by the herd immunity [10].

3000 iterations. In the paper (by the same title) being prepared for publication in *PLoS Computational Biology*, we use different parameter combinations and are able to obtain qualitatively similar results without dropping the realizations that reach the absorbing states within first 3000 iterations. For the square lattice, the population size $N = 2500$, the number of initial infection seed $I_0 = 50$. We assume that vaccination prevents the epidemic if the average final epidemic size is less than twice the size of I_0.

In our basic model, we assume that individuals have homogenous perceptions of the cost of vaccination — C_v is the same for all individuals. In our extended model, we consider two groups of individuals: believers of vaccine effectiveness and non-believers. For the nonbelievers, an additional vaccination cost $\theta > 0$ is incurred. The perceived payoffs for the two groups differ in the following way. For believers, the possible payoffs are the same as those described above. For nonbelievers, we have:

$P(i,t) = -C_v - \theta$ if i is vaccinated and is not infected;

$P(i,t) = -C_v - \theta - 1$ if i is vaccinated and is infected;

$P(i,t) = -1$ if i is not vaccinated and is infected;

$P(i, t) = 0$ if i is not vaccinated and is not infected.

We investigate two scenarios for our extended model: one where such beliefs about ineffective vaccination are fixed, and one where the beliefs are contagious, and spread in a same way as the imitation dynamics in vaccination decisions based on payoff differences. In this way, we explore systems in which both social contagions and epidemiological contagions are coupled to one another, and offer insight into the resulting disease-behavior system that exhibits dynamics that do not occur when the two subsystems are isolated from one another [65].

Results

Homogeneous perceptions of cost of vaccination

In this section, we present results from our basic model, where we assume that individuals have homogenous perceptions of the cost of vaccination. We consider a population of individuals arranged on a square lattice where each individual has eight immediately adjacent neighbors.

Previous research has shown that individuals who carefully pay attention to his neighbors' payoffs and imitate the behavior of successful neighbors will end up attempting to free-ride more than they rationally 'ought' to [10]. In this paper, we discover that when the initial vaccination rate is low, this effect is even more pronounced. For example, Fig 2(A) shows that when infection is 20 times as costly as vaccination ($C_v = 0.05$), vaccination level for $V_0 = 0.05$ reaches approximately 50% while vaccination level for $V_0 = 0.95$ reaches approximately 70%. A low initial vaccination rate lowers vaccination coverage by approximately 20% as compared to a high initial vaccination rate. Fig 2(B, C) show snapshots of the system at equilibrium with high and low initial vaccination rates, respectively. It is visually apparent that the when the initial vaccination rate is low, more people opt to free ride, which results in larger disease outbreak. Fig S1 shows the time courses of changes of subpopulations of the iteration shown in Fig 2(B, C).

As shown in Fig 3(A), equilibrium level falls with increasing C_v. When C_v increases, the equilibrium vaccination level follows a rotated 'S' shape: the vaccination level is close to 1 when cost is low, then it drops rapidly in the range $C_v \approx 0.03$ to 0.08. Above a cost threshold of $C_v \approx 0.12$, no one chooses vaccination and the epidemic reaches its maximum size like there is no option to vaccinate. This result is qualitative the same as results in [10]. In particular, for the range of vaccination cost appropriate to influenza (i.e. $C_v \approx 0.002$ to 0.08) [10], a high initial vaccination rate and a low initial vaccination rate result in two separate equilibrium vaccination rates. The difference is most pronounced in the range of vaccination cost $C_v \approx 0.02$ to 0.08.

Our analysis also shows the relationship between vaccination effectiveness and equilibrium vaccination rate. As shown in Fig 3(B), vaccination rate rises with increasing E. When E increases, the equilibrium vaccination level also follows a rotated 'S' shape: the vaccination level is zero when the vaccine is completely ineffective ($E = 0$), then it

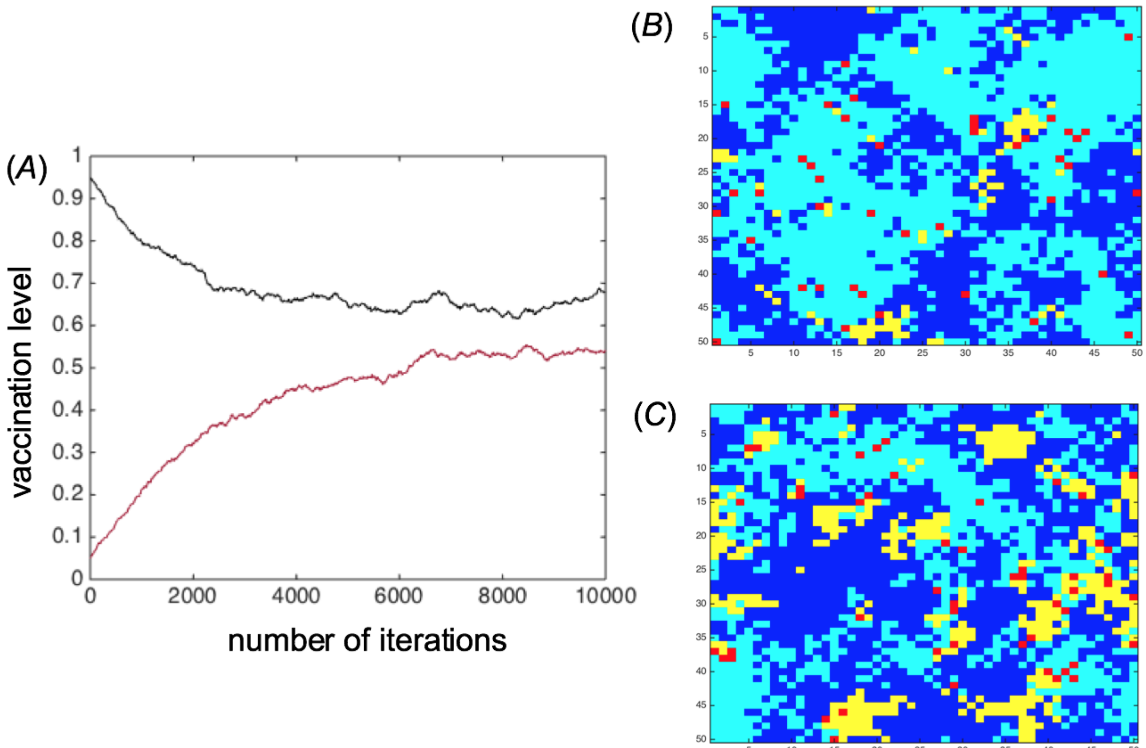


Fig 2. Vaccination rates in non-well-mixed populations at equilibrium. (A) The fractions of the vaccinated evolve as the number of iterations increases. The black line represents simulation results when the initial vaccination rate $V_0 = 0.95$. The red line represents simulation results when the initial vaccination rate $V_0 = 0.05$. Parameters: the population size $N = 2500$ with Moore neighborhood, the number of initial infection seed $I_0 = 50$, per day per infected neighbor transmission rate $beta = 0.025$, per day recovery rate $\gamma = 0.10$, selection intensity $K = 0.1$, cost of vaccination $C_v = 0.05$, vaccination effectiveness E$= 0.80$. (B, C) Snapshots of the system at equilibrium with high and low initial vaccination rates, respectively. Dark blue denotes unvaccinated individuals who are uninfected (successful free riders). Light blue denotes vaccinated individuals who are uninfected. Yellow denotes unvaccinated individuals who are infected. Red denotes vaccinated individuals who are infected.

increases rapidly in the range $E \approx 0.2$ to 0.6. Between $E \approx 0.7$ to 0.9, we observe an overshoot of vaccine uptake level as the effectiveness of vaccination increases. Past research has documented this overshoot in well-mixed populations in a similar range of vaccination effectiveness [2]. It has been shown that there is a tradeoff effect between vaccination effectiveness and vaccination uptake level: when vaccination effectiveness is already high and when it increases further, it encourages more free-riding and leads to decreases in vaccination uptake. However, the disease is still better mitigated because the number is traded for efficiency: though the number of people who vaccinate decreases, still more people are effectively protected by vaccines. (For proof, see [2].) This paper

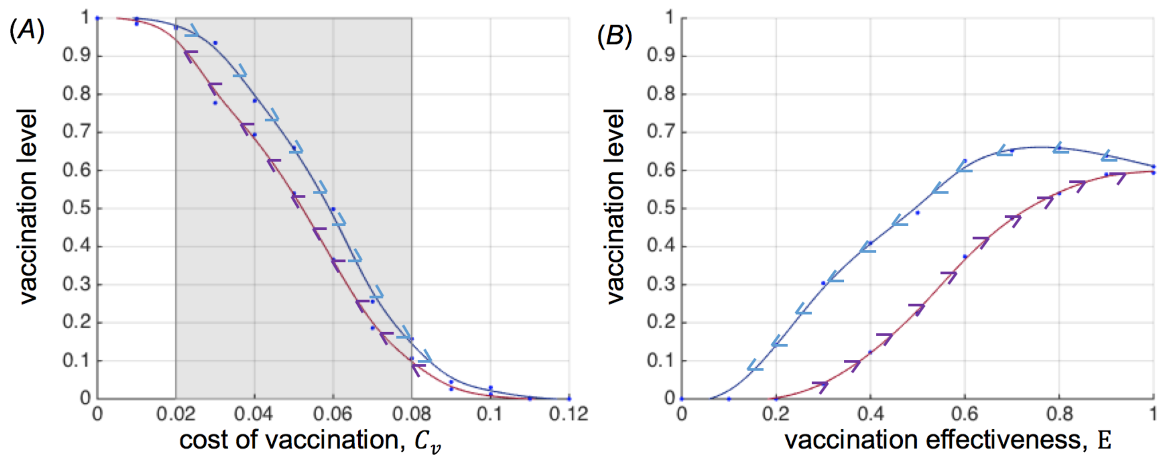


Fig 3. Bi-stability of vaccination rates caused by imperfect vaccination. (A) The fractions of the vaccinated at equilibrium are shown as functions of the relative cost of vaccination C_v. The lines are fitted values by using the smoothing spline method. The black line represents simulation results when the initial vaccination rate $V_0 = 0.95$. The red line represents simulation results when the initial vaccination rate $V_0 = 0.05$. Parameters: the population size $N = 2500$, the number of initial infection seed $I_0 = 50$, per day per infected neighbor transmission rate $\beta = 0.025$, per day recovery rate $\gamma = 0.10$, selection intensity $K = 0.1$, vaccination effectiveness E$= 0.80$. (B) The fractions of the vaccinated at equilibrium are shown as functions of the vaccination effectiveness E. The lines are fitted values by using the smoothing spline method. The black line represents simulation results when the initial vaccination rate $V_0 = 0.95$. The red line represents simulation results when the initial vaccination rate $V_0 = 0.05$. Parameters: the population size $N = 2500$, the number of initial infection seed $I_0 = 50$, per day per infected neighbor transmission rate $beta = 0.025$, per day recovery rate $\gamma = 0.10$, selection intensity $K = 0.1$, cost of vaccination $C_v = 0.05$.

shows the results are qualitatively similar for non-well-mixed populations. Moreover, we discover a bi-stability of equilibrium vaccination rate, which we believe is the first time reported for vaccination decisions. When the vaccine is completely effective ($E = 1$), vaccine uptake level is approximately 0.6.

For a range of vaccination effectiveness, a high initial vaccination rate and a low initial vaccination rate result in two separate equilibrium vaccination rates. We note an important fact that two separate equilibrium vaccination levels only exist when vaccination effectiveness $E \neq 1$. As shown in Fig 3(B), when vaccines are completely effective in preventing the disease, equilibrium vaccination levels for high initial vaccination and low initial vaccination converge to approximately 0.6. When vaccines are not completely effective, a low initial vaccination rate always lowers vaccination coverage as compared to a high initial vaccination rate. The difference can be as large as 30% (when E$= 0.4$) in our simulations.

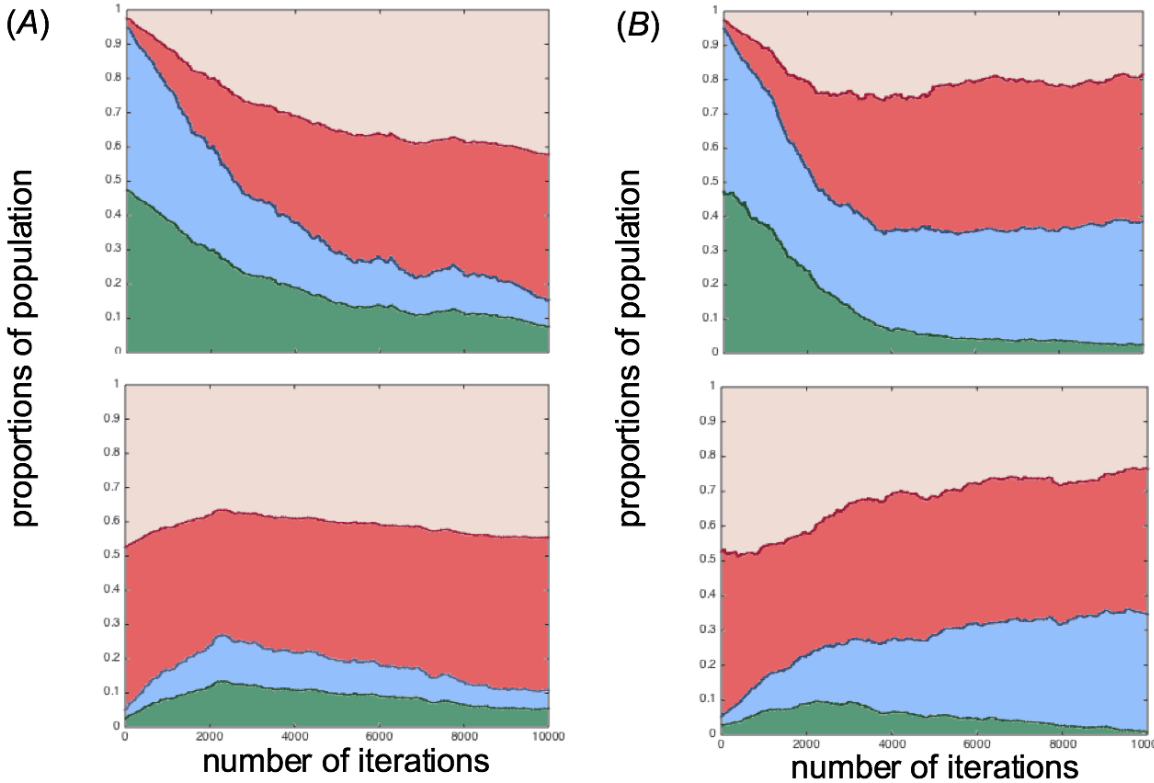


Fig 4. Vaccination dynamics in non-well-mixed populations with heterogeneous beliefs. Green: nonbelievers who vaccinate, blue: believers who vaccinate, red: nonbelievers who do not vaccinate, beige: believers who do not vaccinate. (A) shows the evolution of the fractions of the four subpopulations as the number of iterations increases when beliefs of ineffective vaccines are fixed. The upper panel shows the scenario when the initial vaccination rate $V_0 = 0.95$. The bottom panel shows the scenario when the initial vaccination rate $V_0 = 0.05$. Parameters: the population size $N = 2500$, believer population $N_b = 1250$, the number of initial infection seed $I_0 = 50$, per day per infected neighbor transmission rate $\beta = 0.025$, per day recovery rate $\gamma = 0.10$, selection intensity $K = 0.1$, cost of vaccination $C_v = 0.03$, additional vaccination cost $\theta = 0.1$. (B) shows the evolution of the fractions of the four subpopulations as the number of iterations increases when beliefs of effective vaccines are spreading. The upper panel shows the scenario when the initial vaccination rate $V_0 = 0.95$. The bottom panel shows the scenario when the initial vaccination rate $V_0 = 0.05$. Parameters: the population size $N = 2500$, initial believer population $N_{b_0} = 1250$, the number of initial infection seed $I_0 = 50$, per day per infected neighbor transmission rate $\beta = 0.025$, per day recovery rate $\gamma = 0.10$, selection intensity $K = 0.1$, cost of vaccination $C_v = 0.03$, additional vaccination cost $\theta = 0.1$.

Heterogeneous perceptions of cost of vaccination

Our extended model which incorporates heterogenous perception of cost of vaccination, is motivated by the the spread of opinions about vaccination like a social contagion in the

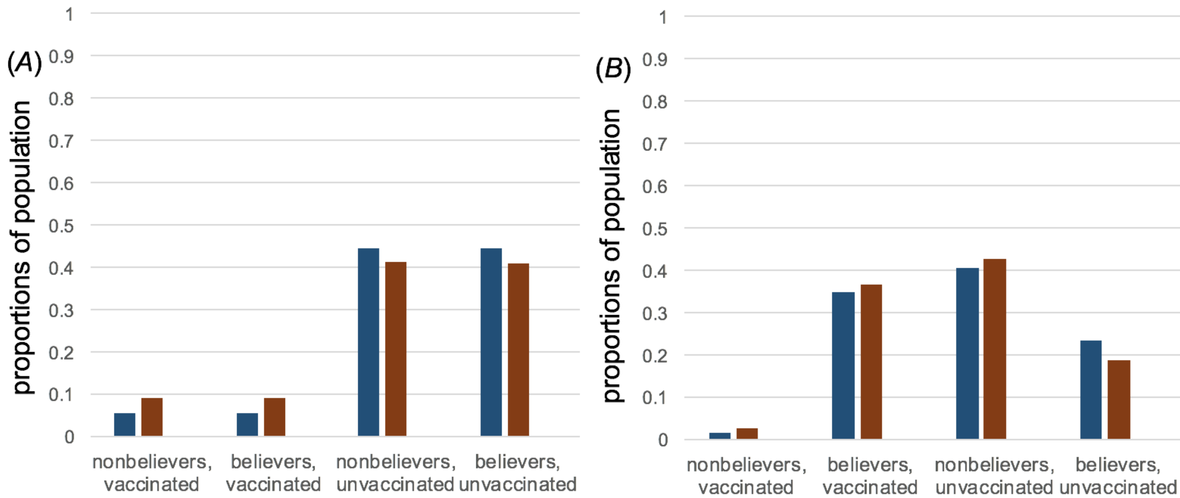


Fig 5. Proportions of four subpopulations in vaccination dynamics with heterogeneous beliefs. Blue bars: the proportions of four subpopulations when $V_0 = 0.05$, red bars: the proportions of four subpopulations when $V_0 = 0.95$. (A) presents the proportions of four subpopulations in Fig4 (A). (B) presents the proportions of four subpopulations in Fig4 (B).

real world [49]. Vaccine confidence and immunization decisions are driven by perceived social norms or collective values. For example, many parents reply on other parents or family members as sources of vaccine-related information. Specifically, decisions to immunize are mediated in part by perceptions of what other parents in the community are doing [9]. In today's world, many diseases, such as smallpox, have been controlled due to a successful vaccination program. Consequently, fear has shifted from many vaccine-preventable diseases to fear of the vaccines. Vaccines are not only victims of their own success, but also struggle to maintain public confidence given the heuristics that often influence risk perceptions and decision-making [63]. It is therefore of particular importance that our model studies how the vaccination dynamics are influenced by social contagion.

We first study the scenario when a fixed population of individuals believe vaccines are ineffective. For this population, they perceive an additional vaccination cost θ. As shown in Fig 4(A), we observe that even with very low actual vaccination cost $C_v = 0.03$, the equilibrium vaccination level for this group of believers as well as for the non-believers become very low as compared to the homogenous population where no one perceives an additional cost. However, the vaccination rate is higher than that in a homogenous population where everyone perceives an additional cost. The vaccination rate among believers and nonbelievers are similar. As shown in Fig 5(A), the effect of two separate equilibria of vaccination levels is preserved.

We then study the scenario when beliefs about vaccination effectiveness are a social contagion and spread in the same way as the spread of disease. As shown in Fig 4(B), we observe that, similar to Fig 4(A), even with very low actual vaccination cost $C_v = 0.03$, the equilibrium vaccination level for this group of believers as well as for the non-believers become lower as compared to the homogenous population where no one perceives an additional cost. The vaccination rate is higher than that in a homogenous population where everyone perceives an additional cost. We observe that the populations of believers and nonbelievers change over the number of iterations. In this simulation, the population of nonbelievers grows at the expense of believers. Moreover, individuals select on vaccination decisions based on their beliefs about vaccination effectiveness. Believers are unlikely to vaccinate in equilibrium while nonbelievers are likely to vaccinate. As shown in Fig 5(B), the effect of two separate equilibria of vaccination levels is also preserved.

Discussion and Conclusion

Previous research has shown voluntary vaccination can be a viable policy for achieving high vaccination coverage and eradicating diseases, but the outcome is sensitive to small changes of (actual or perceived) vaccination cost in social networks [10]. Achieving socially optimal coverage through voluntary vaccination is a problem of cooperation with limited information and uncertainty about outcomes and often fail to protect populations from epidemic [10]. Despite these concerns, vaccine have significantly reduced the levels of morbidity and mortality from infectious diseases [1].

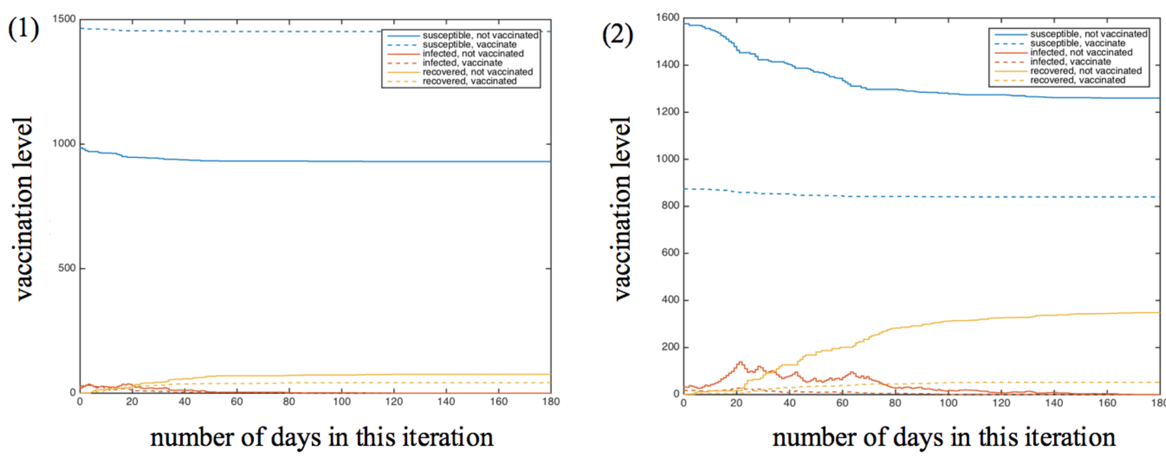
However, recent trends suggest that past gains in reducing vaccine-preventable diseases are threatened with shift in perceptions of disease experience and heightened concerns regarding vaccine safety [63, 64]. Factors such as expanding immunization requirements and increased media coverage of alleged associations between vaccinations and chronic illnesses have heightened concerns regarding vaccine safety [63, 64]. Many individuals also feel that the risk of infection is low because of herd immunity. As a consequence, vaccine hesitancy has increases significantly over the last decade. Vaccine hesitancy has potentially severe consequences. For example, the belief that the measles-mumps-rubella (MMR) vaccine causes autism and irritable bowel syndrome caused a severe decline in MMR vaccine uptake in Britain [1, 10–12]. In 2003, polio was on the verge of global eradication when vaccine hesitancy in northern Nigeria caused an international resurgence of the disease [13, 14]. A resurgence of outbreaks of these vaccine-preventable diseases has brought attention to the issue of vaccine hesitancy and its threat to public health [9].

An emerging literature [1, 6, 10, 15, 17–20] has investigated the epidemiology of individuals facing the free rider problem given the choice of voluntary vaccination. Here, we extend previous work by accounting for imperfect vaccines, whose effects on individuals' vaccination behavior in spatial populations have not been fully answered. We propose a model that incorporates imperfect vaccines into the interaction between disease and vaccination in structured populations. We combine vaccination dynamics with an epidemiological model, in particular the SIR model, to study flu-like diseases.

The results from this paper show incomplete information together with ineffective vaccines in a population of imitators further aggravate the problem of suboptimal level of vaccination if the initial vaccination rate is low. This is because two separate equilibria exist for high initial vaccination and low initial vaccination. This bi-stability effect is observed when the population is homogeneous in terms of beliefs of vaccination effectiveness or heterogeneous with fixed beliefs or spreading beliefs. Taking into considerations of recent trends of vaccine hesitancy, results from this paper provide justification for intensifying vaccination campaigns to boost initial vaccination rate and discourage people from opting out of immunization programs.

Supporting Information

S1 Fig. Vaccination dynamics in non-well-mixed populations. This figure supplements Fig 2. (1) shows the time course of the iteration shown in Fig 2(B). (2) shows the time course of the iteration shown in Fig 2(C). Blue solid lines, susceptible population that is not vaccinated; blue dotted lines, susceptible population that is vaccinated; red solid lines, infected population that is not vaccinated; red dotted lines, infected population that is vaccinated; yellow solid lines, recovered population that is not vaccinated; yellow dotted lines, recovered population that is vaccinated.



Author Contributions

Conceived and designed the model: Ran Zhuo, Feng Fu. Simulated the results: Ran Zhuo. Analyzed the data: Ran Zhuo. Replicated the results: Tommy Khoo (Department of Mathematics, Dartmouth College). Wrote the paper: Ran Zhuo. Reviewed the paper: Feng Fu.

References

1. Bauch CT. Imitation dynamics predict vaccinating behaviour. Proceedings of the Royal Society of London B: Biological Sciences. 2005 Aug 22;272(1573):1669-75.

2. Wu B, Fu F, Wang L. Imperfect vaccine aggravates the long-standing dilemma of voluntary vaccination. PloS one. 2011 Jun 8;6(6):e20577.

3. Fine PE, Clarkson JA. Individual versus public priorities in the determination of optimal vaccination policies. American Journal of Epidemiology. 1986 Dec 1;124(6):1012-20.

4. Bauch CT, Galvani AP, Earn DJ. Group interest versus self-interest in smallpox vaccination policy. Proceedings of the National Academy of Sciences. 2003 Sep 2;100(18):10564-7.

5. Jansen VA, Stollenwerk N, Jensen HJ, Ramsay ME, Edmunds WJ, Rhodes CJ. Measles outbreaks in a population with declining vaccine uptake Science. 2003 Aug 8;301(5634):804-.

6. Basu S, Chapman GB, Galvani AP. Integrating epidemiology, psychology, and economics to achieve HPV vaccination targets. Proceedings of the National Academy of Sciences. 2008 Dec 2;105(48):19018-23.

7. Larson HJ, Jarrett C, Eckersberger E, Smith DM, Paterson P. Understanding vaccine hesitancy around vaccines and vaccination from a global perspective: a systematic review of published literature, 2007?2012. Vaccine. 2014 Apr 17;32(19):2150-9.

8. Omer SB, Salmon DA, Orenstein WA, Dehart MP, Halsey N. Vaccine refusal, mandatory immunization, and the risks of vaccine-preventable diseases. New England Journal of Medicine. 2009 May 7;360(19):1981-8.

9. Gowda C, Dempsey AF. The rise (and fall?) of parental vaccine hesitancy. Human vaccines & immunotherapeutics. 2013 Aug 8;9(8):1755-62.

10. Fu F, Rosenbloom DI, Wang L, Nowak MA. Imitation dynamics of vaccination behaviour on social networks. 1. Proceedings of the Royal Society of London B: Biological Sciences. 2011 Jan 7;278(1702):42-9.

11. Zhang H, Fu F, Zhang W, Wang B. Rational behavior is a ?double-edged sword?when considering voluntary vaccination. Physica A: Statistical Mechanics and its Applications. 2012 Oct 15;391(20):4807-15.

12. Coelho FC, Codeco CT. Dynamic modeling of vaccinating behavior as a function of individual beliefs. PLoS Comput Biol. 2009 Jul 10;5(7):e1000425.

13. Bauch CT, Bhattacharyya S. Evolutionary game theory and social learning can determine how vaccine scares unfold. PLoS Comput Biol. 2012 Apr 5;8(4):e1002452.

14. Hughes V. News feature: a shot of fear. Nature medicine. 2006 Nov 1;12(11):1228-9.

15. Bauch CT, Earn DJ. Vaccination and the theory of games. Proceedings of the National Academy of Sciences of the United States of America. 2004 Sep 7;101(36):13391-4.

16. Pastor-Satorras R, Vespignani A. Epidemic dynamics and endemic states in complex networks. Physical Review E. 2001 May 22;63(6):066117.

17. Vardavas R, Breban R, Blower S. Can influenza epidemics be prevented by voluntary vaccination?. PLoS Comput Biol. 2007 May 4;3(5):e85.

18. Galvani AP, Reluga TC, Chapman GB. Long-standing influenza vaccination policy is in accord with individual self-interest but not with the utilitarian optimum. Proceedings of the National Academy of Sciences. 2007 Mar 27;104(13):5692-7.

19. Perisic A, Bauch CT. Social contact networks and disease eradicability under voluntary vaccination. 1. PLoS Comput Biol. 2009 Feb 6;5(2):e1000280.

20. Bauch CT, Bhattacharyya S, Ball RF. Rapid emergence of free-riding behavior in new pediatric immunization programs. PLoS One. 2010 Sep 15;5(9):e12594.

21. Nowak MA. Evolutionary dynamics. Harvard University Press; 2006 Sep 29.

22. Traulsen A, Nowak MA. Chromodynamics of cooperation in finite populations. PLoS One. 2007 Mar 7;2(3):e270.

23. Brown SP, Taddei F. The durability of public goods changes the dynamics and nature of social dilemmas. PLoS One. 2007 Jul 4;2(7):e593.

24. Poncela J, Gomez-Gardenes J, Floria LM, Sanchez A, Moreno Y. Complex cooperative networks from evolutionary preferential attachment. PLoS one. 2008 Jun 18;3(6):e2449.

25. van Boven M, Klinkenberg D, Pen I, Weissing FJ, Heesterbeek H. Self-interest versus group-interest in antiviral control. PLoS One. 2008 Feb 13;3(2):e1558.

26. Perc M, Wang Z. Heterogeneous aspirations promote cooperation in the prisoner's dilemma game. PLoS One. 2010 Dec 6;5(12):e15117.

27. Zhang BY, Cressman R, Tao Y. Cooperation and stability through periodic impulses. PloS one. 2010 Mar 29;5(3):e9882.

28. Szolnoki A, Szabo G, Perc M. Phase diagrams for the spatial public goods game with pool punishment. Physical Review E. 2011 Mar 7;83(3):036101.

29. Wang Z, Murks A, Du WB, Rong ZH, Perc M. Coveting thy neighbors fitness as a means to resolve social dilemmas. Journal of theoretical biology. 2011 May 21;277(1):19-26.

30. Szolnoki A, Perc M. Reward and cooperation in the spatial public goods game. EPL (Europhysics Letters). 2010 Nov 29;92(3):38003.

31. Perc M, Szolnoki A. Coevolutionary games – a mini review. BioSystems. 2010 Feb 28;99(2):109-25.

32. Gross T, D'Lima CJ, Blasius B. Epidemic dynamics on an adaptive network. Physical review letters. 2006 May 24;96(20):208701.

33. Fukuda E, Kokubo S, Tanimoto J, Wang Z, Hagishima A, Ikegaya N. Risk assessment for infectious disease and its impact on voluntary vaccination behavior in social networks. Chaos, Solitons & Fractals. 2014 Nov 30;68:1-9.

34. Cardillo A, Reyes-Suarez C, Naranjo F, Gomez-Gardenes J. Evolutionary vaccination dilemma in complex networks. Physical Review E. 2013 Sep 5;88(3):032803.

35. Wang Z, Zhang H, Wang Z. Multiple effects of self-protection on the spreading of epidemics. Chaos, Solitons & Fractals. 2014 Apr 30;61:1-7.

36. Zhang HF, Wu ZX, Tang M, Lai YC. Effects of behavioral response and vaccination policy on epidemic spreading-an approach based on evolutionary-game dynamics. Scientific reports. 2014 Jul 11;4.

37. Traulsen A, Nowak MA, Pacheco JM. Stochastic dynamics of invasion and fixation. Physical Review E. 2006 Jul 17;74(1):011909.

38. Traulsen A, Semmann D, Sommerfeld RD, Krambeck HJ, Milinski M. Human strategy updating in evolutionary games. 1. Proceedings of the National Academy of Sciences. 2010 Feb 16;107(7):2962-6.

39. Tversky A, Kahneman D. Availability: A heuristic for judging frequency and probability. Cognitive psychology. 1973 Sep 30;5(2):207-32.

40. Johnson EJ, Tversky A. Affect, generalization, and the perception of risk. Journal of personality and social psychology. 1983 Jul;45(1):20.

41. Palekar R, Pettifor A, Behets F, MacPhail C. Association between knowing someone who died of AIDS and behavior change among South African youth. AIDS and Behavior. 2008 Nov 1;12(6):903-12.

42. Eames KT. Networks of influence and infection: parental choices and childhood disease. Journal of The Royal Society Interface. 2009 Sep 6;6(38):811-4.

43. Sudfeld CR, Navar AM, Halsey NA. Effectiveness of measles vaccination and vitamin A treatment. International journal of epidemiology. 2010 Apr 1;39(suppl 1):i48-55.

44. Hoffman SL. Malaria vaccine development: a multi-immune response approach. American Society for Microbiology (ASM); 1996.

45. Chen FH. A susceptible-infected epidemic model with voluntary vaccinations. Journal of mathematical biology. 2006 Aug 1;53(2):253-72.

46. Reluga TC, Galvani AP. A general approach for population games with application to vaccination. Mathematical biosciences. 2011 Apr 30;230(2):67-78.

47. Cornforth DM, Reluga TC, Shim E, Bauch CT, Galvani AP, Meyers LA. Erratic flu vaccination emerges from short-sighted behavior in contact networks. PLoS Comput Biol. 2011 Jan 27;7(1):e1001062.

48. Osterholm MT, Kelley NS, Sommer A, Belongia EA. Efficacy and effectiveness of influenza vaccines: a systematic review and meta-analysis. The Lancet infectious diseases. 2012 Jan 31;12(1):36-44.

49. Bauch CT, Galvani AP. Social factors in epidemiology. Science. 2013 Oct 4;342(6154):47-9.

50. Gillespie DT. A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. Journal of computational physics. 1976 Dec 1;22(4):403-34.

51. Breban R, Vardavas R, Blower S. Mean-field analysis of an inductive reasoning game: application to influenza vaccination. Physical review E. 2007 Sep 24;76(3):031127.

52. Breban R. Health newscasts for increasing influenza vaccination coverage: an inductive reasoning game approach. PloS one. 2011 Dec 21;6(12):e28300.

53. Traulsen A, Claussen JC, Hauert C. Coevolutionary dynamics: from finite to infinite populations. Physical review letters. 2005 Dec 2;95(23):238701.

54. Wu B, Altrock PM, Wang L, Traulsen A. Universality of weak selection. Physical Review E. 2010 Oct 13;82(4):046106.

55. Blume LE. The statistical mechanics of strategic interaction. Games and economic behavior. 1993 Jul 31;5(3):387-424.

56. Szabo G, Toke C. Evolutionary prisoner?s dilemma game on a square lattice. Physical Review E. 1998 Jul 1;58(1):69.

57. Perc M. Coherence resonance in a spatial prisoner's dilemma game. New Journal of Physics. 2006 Feb 14;8(2):22.

58. Szolnoki A, Perc M, Szabo G. Topology-independent impact of noise on cooperation in spatial public goods games. Physical Review E. 2009 Nov 19;80(5):056109.

59. Rasanen K, Kruuk LE. Maternal effects and evolution at ecological time?scales. Functional Ecology. 2007 Jun 1;21(3):408-21.

60. Asch DA, Baron J, Hershey JC, Kunreuther H, Meszaros J, Ritov I, Spranca M. Omission bias and pertussis vaccination. 1. Medical decision making. 1994 Apr 1;14(2):118-23.

61. Christakis NA, Fowler JH. The spread of obesity in a large social network over 32 years. New England journal of medicine. 2007 Jul 26;357(4):370-9.

62. May RM, Levin SA, Sugihara G. Complex systems: Ecology for bankers. Nature. 2008 Feb 21;451(7181):893-5.

63. Siddiqui M, Salmon DA, Omer SB. Epidemiology of vaccine hesitancy in the United States. Human vaccines & immunotherapeutics. 2013 Dec 24;9(12):2643-8.

64. Glanz JM, McClure DL, Magid DJ, Daley MF, France EK, Hambidge SJ. Parental refusal of varicella vaccination and the associated risk of varicella infection in children. Archives of pediatrics & adolescent medicine. 2010 Jan 4;164(1):66-70.

65. Fu F, Christakis NA, Fowler JH. Dueling biological and social contagions. Scientific Reports. 2017;7.