ARTICLE

Crosstalk in concurrent repeated games impedes direct reciprocity and requires stronger levels of forgiveness

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Direct reciprocity is a mechanism for cooperation among humans. Many of our daily interactions are repeated. We interact repeatedly with our family, friends, colleagues, members of the local and even global community. In the theory of repeated games, it is a tacit assumption that the various games that a person plays simultaneously have no effect on each other. Here we introduce a general framework that allows us to analyze "crosstalk" between a player's concurrent games. In the presence of crosstalk, the action a person experiences in one game can alter the person's decision in another. We find that crosstalk impedes the maintenance of cooperation and requires stronger levels of forgiveness. The magnitude of the effect depends on the population structure. In more densely connected social groups, crosstalk has a stronger effect. A harsh retaliator, such as Tit-for-Tat, is unable to counteract crosstalk. The crosstalk framework provides a unified interpretation of direct and upstream reciprocity in the context of repeated games.

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S ocial dilemmas are situations where mutual cooperation is better than mutual defection and yet there is an incentive to defect[1,2]. Cooperation is normally opposed by natural selection unless mechanisms for the evolution of cooperation are in place[3]. One such mechanism is direct reciprocity, which is based on repeated interactions between the same two players[4,5]. In repeated social dilemmas, humans often learn to use adaptive rules, telling them when to cooperate, when to defect, and how to motivate others to cooperate[6–8]. Cooperation can be achieved if people adopt conditional cooperative strategies such as Tit-for-Tat[5], Generous Tit-for-Tat[9,10], or Win-stay, Lose-shift[11,12]. Conditional cooperation, paired with some amount of generosity, can maintain a healthy level of cooperation[13–21]. It can evolve even if initially rare[22–26].

Most previous models of direct reciprocity (with a few notable exceptions[27–30]) have either assumed that (i) individuals only engage in one repeated game at a time or that (ii) an individual's action in one game is independent of all its other interactions. Because humans often engage in many games simultaneously, the first assumption seems to be violated in most practical scenarios. Moreover, evidence from experimental studies suggests that also the second assumption of independence may not always apply[31–38]. We say that a player's decision is subject to "crosstalk" when an interaction that a player has in one repeated game influences how the very same player behaves in another repeated game (Fig. 1a). For example, consider the interactions in a group of three individuals, "Alice", "Bob", and "Charlie" (Fig. 1b). Suppose that after a series of previous encounters, Bob is prompted for a decision whether to cooperate with Alice in the next round. In her last interaction with Bob, Alice has cooperated. Therefore, Bob who uses Tit-for-Tat, would now cooperate with Alice. But Bob's last interaction had occurred with Charlie and in that interaction Charlie had defected. Crosstalk now means there is some chance that Bob defects with Alice although direct reciprocity would mandate Bob to cooperate. Bob's state with respect to Charlie influences his decision with respect to Alice.

Such crosstalk can result from various psychological processes. For example, experiments on upstream reciprocity suggest that subjects who have received help in their previous interaction often consciously choose to "pay it forward"[22,31–33]. Alternatively, crosstalk may also occur when subjects have limited working memory[34–36]. In that case, subjects may confuse their co-players' past actions, which may in turn lead them to reward the wrong person for past cooperative behaviors. We propose a mathematical framework that allows us to quantify how crosstalk affects the cooperation dynamics within a population. We show that, in the presence of crosstalk, a single defector can lead to the complete breakdown of cooperation in an arbitrarily large group of conditional cooperators. Nevertheless, cooperation can prevail if the population is structured and if subjects are sufficiently forgiving. For our model, we do not need to specify the particular psychological process at work: the resulting behavioral dynamics are independent of whether crosstalk is the result of a conscious decision (as in upstream reciprocity), or the consequence of a subconscious error (as when individuals confuse the past actions of their co-players). However, the interpretation of our results will often depend on the specific psychological mechanism that gives rise to crosstalk. We revisit this matter in the "Discussion" section.

Results
Framework for crosstalk between concurrent repeated games. We consider a group of N individuals. Each individual plays a pairwise repeated prisoner's dilemma (PD) with each interaction partner. These repeated games occur concurrently. At each time step, we choose a random pair of players for a single interaction

(Fig. 1b). Each player uses a reactive strategy, defined by two parameters, p and q, which denote the probability to cooperate if the same co-player in the previous round has either cooperated or defected, respectively. The class of reactive strategies includes many well-known examples, such as always-cooperate (ALLC), always-defect (ALLD), tit-for-tat (TFT: Supplementary Fig. 1b), and Generous Tit-for-Tat[10] (GTFT: Supplementary Fig. 1d). Reactive strategies can be implemented by stochastic two-state automata[39–42]. The two states are labeled C and D (see Supplementary Fig. 1a). In the next interaction, a player cooperates if she is in state C and defects if she is in state D. Cooperators pay a cost c for their co-player to receive a benefit $b > c$. Defectors do not incur a cost and their co-player does not receive a benefit. The player's strategy determines how the player's state is updated after an interaction has taken place.

In our setup, each player uses a specific strategy for all of her interactions, but has distinct automata to hold the games with all of her different co-players in memory (Supplementary Fig. 2). For example, a player using TFT can be in different states (C or D) with different co-players, but uses the same strategy to update her states against all of her co-players. The separate automata enable players to remember previous interactions and to react in future rounds according to their respective history with each co-player.

Crosstalk between two repeated games occurs if a player's state with respect to one interaction partner displaces the player's state with respect to another player (Supplementary Fig. 2). Specifically, we assume that, before each interaction, there is a probability γ that the players' state with respect to the current co-player is replaced by the state with respect to the previous co-player (other variants of crosstalk will be discussed below). The crosstalk rate $\gamma \in [0, 1]$ specifies how often crosstalk occurs. In the special case of no crosstalk, $\gamma = 0$, players perfectly distinguish between all their opponents, and we recover the scenario considered in previous studies of direct reciprocity[2,5]. For positive crosstalk rates, cooperative and defective behaviors can cascade in the players' social network: a player's action in one game can affect how the co-player acts in a different game, which in turn may influence again other games (Fig. 1). Therefore, crosstalk causes ripples that propagate in social networks. The overall effect of crosstalk depends on the structure of the population. We represent this structure by arranging players on a graph[43–45], where edges between players denote interactions (Fig. 2; "Methods" section). While our framework is applicable to arbitrary population structures, we illustrate the effects of crosstalk using four regular networks (Fig. 3a), ranging from a circle (where each player has exactly two interaction partners) to the complete graph (where all players interact with everyone else).

Cooperative and defective behavior spreads across population. We utilize stochastic computer simulations to study the cooperation frequency in a population over time, and derive mathematical recursions to calculate the long-run payoffs in the steady state ("Methods" section). To illustrate how crosstalk leads to the spread of defection in a generally cooperative society, we place a single ALLD player in a network of $N - 1$ conditionally cooperative players (Figs. 2 and 3a). When the conditionally cooperative players use TFT (which is given by $p = 1$, $q = 0$) and crosstalk occurs, $\gamma > 0$, the ALLD player can turn all remaining players into defectors eventually (Fig. 2a), independent of the population structure and the crosstalk rate (Supplementary Fig. 3). The spread of defection can be prevented if the cooperative players use more generous strategies, with $p = 1$ and $0 < q < 1$. We refer to such strategies as GTFT. The impact of different q values will be discussed below. At first, we choose $q = 1/3$. If the single ALLD player is placed among GTFT players,
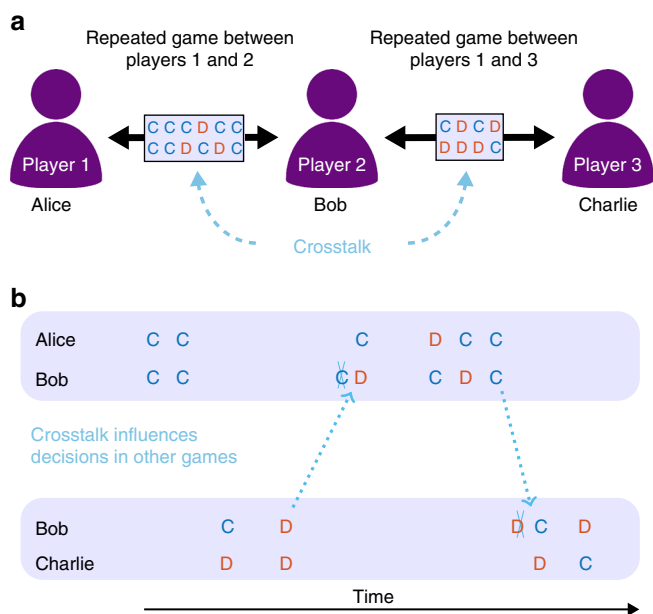
Fig. 1 Crosstalk between repeated games. **a** Bob is engaged simultaneously in independent, repeated games with Alice and Charlie. Crosstalk means that the moves that occur between Alice and Bob can affect Bob's decisions towards Charlie. **b** Alice and Bob as well as Bob and Charlie simultaneously play a repeated Prisoner's Dilemma. The rounds of the two games occur at particular times. In each round the players can either cooperate (C) or defect (D). The outcome of a round in one game can influence the subsequent round in the other game. Crosstalk is indicated by dotted arrows

cooperation frequencies converge to a positive value (Fig. 2b), with the eventual equilibrium rates depending on the population structure and on the crosstalk rate (Supplementary Fig. 3). We can also observe the opposite effect: a single ALLC player can increase the cooperation rates in a population of stochastic TFT players using $p = 1 - \epsilon$ and $q = \epsilon$ (Supplementary Fig. 4c).

Comparing the effect of different population structures, we find that a GTFT population can maintain cooperation more easily if players are arranged on a circle instead of a complete graph (Fig. 3a, b, Supplementary Fig. 5). For a population size of $N = 16$, the cooperators obtain a higher average payoff than the defector for crosstalk rates up to $\gamma = 0.85$ on a circle, and for up to $\gamma = 0.41$ on a complete graph. In networks with a low degree, players are more likely to give the adequate response with respect to their current co-player, because, if crosstalk occurs, the current co-player is more likely to coincide with the previous co-player such that crosstalk becomes inconsequential. For this reason, all other explored population structures exhibit crosstalk thresholds between the circle and the complete graph (Fig. 3b).

To investigate the recovery properties after a mistake, we computed the amount of time that a population of conditional cooperators with strategy $(1, q)$ and $q > 0$ needs to return to full cooperation after a single defection event. We find that crosstalk leads to a significantly faster recovery (Supplementary Fig. 6). Intuitively, when the crosstalk rate is high, a player's automata are updated more frequently (once before the interaction takes place, and once after the interaction). Because the players apply strategies with $p = 1$ and $q > 0$, each updating event is biased towards increasing cooperation: every cooperative act puts the co-player into a cooperative state, whereas defective acts are forgiven with probability q. Moreover, we show that the recovery time is monotonically increasing with the average degree (k) of the population structure and monotonically decreasing with the
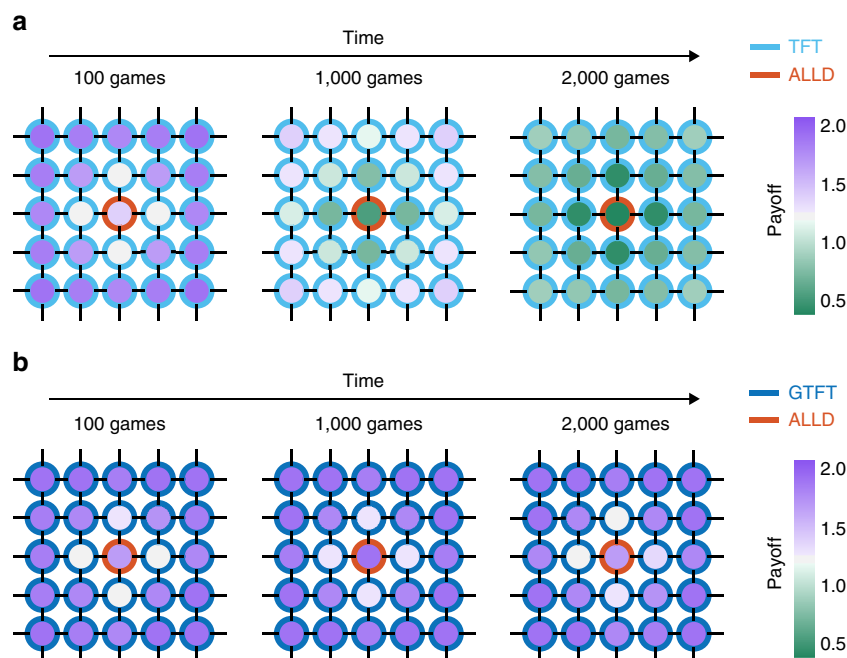

Fig. 2 Cooperative and defective behavior can spread across a population in the presence of crosstalk. Twenty-four conditional cooperators (blue framed nodes, panels) and one ALLD (Always-Defect) player (red framed node, placed in the center) populate a 5 × 5 lattice. The fill color of the nodes depicts the expected payoff of the players after 100, 1000, and 2000 games. **a** If the conditional cooperators use TFT (Tit-for-Tat), crosstalk leads to the spread of defection from the ALLD player to all other group members. Cooperation goes extinct. **b** GTFT (Generous Tit-for-Tat) is an error-correcting strategy and can thereby suppress the spread of defection by crosstalk. Only the players in the neighborhood of the ALLD player have reduced payoff. Parameter values: crosstalk rate $\gamma = 0.5$, benefit $b = 3$, and cost $c = 1$. For GTFT (defined by $p = 1$ and $0 < q < 1$), we used $q = 1/3$
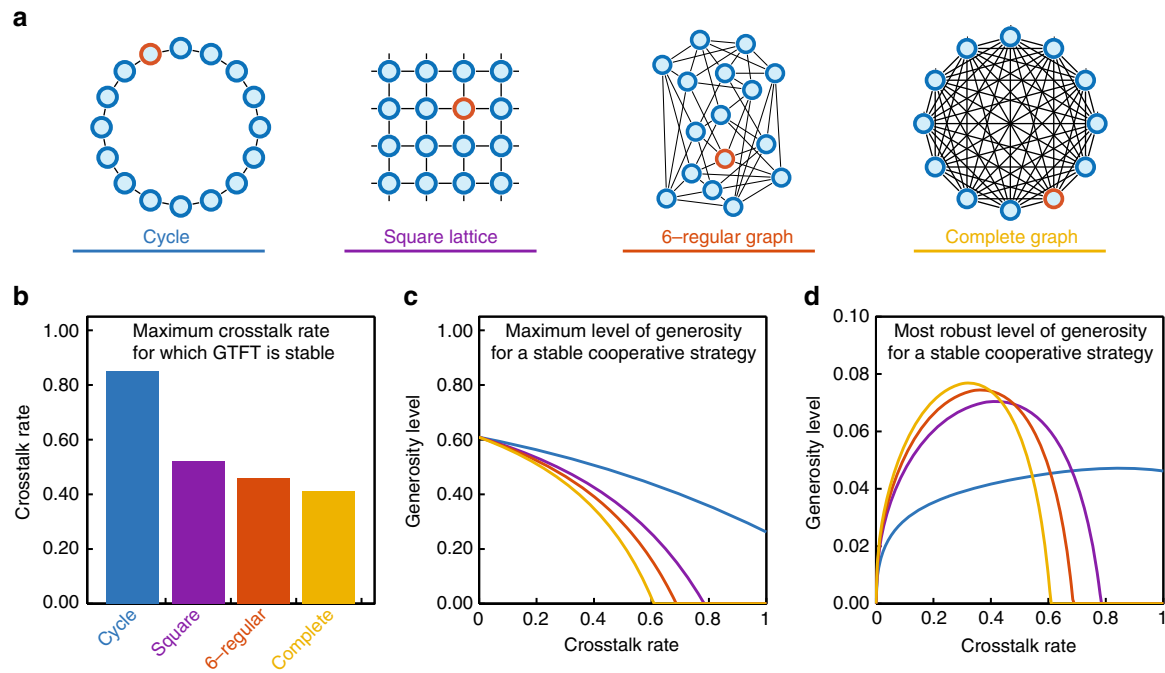
Fig. 3 Population structure and crosstalk rate substantially affect stationary payoffs and evolutionary stability. **a** Examples of the investigated population structures: cycle, square lattice, 6-regular graph, complete graph. Defectors (red nodes) are randomly placed within the population. **b** Maximally tolerated crosstalk rate (γ) in various population structures such that the payoff of the ALLD player remains below the payoff of the GTFT players (for a generosity parameter q fixed to 1/3). **c** Maximum level of generosity (q_M) such that the average payoff of the GTFT players exceeds the payoff of the ALLD player. The circle allows players to be most generous when crosstalk is common. **d** Most robust level of generosity (q_R) maximizing the relative payoff advantage of the GTFT players compared to the ALLD player. When crosstalk is rare, a small increase in the crosstalk rate allows players to be more generous, to decrease the chance that defection spreads across the population. However, when crosstalk becomes common, a further increase of γ requires the players to become less generous to constrain the payoff of the ALLD player. Parameter values: number of players $N = 16$ (one ALLD player), benefit $b = 3$, and cost $c = 1$

probability to cooperate after defection (q; see Supplementary Note 1 for more details).

Crosstalk requires the right level of forgiveness. We calculate the generosity parameter q of GTFT to optimally cope with crosstalk. To this end, we consider two different optimality criteria. First, we calculate the most generous strategy that is able to resist invasion by a single ALLD player. That is, for a fixed population structure and a given crosstalk rate, we derive the reactive strategy $(1, q_M)$ with maximum q_M such that $N-1$ players with this strategy get at least the same average payoff as the single defector. Analytical calculations for the complete graph and numerical results for all other population structures show that higher crosstalk rates and higher network degrees (that is a higher number of neighbors) require the cooperative players to be less generous (Fig. 3c, "Methods" section). For the second optimality criterion, we calculate the cooperative strategy with the most robust level of generosity q_R such that $N-1$ players with strategy $(1, q_R)$ have the highest relative payoff advantage compared to the single ALLD player. The most robust level of generosity exhibits a non-monotonic dependence on the crosstalk rate (Fig. 3d). In the absence of crosstalk, $\gamma = 0$, the perfectly reciprocal TFT strategy is most robust against invasion of ALLD. As the crosstalk rate increases, the most robust level of generosity q_R first increases, but then decreases again. Intuitively, for the robustness of a conditionally cooperative population against ALLD, high values of the generosity parameter q have two opposing effects. On one hand, high values of q make it less likely that the defectors' actions propagate through the network. On the other hand, high values of q also let the players be more forgiving against the defector, and hence increase the payoff of the ALLD player. When crosstalk is rare, conditional cooperators can prevent the spread of defection by choosing a small value for q. Once crosstalk is sufficiently frequent, however, players can no longer fully prevent defection from spreading. Instead, they rather need to keep the defector's payoff low, by choosing a smaller q value. These results confirm that in the presence of crosstalk, $\gamma > 0$, subjects should show some amount of generosity ($q > 0$), but not too much; we find $q < q_M$, with q_M depending on the crosstalk rate and on the population structure. Only for the circle, cooperation can prevail even when crosstalk is abundant (Fig. 3d).

The above analysis is based on a comparison between conditional cooperators and a specific invader, ALLD. More generally, we find that conditionally cooperative strategies $(1, q)$ with $q < q_M$ in fact resist invasion by all possible invading strategies (p', q') for the complete graph. This analysis also reveals that there are three classes of strategies in total that are stable against arbitrary invaders (Supplementary Note 1). The first class consists of the conditionally cooperative strategies just described. The second class consists of uncooperative strategies $(p, 0)$, with p sufficiently small (see Supplementary Note 1 for the exact condition). In particular, this class contains ALLD. When adopted by all players in a population, strategies of this class eventually lead to full defection. Finally, the third class consists of strategies (p, q) analogous to equalizer strategies of direct reciprocity[46–49]. When applied by all residents in the population, equalizer strategies guarantee that the payoff of a single invader is independent of the invader's strategy.

Crosstalk impedes the evolution of cooperation. These results raise the question to which extent subjects themselves would learn to apply cooperative strategies with a sustainable degree of
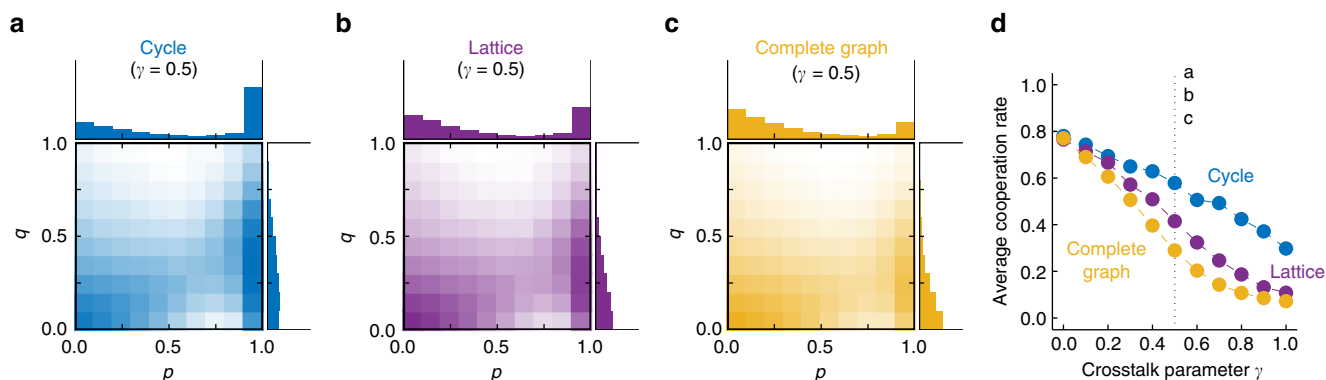
Fig. 4 Cooperative strategies evolve for various crosstalk rates and population structures. **a–c** Abundance of different reactive strategies (p, q) over the course of an evolutionary process when the crosstalk rate is fixed to $\gamma = 0.5$. The probability to cooperate if the co-player in the previous round either cooperated or defected is denoted by p and q. On a cycle and a lattice, GTFT strategies evolved, whereas the same settings did not allow for the evolution of cooperative strategies on a complete graph. **d** Resulting average cooperation rates across different crosstalk rates. The dotted line indicates the crosstalk rate used in **a–c**. See "Methods" section for setup of the simulations. Parameter values: population size $N = 16$, benefit $b = 10$, cost $c = 1$, intermediate selection strength $s = 1$

generosity. To explore that question, we implemented a simple model of cultural evolution where players are allowed to adopt new strategies over time, based on their current strategy's success ("Methods" section). According to this process, strategies that yield a comparably high payoff are more likely to be imitated by other players[50,51]. In addition, players may occasionally also experiment with new stochastic strategies, which introduces novel behaviors into the population. These two events, imitation and exploration, take the role of selection and mutation in models of biological evolution. We show that a birth-death process as used in many biological applications yields the same results (Supplementary Note 1). We simulated the evolutionary dynamics for various population structures and crosstalk rates, assuming that experimentation events are relatively rare[23]. In the plane of reactive strategies, we observe that for most of the time, players either apply defective strategies with $p \approx q \approx 0$, or cooperative strategies with $p \approx 1$ and $0 < q < q_{\mathrm{M}}$ (Fig. 4a–c). None of these strategies are evolutionarily stable[52]. Instead, when residents apply one of these strategies, neutral or nearly neutral mutants can often invade and pave the way for mutants of another strategy class[42]. The relative weight of these two strategy classes depends on the crosstalk rate and on the population structure (Fig. 4d). While cooperative strategies readily evolve on the cycle even for substantial crosstalk rates, they become less abundant as the population structure changes to a square lattice, or to a complete graph.

To understand the effect of crosstalk in more detail, we analyzed how easily other strategies fix in a resident population that either consists of ALLD players or GTFT players (Supplementary Fig. 7). Without crosstalk, GTFT is much more successful in resisting mutant invasions. On average, more mutants need to be introduced until the first mutant fixes. Moreover, successful mutants typically have a strategy that is very similar to GTFT (whereas ALLD is typically invaded by TFT-like strategies rather quickly). However, as the crosstalk rate increases, the invasion time into GTFT drops considerably, and successful mutants no longer need to be cooperative themselves.

Interestingly, we find that crosstalk favors the stability of extortionate strategies. With an extortionate strategy, players can guarantee that they never get a lower payoff than their co-player, while simultaneously acting such that it is in the co-player's best interest to cooperate unconditionally[47]. In classical models of direct reciprocity, extortionate strategies are unstable and they can only succeed if the population size is small[18,19,53]. In contrast, extortionate strategies can thrive even in large populations when

crosstalk is sufficiently abundant (Supplementary Fig. 8). However, this success comes at a cost. By becoming stable, extortionate strategies lose one of their most appealing properties: when crosstalk is abundant, a rare invader in an extortionate population does no longer benefit from being unconditionally cooperative. Instead, the best response is to be extortionate as well (see Supplementary Note 1 for details).

To analytically understand the impact of crosstalk on the evolutionary dynamics, we explored a deterministic model of evolution in well-mixed populations[54–56]. The singular strategies of these dynamics consist exactly of the three strategy sets that resist invasion by rare mutants that we described in the previous section: conditional cooperators, defectors, and equalizers. Which of these strategy classes is reached in the course of evolution now depends on the initial population (Supplementary Fig. 9a). As the crosstalk rate increases, the number of initial populations that eventually end up in a conditionally cooperative state decreases (Supplementary Fig. 9b). In this deterministic model, crosstalk thus acts by reducing the basin of attraction of the cooperative equilibria.

Alternative models of crosstalk. So far, we have analyzed one particular model of crosstalk: when prompted for the next decision, a player instead reacts to her most recent interaction, and this interaction could have been with someone else. But other implementations are conceivable.

For example, the memory state that a player holds for her current co-player could be replaced by the memory state of a random co-player, who may not coincide with the current or the most recent co-player. In this case, when deciding what to do for the next round in a particular game, the player uses with probability γ the state of a random game that she is holding in memory. We find that this alternative implementation of crosstalk differs in its short-term dynamics but converges to the same steady state as our original model (Supplementary Fig. 10). Thus, Figs. 3 and 4 immediately apply to this type of crosstalk as well.

Alternatively, a player's decision could depend not only on the previous interaction with one particular opponent. Instead, the player might consider an average across her recent experiences with all her co-players. We therefore introduce aggregate reactive strategies (Supplementary Note 1). Players using these strategies compute a weighted cooperation score across all their co-players. This cooperation score incorporates the last action of the current

co-player with weight $1 - \gamma$ and the average cooperation rate across all co-players' last actions with weight γ. The obtained score is then compared to an exogenous cooperation threshold τ. Players cooperate with probability p if the weighted cooperation score exceeds τ; otherwise they cooperate with probability q. In particular, if the crosstalk rate γ is zero, these strategies again correspond to the classical reactive strategies of direct reciprocity[2,10]. We explore the effects of γ and τ by considering a single defector in a population of conditional cooperators. The conditional cooperators apply a strategy with $p = 1$, $q = 1/3$ and some value τ, a strategy to which we refer to as Aggregate Generous Tit-for-Tat (AGTFT). While the cooperation dynamics of this model are qualitatively different from our previous results, we again find that higher crosstalk rates impede the stability of cooperation across all population structures (Supplementary Figs. 11 and 12).

Discussion

Classical models of direct reciprocity require that players provide a targeted response to each of their co-players[2,5]. Experimental results and everyday experience indicate that players' decisions can be affected by unrelated events that occur in their interactions with others[31–38]. Crosstalk arises when a player has simultaneous repeated interactions with several opponents. Importantly, crosstalk is different from previous approaches that combined direct and indirect (downstream) reciprocity. In models of downstream reciprocity, a player's strategy depends on the co-player's reputation, and hence on the co-players' interactions with others[38,57–64]. A combination of direct reciprocity and downstream reciprocity can promote cooperation because a single defection in one game may lead several unaffected co-players to retaliate against the defector[27–29]. However, downstream reciprocity makes stronger assumptions on the information players have when making their decision. It requires a player to observe other players' interactions or reputations to respond accordingly. In contrast, crosstalk is a much more elementary mechanism. It occurs "within" each player and does not rely on additional external information about independent interactions of unrelated players. Our notion of crosstalk is general: it captures that a player's decision in one game can be affected by the player's previous experience in another game, but it does not depend on the psychological process responsible for this interdependency.

Depending on the specific process at work, crosstalk is amendable to different interpretations. Our framework can be taken as a model of upstream reciprocity in the context of repeated games. Under this interpretation, cooperation or defection received from one person is sometimes consciously "paid forward" to another person. Previous analytical models have either focused on direct reciprocity or on upstream reciprocity separately[2,65,66]. The framework of crosstalk allows us to explore the consequences when both modes of reciprocity act simultaneously, and possibly interfere with each other. We recover previous results[65–67] that upstream reciprocity alone is most likely to yield cooperation when the population is highly structured. However, our results suggest that cooperation can even be maintained in well-mixed populations when upstream reciprocity is sufficiently coupled with direct reciprocity (i.e., when the crosstalk rate γ is sufficiently small).

Alternatively, crosstalk can serve as a model of individuals with limited working memory. According to this interpretation, crosstalk occurs when individuals confuse their various co-players, which introduces a type of behavioral noise into the cooperation dynamics. This noise is different from simple implementation errors considered in previous models[2,9,18,19,36,68,69]. Implementation errors only affect the repeated game in which they occur (Supplementary Fig. 4a, b). But crosstalk spreads from one game to another and therefore through the population (Supplementary Fig. 4). Only in the presence of crosstalk, a single defector can turn a whole population of TFT players into defectors.

We consider upstream reciprocity and confusion as different psychological processes which independently can give rise to crosstalk. Although these two processes are subject to different interpretations, according to the above discussed implementation, they lead to the same cooperation dynamics within a population. High degrees of upstream reciprocity, just as high degrees of confusion, undermine the ability of direct reciprocity to sustain cooperation.

Crosstalk provides a general framework with applications beyond the examples studied here. Future models could explore, for example, crosstalk between independent games that differ in their payoff structure[70], or when subjects engage in simultaneous games that involve more than two players. Similarly, one may study interactions in which the crosstalk rate itself depends on exogenous parameters, such as the number of neighbors, or the benefit of cooperation. Finally, we explored a model in which players aggregate across their last experience with all co-players. Further generalizations are conceivable. For example, players may defect against all their co-players as long as at least one of their automata is in the D state, or they may remember more than their co-player's last action[26,71]. Under crosstalk, the players' individual games are no longer considered in isolation, but they are embedded into the context of all concurrently ongoing interactions. Crosstalk requires stronger mechanisms for forgiveness especially in a more highly connected world. A harsh retaliator such as Tit-for-Tat is particularly unable to deal with crosstalk. This is an interesting message for our current society.

Methods

Computer simulations. To simulate the effect of crosstalk on the cooperation dynamics among players with fixed strategies, we consider a population of size N playing a repeated Prisoner's Dilemma (PD). The population is given by a graph where the nodes represent the players, and the edges reflect all possible interactions between players. Only players connected by an edge can be paired to play the PD. Players use separate two-state automata for each of their neighbors on the interaction graph[41]. The two states of each automaton are labeled C (cooperation) and D (defection). These states are updated according to the player's reactive strategy (p, q), see Supplementary Figs. 1 and 2. The parameter p denotes the probability to move to state C if the co-player has cooperated in the previous game (whereas the complementary probability $1 - p$ gives the likelihood to move to state D). Similarly, q denotes the probability to move to state C if the co-player has defected (and $1 - q$ is the respective probability to move to state D).

In each round, an edge of the interaction graph is chosen uniformly at random. A single PD is played among the two players adjacent to the chosen edge. With probability $1 - \gamma$ a player acts according to the respective automaton state associated with this co-player; with probability γ crosstalk occurs and the player refers to the state of the automaton updated in her last interaction instead. After the game, the automata states are updated according to the game outcome and the players' strategies. This elementary step is then iterated for a large number of rounds. For the simulation results depicted in Supplementary Fig. 5, we simulated 4000 games per realization (on average 500 games per player) and averaged across 10^4 realizations to obtain the stationary payoff of GTFT and ALLD players for a given population structure and crosstalk rate.

So far, we assumed that every edge in the interaction graph is chosen with the same probability. However, some interactions can occur with a higher frequency than others. To investigate the effects of different interaction frequencies, we studied the spread of defective behavior in a population of GTFT players populating a 5×5 lattice (Supplementary Fig. 13). We increased the interaction probability of all players on the central horizontal line by 10-fold (see orange edges) and observe how defective behavior spreads much faster along the horizontal axis than along the vertical axis. Within the analytical framework, interaction probabilities w_{ij} are given by the connectivity matrix W (see next section for details).

In the second studied type of crosstalk, again with probability γ crosstalk occurs and the player refers to the state of a random automaton, chosen from all her interaction partners with equal probability (Supplementary Figs. 2 and 10).

Analytical derivation of steady-state payoffs. To derive an explicit representation for the payoffs that players receive in the long run, we suppose that each player i adopts some fixed reactive strategy (p_i, q_i). The population structure is given by an $N \times N$ connectivity matrix $W = (w_{ij})$. The entries w_{ij} give the probability that the next interaction in that population occurs between players i and j. In particular, the connectivity matrix W is symmetric $w_{ij} = w_{ji}$, and satisfies $w_{ii} = 0$ and $\sum_{i<j} w_{ij} = 1$. As in the computer simulations, we focus on networks in which each link is played with equal probability. That is, if player i and j are connected, then $w_{ij} = w$ for some constant $w > 0$ that depends on the network structure, but is independent of the players i and j. For example, because there are $N(N-1)/2$ different links in a complete graph, well-mixed populations can be represented by a connectivity matrix with $w_{ij} = 2/(N(N-1))$ for all $i \neq j$. As another example, populations on a cycle are represented by $w_{ij} = 1/N$ if i and j occupy neighboring sites, and $w_{ij} = 0$ for all other i, j.

Let $\overline{w}_i = \sum_{j=1}^N w_{ij}$ denote the probability that the next interaction in the population involves player i. Moreover, let y_{ij}^t be the probability that player i is in state C against player j at time t, and let y_i^t be the probability that player i is in state C with respect to her previous co-player. We can calculate y_{ij}^{t+1} using the following recursion

$$
\begin{aligned}
y_{ij}^{t+1} = \quad & \underbrace{(1 - w_{ij}) y_{ij}^t}_{\text{If player } i \text{ did not interact with player } j \text{ in previous round}} \\
+ \quad & \underbrace{(1 - \gamma) w_{ij} \cdot \left(y_{ji}^t p_i + \left(1 - y_{ji}^t\right) q_i \right)}_{\text{Players } i \text{ and } j \text{ interacted, and player } j\text{'s action was not subject to crosstalk}} \\
+ \quad & \underbrace{\gamma w_{ij} \cdot \left(y_j^t p_i + \left(1 - y_j^t\right) q_i \right)}_{\text{Players } i \text{ and } j \text{ interacted, and player } j\text{'s action was subject to crosstalk}} .
\end{aligned}
\tag{1}
$$

To calculate the player's long run cooperation frequencies, we note that in the steady state, cooperation rates are independent of the time period, and hence $y_{ij}^{t+1} = y_{ij}^t =: y_{ij}$. Moreover, because interactions are fully random, the stationary probability y_i that player i is in state C with respect to her previous co-player simplifies to $y_i = \sum_{k=1}^N \frac{w_{ik}}{\overline{w}_i} y_{ik}$, which is the weighted average that player i is in state C with respect to a random co-player. In that case, we can rewrite Eq. (1) as

$$
y_{ij} - (1 - \gamma)(p_i - q_i) y_{ji} - \gamma(p_i - q_i) y_j = q_i.
\tag{2}
$$

The Eqs. (2) represent a system of $N(N-1)$ linear equations in the unknowns y_{ij} with $i \neq j$. By solving this inhomogeneous system, we can calculate the stationary frequency $\hat{y}_{ij}$ to find player i in state C with respect to player j. Given the stationary frequencies $\hat{y}_{ij}$, we can calculate the payoff π_i of player i by averaging over all co-players,

$$
\pi_i = \sum_{j=1}^N \frac{w_{ij}}{\overline{w}_i} \cdot \left[\left((1 - \gamma) \hat{y}_{ji} + \gamma \hat{y}_j \right) \cdot b - \hat{y}_{ij} \cdot c \right].
\tag{3}
$$

We note that this method applies to general crosstalk rates γ, general population structures, and general population compositions (e.g., populations with more than two different strategies present). As shown in Supplementary Fig. 5, these analytically derived payoffs are in excellent agreement with the computer simulations. In the Supplementary Note 1, we show how Eqs. (2) and (3) can be further simplified for well-mixed populations. In that case, we can also provide explicit expressions for how generous cooperative strategies of the form $(1, q)$ are allowed to be to resist invasion of ALLD (as depicted in Fig. 3c, d).

Setup of the evolutionary simulations. To explore the evolution of strategies under crosstalk, we consider a simple model of cultural evolution, the pairwise comparison process[50,51]. As common in studies on the evolution of strategies in repeated games[10–25,40,41], we assume a separation of time scales: the time it takes individuals to play their repeated games is short compared to the evolutionary timescale at which individuals adopt new strategies. This assumption allows us to use the players' stationary payoffs, as given by Eq. (3), when simulating the evolutionary trajectory of a population.

For the evolutionary simulations, we consider a population with fixed population structure and fixed crosstalk rate γ. In each evolutionary time step, there are two possible events, imitation or random strategy exploration. To model imitation events, we assume that two individuals are randomly drawn from the population. We refer to these two individuals as the "learner" and the "role model", respectively. Herein, we aim to compare the effect of crosstalk across different population structures. To allow for a fair comparison, we assume that, while payoffs are calculated for the given population structure, strategy updating occurs globally. As a consequence, the learner and the role model do not need to be neighbors in the direct interaction network. With this assumption, we rule out the formation of cooperative clusters, which would additionally favor the evolution of cooperation in networks with a low degree[44]. After selecting the learner and the role model, their payoffs π_L and π_R are calculated according to Eq. (3). We assume that the learner adopts the role model's strategy with probability $\rho = [1 + \exp(-s(\pi_R - \pi_L))]^{-1}$. The parameter $s \geq 0$ measures the strength of selection. When selection is

weak, $s \ll 1$, payoffs are largely irrelevant for imitation and the imitation probability approaches 1/2, irrespective of the players' strategies. When selection is strong, $s \gg 1$, players tend to adopt only those strategies that yield a higher payoff than their own strategy. In addition to these imitation events, we allow for random strategy exploration. When such an exploration event occurs, one player is randomly drawn from the population. This player then adopts a new strategy (p, q), which is uniformly drawn from all reactive strategies. Following the approach of Imhof and Nowak[23], we assume that these exploration events are rare. As a consequence, the population is homogeneous most of the time. Only occasionally, a mutant strategy enters the population due to random strategy exploration. This mutant strategy than either goes extinct or fixes before the next exploration event occurs. By simulating this process over a long timespan, we can record how often the population applies certain strategies (p, q), and we can compute the resulting average cooperation rate over an evolutionary timescale. In Fig. 4, we show corresponding results for the cycle, the square lattice, and for the complete graph, assuming parameter values of population size $N = 16$, benefit $b = 10$, cost $c = 1$, and selection strength $s = 1$. Other parameter values lead to qualitatively similar results, provided that selection is sufficiently strong and that the benefit of cooperation is sufficiently high to allow for the evolution of cooperation. In the Supplementary Note 1, we show that analogous results apply when we consider a birth-death process instead of the pairwise imitation process considered herein.

References

1. Dawes, R. M. Social dilemmas. *Annu. Rev. Psychol.* **31**, 169–193 (1980).
2. Sigmund, K. *The Calculus of Selfishness* (Princeton Univ. Press, 2010).
3. Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314**, 1560–1563 (2006).
4. Trivers, R. L. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57 (1971).
5. Axelrod, R. *The evolution of Cooperation* (Basic Books, NY, 1984).
6. Grujic, J. et al. A comparative analysis of spatial prisoner's dilemma experiments: Conditional cooperation and payoff irrelevance. *Sci. Rep.* **4**, 4615 (2014).
7. Fudenberg, D., Dreber, A. & Rand, D. G. Slow to anger and fast to forgive: cooperation in an uncertain world. *Am. Econ. Rev.* **102**, 720–749 (2012).
8. Rand, D. G. & Nowak, M. A. Human cooperation. *Trends Cogn. Sci.* **117**, 413–425 (2013).
9. Molander, P. The optimal level of generosity in a selfish, uncertain environment. *J. Confl. Resolut.* **29**, 611–618 (1985).
10. Nowak, M. A. & Sigmund, K. Tit for tat in heterogeneous populations. *Nature* **355**, 250–253 (1992).
11. Nowak, M. A. & Sigmund, K. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* **364**, 56–58 (1993).
12. Hauert, C. & Schuster, H. G. Effects of increasing the number of players and memory size in the iterated prisoner's dilemma: a numerical approach. *Proc. R. Soc. B* **264**, 513–519 (1997).
13. Frean, M. R. The prisoner's dilemma without synchrony. *Proc. R. Soc. B* **257**, 75–79 (1994).
14. Szolnoki, A., Perc, M. & Szabó, G. Phase diagrams for three-strategy evolutionary prisoner's dilemma games on regular graphs. *Phys. Rev. E* **80**, 056104 (2009).
15. van Segbroeck, S., Pacheco, J. M., Lenaerts, T. & Santos, F. C. Emergence of fairness in repeated group interactions. *Phys. Rev. Lett.* **108**, 158104 (2012).
16. Grujic, J., Cuesta, J. A. & Sanchez, A. On the coexistence of cooperators, defectors and conditional cooperators in the multiplayer iterated prisoner's dilemma. *J. Theor. Biol.* **300**, 299–308 (2012).
17. Fischer, I. et al. Fusing enacted and expected mimicry generates a winning strategy that promotes the evolution of cooperation. *Proc. Natl Acad. Sci. USA1* **10**, 10229–10233 (2013).
18. Hilbe, C., Nowak, M. A. & Sigmund, K. The evolution of extortion in iterated prisoner's dilemma games. *Proc. Natl Acad. Sci. USA* **110**, 6913–6918 (2013).
19. Stewart, A. J. & Plotkin, J. B. From extortion to generosity, evolution in the iterated prisoner's dilemma. *Proc. Natl Acad. Sci. USA* **110**, 15348–15353 (2013).
20. Szolnoki, A. & Perc, M. Defection and extortion as unexpected catalysts of unconditional cooperation in structured populations. *Sci. Rep.* **4**, 5496 (2014).
21. Akin, E. What you gotta know to play good in the iterated prisoner's dilemma. *Games* **6**, 175–190 (2015).
22. Nowak, M. A., Sasaki, A., Taylor, C. & Fudenberg, D. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646–650 (2004).

23. Imhof, L. A. & Nowak, M. A. Stochastic evolutionary dynamics of direct reciprocity. *Proc. R. Soc.* **B277**, 463–468 (2010).

24. Pinheiro, F. L., Vasconcelos, V. V., Santos, F. C. & Pacheco, J. M. Evolution of all-or-none strategies in repeated public goods dilemmas. *PLoS Comput. Biol.* **10**, e1003945 (2014).

25. Baek, S. K., Jeong, H. C., Hilbe, C. & Nowak, M. A. Comparing reactive and memory-one strategies of direct reciprocity. *Sci. Rep.* **6**, 25676 (2016).

26. Stewart, A. J. & Plotkin, J. B. Small groups and long memories promote cooperation. *Sci. Rep.* **6**, 26889 (2016).

27. Raub, W. & Weesie, J. Reputation and efficiency in social interactions: an example of network effects. *Am. J. Sociol.* **96**, 626–654 (1990).

28. Pollock, G. & Dugatkin, L. A. Reciprocity and the emergence of reputation. *J. Theor. Biol.* **159**, 25–37 (1992).

29. Roberts, G. Evolution of direct and indirect reciprocity. *Proc. R. Soc.* **B275**, 173–179 (2008).

30 Bear A. & Rand, D. G. Intuition, deliberation, and the evolution of cooperation. *Proc. Natl Acad. Sci. USA* **113**, 936–941 (2016).

31. Tsvetkova, M. & Macy, M. W. The social contagion of generosity. *PLoS ONE* **9**, e87275 (2014).

32. Gray, K., Ward, A. F. & Norton, M. I. Paying it forward: generalized reciprocity and the limits of generosity. *J. Exp. Psychol.* **143**, 247–254 (2014).

33. Fowler, J. H. & Christakis, N. A. Cooperative behavior cascades in human social networks. *Proc. Natl Acad. Sci.* **107**, 5334–5338 (2010).

34. Milinski, M. & Wedekind, C. Working memory constrains human cooperation in the prisoner's dilemma. *Proc. Natl Acad. Sci. USA* **95**, 13755–13758 (1998).

35. Soutschek, A. & Schubert, T. The importance of working memory updating in the prisoner's dilemma. *Psychol. Res.* **80**, 172–180 (2015).

36. Stevens, J. R., Volstorf, J., Schooler, L. J. & Rieskamp, J. Forgetting constrains the emergence of cooperative decision strategies. *Front. Psychol.* **1**, 235 (2011).

37. Molleman, L., van den Broek, E. & Egas, M. Personal experience and reputation interact in human decisions to help reciprocally. *Proc. R. Soc. B* **280**, 20123044 (2013).

38. Rockenbach, B. & Milinski, M. The efficient interaction of indirect reciprocity and punishment. *Nature* **444**, 718–723 (2006).

39. Nowak, M. A., Sigmund, K. & El-Sedy, E. Automata, repeated games and noise. *J. Math. Biol.* **33**, 703–722 (1995).

40. van Veelen, M., García, J., Rand, D. G. & Nowak, M. A. Direct reciprocity in structured populations. *Proc. Natl Acad. Sci. USA* **109**, 9929–9934 (2012).

41. Zagorsky, B. M., Reiter, J. G., Chatterjee, K. & Nowak, M. A. Forgiver triumphs in alternating prisoner's dilemma. *PLoS ONE* **8**, e80814 (2013).

42. Garcia, J. & van Veelen, M. In and out of equilibrium I: evolution of strategies in repeated games with discounting. *J. Econ. Theory* **161**, 161–189 (2016).

43. Lieberman, E., Hauert, C. & Nowak, M. A. Evolutionary dynamics on graphs. *Nature* **433**, 312–316 (2005).

44. Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**, 502–505 (2006).

45. Allen, B. et al. Evolutionary dynamics on any population structure. *Nature* **544**, 227–230 (2017).

46. Boerlijst, M. C., Nowak, M. A. & Sigmund, K. Equal pay for all prisoners. *Am. Math. Mon.* **104**, 303–307 (1997).

47. Press, W. H. & Dyson, F. D. Iterated prisoner's dilemma contains strategies that dominate any evolutionary opponent. *Proc. Natl Acad. Sci. USA* **109**, 10409–10413 (2012).

48. Akin, E. in *Ergodic Theory, Advances in Dynamics* (ed Assani, I.) 77–107 (de Gruyter, 2016).

49. Hilbe, C., Traulsen, A. & Sigmund, K. Partners or rivals? strategies for the iterated prisoner's dilemma. *Games Econ. Behav.* **92**, 41–52 (2015).

50. Szabó, G. & Töke, C. Evolutionary prisoner's dilemma game on a square lattice. *Phys. Rev. E* **58**, 69–73 (1998).

51. Traulsen, A., Nowak, M. A. & Pacheco, J. M. Stochastic dynamics of invasion and fixation. *Phys. Rev. E* **74**, 011909 (2006).

52. Maynard Smith, J. & Price, G. R. The logic of animal conflict. *Nature* **246**, 15–18 (1973).

53. Adami, C. & Hintze, A. Evolutionary instability of zero-determinant strategies demonstrates that winning is not everything. *Nat. Commun.* **4**, 2193 (2013).

54. Hofbauer, J. & Sigmund, K. Adaptive dynamics and evolutionary stability. *Appl. Math. Lett.* **3**, 75–79 (1990).

55. Hofbauer, J. & Sigmund, K. *Evolutionary Games and Population Dynamics.* (Cambridge University Press, Cambridge, 1998).

56. Metz, J. A. J., Geritz, S. A. H., Meszena, G., Jacobs, F. J. A. &van Heerwaarden, J. S. in *Stochastic and Spatial Structures of Dynamical Systems* (eds van Strien, S. J. & Lunel, S. M. V.) 183–231 (North Holland, Amsterdam, 1996).

57. Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity by image scoring. *Nature* **393**, 573–577 (1998).

58. Wedekind, C. & Milinski, M. Cooperation through image scoring in humans. *Science* **288**, 850–852 (2000).

59. Leimar, O. & Hammerstein, P. Evolution of cooperation through indirect reciprocity. *Proc. R. Soc.* **B268**, 745–753 (2001).

60. Ohtsuki, H. & Iwasa, Y. How should we define goodness?-reputation dynamics in indirect reciprocity. *J. Theor. Biol.* **231**, 107–120 (2004).

61. Panchanathan, K. & Boyd, R. Indirect reciprocity can stabilize cooperation without the second-order free-rider problem. *Nature* **432**, 499–502 (2004).

62. Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity. *Nature* **437**, 1291–1298 (2005).

63. Uchida, S. & Sigmund, K. The competition of assessment rules for indirect reciprocity. *J. Theor. Biol.* **263**, 13–19 (2009).

64. Sasaki, T., Yamamoto, H., Okada, I. & Uchida, S. The evolution of reputation-based cooperation in regular networks. *Games* **8**, 8 (2017).

65. Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. Evolution of cooperation by generalized reciprocity. *Proc. R. Soc. Lond. B: Biol. Sci.* **272**, 1115–1120 (2005).

66. Rankin, D. J. & Taborsky, M. Assortment and the evolution of generalized reciprocity. *Evolution* **63**, 1913–1922 (2009).

67. Nowak, M. A. & Roch, S. Upstream reciprocity and the evolution of gratitude. *Proc. R. Soc. Lond. B: Biol. Sci.* **274**, 605–610 (2007).

68. Wu, J. & Axelrod, R. How to cope with noise in the iterated prisoner's dilemma. *J. Confl. Resolut.* **39**, 183–189 (1995).

69. Brandt, H. & Sigmund, K. The good, the bad and the discriminator—errors in direct and indirect reciprocity. *J. Theor. Biol.* **239**, 183–194 (2006).

70. Bernheim, D. & Whinston, M. D. Multimarket contact and collusive behavior. *Rand. J. Econ.* **21**, 1–26 (1990).

71. Hilbe, C., Martinez-Vaquero, L. A., Chatterjee, K. & Nowak, M. A. Memory-n strategies of direct reciprocity. *Proc. Natl Acad. Sci. USA* **114**, 4715–4720 (2017).

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Author contributions

J.G.R., C.H., D.G.R., K.C., and M.A.N.: Designed the research; J.G.R., C.H., D.G.R., K.C., and M.A.N.: Performed the research; J.G.R., C.H., D.G.R., K.C., and M.A.N.: Wrote the paper.

Additional information

Supplementary Figures

Supplementary Figure 1: Reactive strategies implemented by two-state automata. The blue circle depicts the state where the player cooperates (c) and the red circle depicts the state where the player defects (d) in the next game. After a game, depending on the action (c or d) of the co-player, the state changes according to the given probabilities. **a** | A stochastic reactive strategy is encoded by the tuple (p, q) denoting the probability to cooperate if the co-player in the previous round either cooperated or defected, respectively. **b-d** | The well-known strategies Tit-for-Tat (TFT), Stochastic Tit-for-Tat (STFT), and Generous Tit-for-Tat (GTFT; $0 < q < 1$) implemented by stochastic two-state automata.
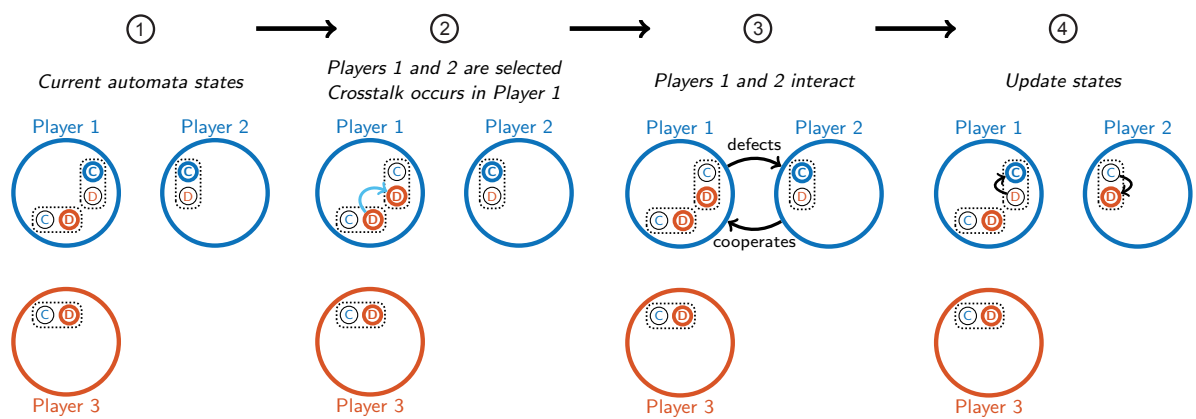
Supplementary Figure 2: Crosstalk in concurrent repeated games. Players (large circles) use reactive strategies implemented by a separate two-state automata for each interaction partner. The current state is emphasized in bold font (panel 1). Two random players (here players 1 and 2) are selected to play a PD (Prisoner's Dilemma; panel 2). Crosstalk between independent automata within the involved players 1 and 2 happens with a small probability γ. Crosstalk might change the action in the following interaction. By chance, state D of the automaton implementing the interaction of player 1 with player 3 is copied to the automaton implementing the interaction of player 1 with player 2 (indicated by a blue arrow). Here player 1 defects (due to crosstalk) and player 2 cooperates (panel 3). The states of the automata are updated according to the player's strategy (panel 4). Player 1 plays TFT (Tit-for-Tat) and moves to state C. Player 2 plays TFT and moves to state D.
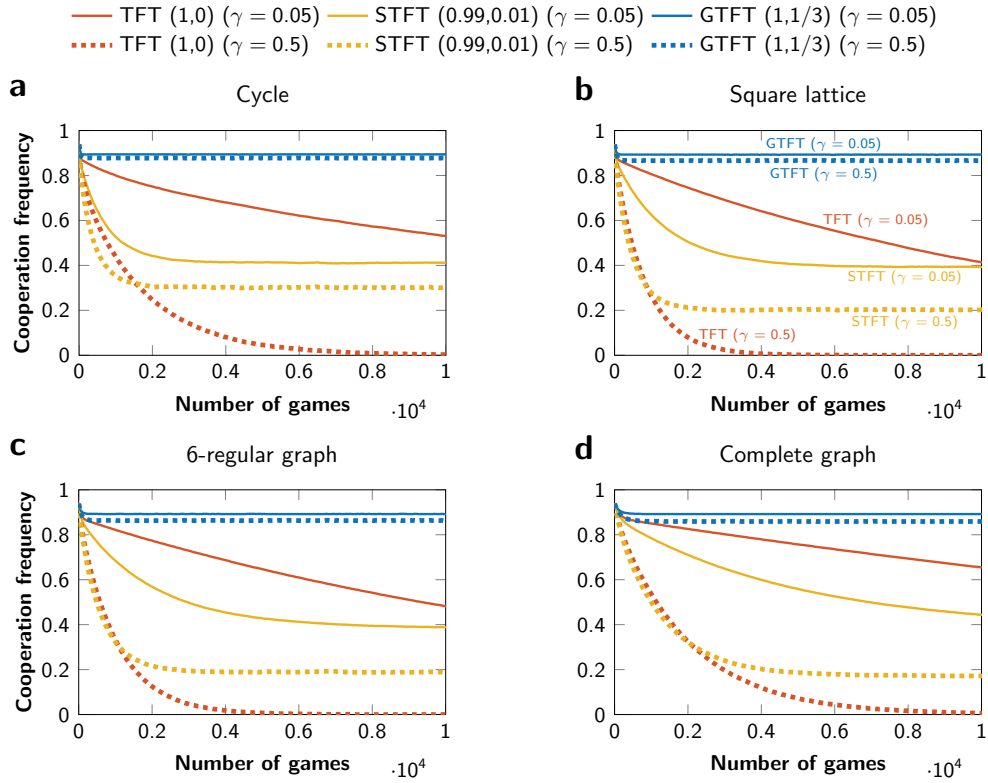
Supplementary Figure 3: Generous Tit-for-Tat (GTFT) maintains high levels of cooperation in the presence of crosstalk over time. The level of cooperation is determined by the frequency that players are in the cooperative state, averaged over all players in the population. Full lines correspond to a crosstalk rate of $\gamma = 0.05$ and dotted lines correspond to a crosstalk rate of $\gamma = 0.5$. **a-d** | Since TFT (Tit-for-Tat) is not an error-correcting strategy, its cooperation frequency converges to zero for any $\gamma > 0$. Stochastic Tit-for-Tat (STFT) can secure a basic level of cooperation as it sometimes forgives defection. Across all population structures GTFT (Generous Tit-for-Tat) maintains a high level of cooperation. High crosstalk rates lead to a faster spreading of defective behavior for both TFT and STFT whereas population structures with a low connectivity delay the spreading of defection (e.g., cycle or square lattice). All players use a given conditional cooperative strategy except one random player always defects (ALLD). Number of players is $N = 16$ (one of those is the ALLD player). Simulation results are averages over 10^4 realizations.
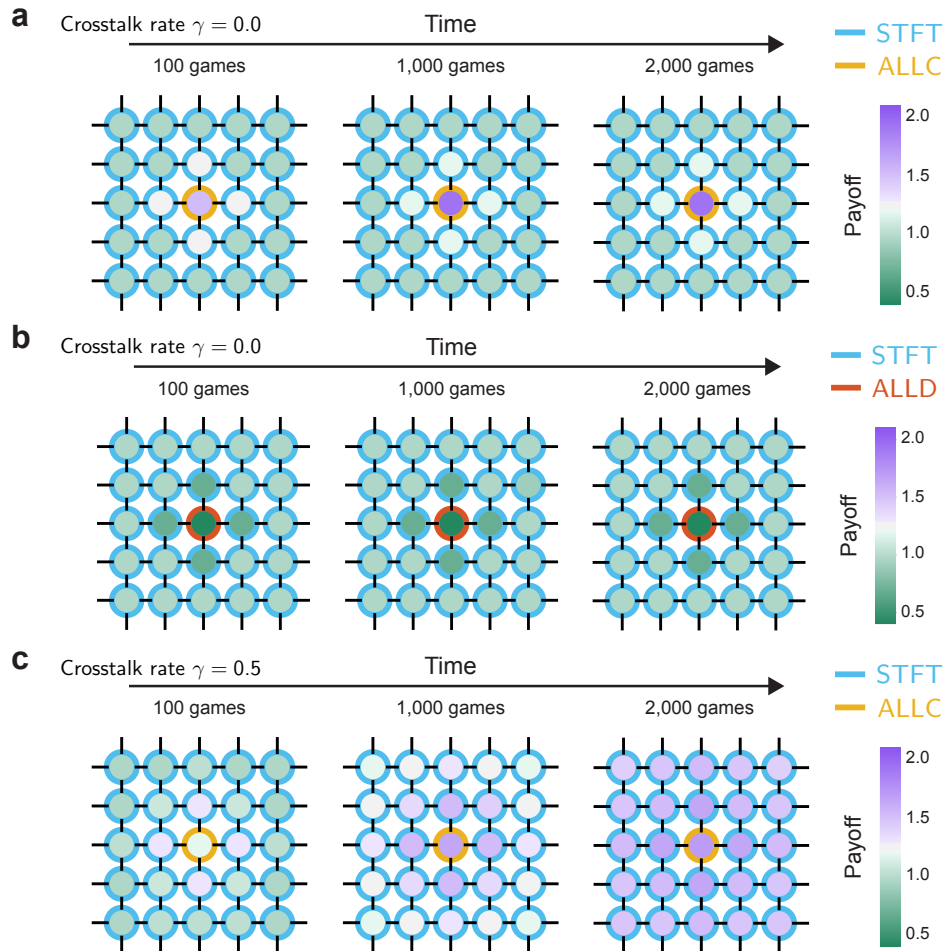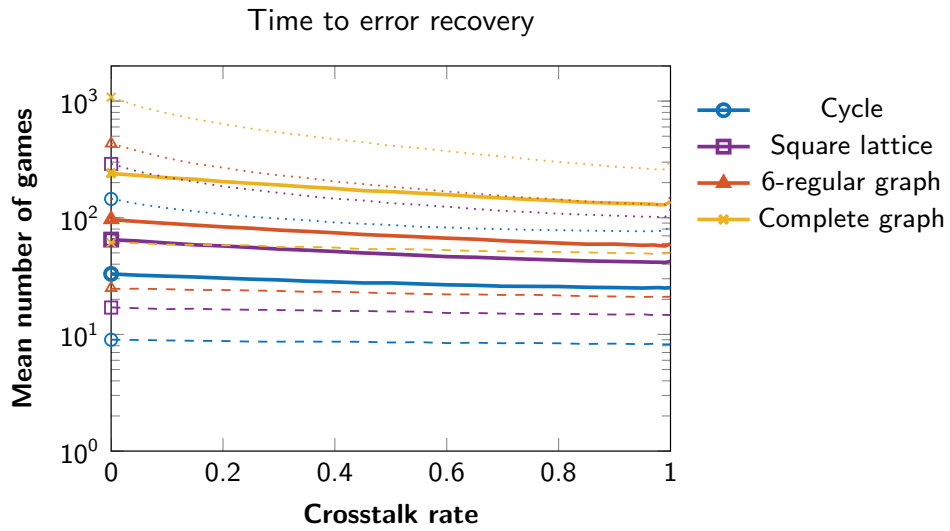
Supplementary Figure 4: Cooperative and defective behavior can spread with crosstalk but not without. Twenty-four erroneous conditional cooperators (STFT $p = 0.999$, $q = 0.001$; blue framed nodes) and one ALLD (red framed node, placed in the center) or ALLC (yellow framed node) player populate a 5x5 lattice. The fill color of the nodes depicts the expected payoff of the players after 100, 1,000 and 2,000 games. **a-b** | In the absence of crosstalk ($\gamma = 0.0$) cooperative and defective behavior can not spread. The erroneous ALLC ($p = 0.999$, $q = 0.999$) or ALLD ($p = 0.001$, $q = 0.001$) player only affect the payoff of its STFT neighbors. **c** | In the presence of crosstalk ($\gamma = 0.5$) cooperation spreads from the ALLC player via crosstalk to all STFT players. We assume that in the first round, the STFT players are equally likely to cooperate or to defect, which is their stationary cooperation frequency in a homogeneous population of STFT players. Parameter values: benefit $b = 3$, and cost $c = 1$.

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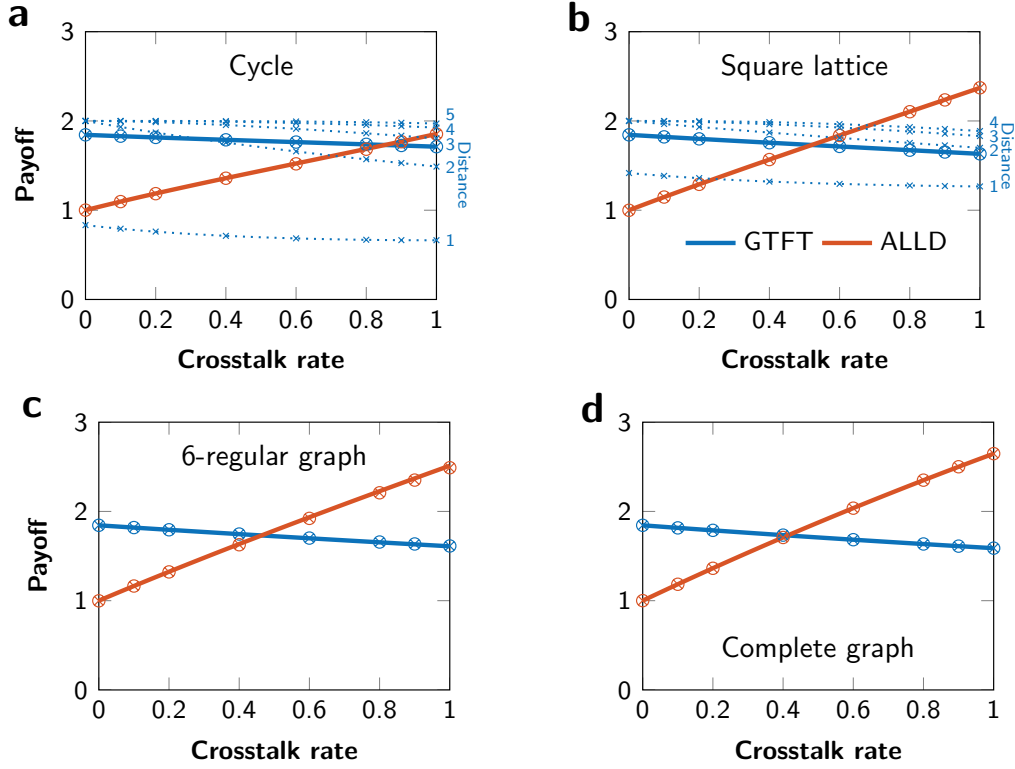
Supplementary Figure 5: Stationary payoff varies across population structures and crosstalk rates.
Stationary payoff of GTFT ($p = 1, q = 1/3$) and ALLD $(0, 0)$ players versus the crosstalk rate in different
population structures. One ALLD player is randomly placed on the graph, among $N - 1$ GTFT players. Full lines
show numerically exact results for the average payoff of all GTFT players (blue) and of the ALLD player (red)
in the steady state. Dotted lines show the steady state payoff of individual players with a given distance to the
ALLD player. Circles and crosses show the respective simulation results. The larger the distance of a GTFT player
to an ALLD player, the less likely a player's payoff is affected by the ALLD player. Players with distance 1 are
adjacent to the ALLD player. **a–d** | On the cycle, the average payoff of the GTFT players exceeds the defector's
payoff up to a crosstalk rate of $\gamma \approx 0.85$, whereas for well-mixed populations the critical crosstalk rate is much
lower, $\gamma \approx 0.41$. The other two population structures exhibit crosstalk thresholds in between these two extremes.
Parameter values: number of players $N = 16$ (one ALLD player), benefit $b = 3$, and costs $c = 1$. Simulation
results are averages over 10^4 realizations.

Supplementary Figure 6: Mean time until a population of conditional cooperators returns to full cooperation after a single error. Higher crosstalk rates (γ) as well as probabilities to cooperate after defection (q) decrease the number of games to recover from an error such that the whole population returns to full cooperation. For the case of $\gamma = 0$, analytical results are denoted by blue circles for the cycle, purple squares for the square lattice, red triangles for the 6-regular graph, and yellow crosses for the complete graph (see Section 2.1 for further details). Parameter values: number of GTFT players $N = 16$, all GTFT players ($p = 1$; full lines: $q = 1/3$, dotted lines: $q = 0.1$; dashed lines: $q = 2/3$), benefit $b = 3$, and costs $c = 1$. Simulation results are averages over 10^5 realizations.
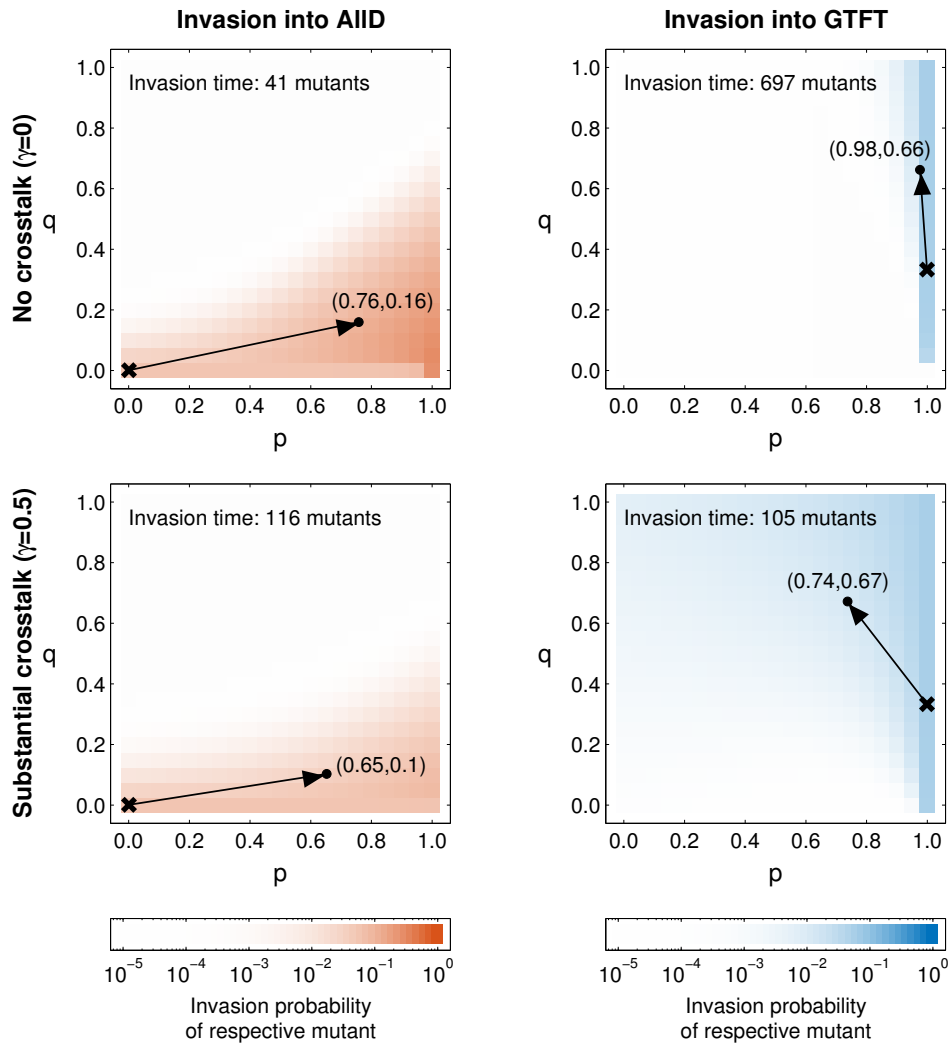
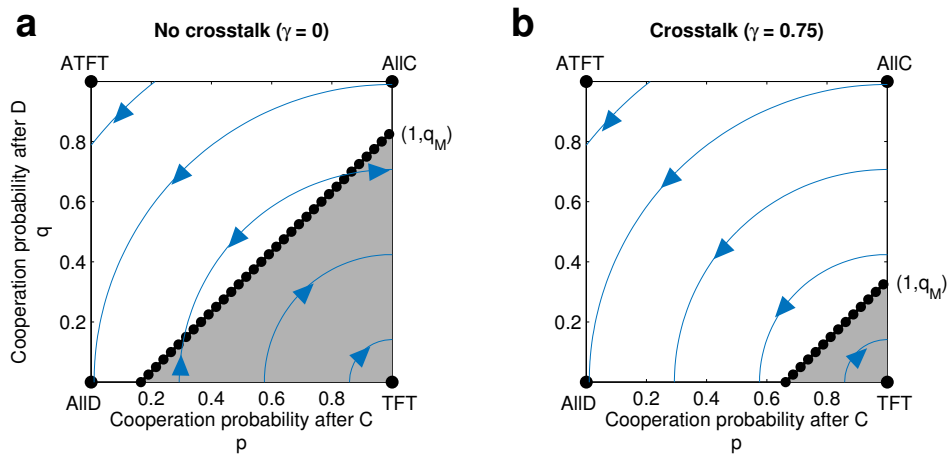**Supplementary Figure 7: Higher crosstalk rates simplify the invasion of selfish strategies into GTFT.** For two different resident strategies, ALLD and GTFT, we have calculated how easily mutants can invade. To this end, we have considered a fine grid of mutant strategies (p, q) with $p, q \in \{0, 0.005, 0.010, \ldots, 1\}$. For each of these mutant strategies, we have calculated its fixation probability into the respective resident strategy. The value of the fixation probability is represented by the color of the respective square at (p, q). In addition, we have simulated how many mutant invasions the resident strategies can resist if mutants are randomly drawn from that grid (reported in the upper left of each panel). We have also recorded the average trait values of successful mutants (indicated by the arrow). We find that ALLD is typically invaded by conditionally cooperative strategies, and that the invasion time increases with the crosstalk rate. For GTFT, we find that in the absence of crosstalk, it takes a considerable number of mutants until the first mutant reaches fixation. Moreover, the successful mutant is typically a cooperative strategy itself. As the crosstalk rate increases, however, the invasion time into GTFT decreases, and successful mutants do no longer need to be cooperative. Parameters: population size $N = 16$, benefit $b = 10$, cost, $c = 1$, selection strength $s = 1$. The strategies are subject to small amounts of noise, ALLD $= (0.001, 0.001)$ and GTFT $= (0.999, 0.333)$.

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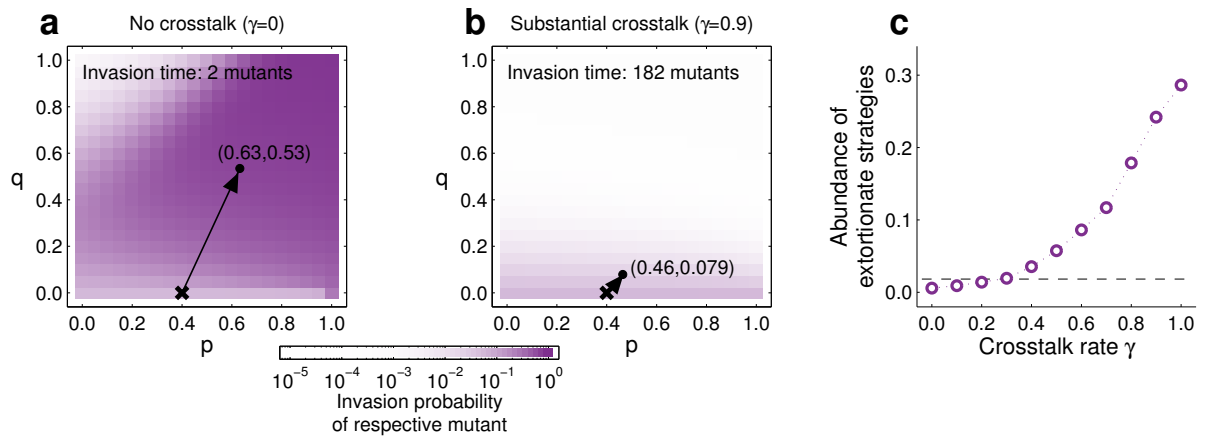
Supplementary Figure 8: Higher crosstalk rates can stabilize extortion. a,b | Similar to the invasion analysis for ALLD and GTFT reported in **Supplementary Fig. 7**, we explored how many mutant invasions it takes until an extortionate resident population is successfully replaced. Without crosstalk, extortionate strategies are quickly replaced by more cooperative strategies. This result is in line with previous observations that extortion is unstable in typical models of direct reciprocity [1]. However, once there is substantial crosstalk, it takes more mutant strategies until an extortionate resident population is invaded, and successful mutants are similar to the extortionate strategy. **c** | To quantify the overall success of extortion in well-mixed populations, we have recorded how often the evolutionary process visits a δ-neighborhood of the set of all extortionate strategies (see also Refs. [1, 2]). For comparison, the dashed line indicates how often this neighborhood is visited in the case of neutral evolution (when the selection strength s is zero). As the crosstalk rate approaches $\gamma = 1$, the set of extortionate strategies is visited more than 10 times more often than expected under neutrality. Thus, when crosstalk is common, selection favors extortionate strategies. Parameters: population size $N = 16$, $b = 10$, $c = 1$, $s = 1$. For the invasion analysis, we have used the extortionate resident strategy (0.4,0), and for the δ-neighborhood, we have used $\delta = 0.02$.

Supplementary Figure 9: Deterministic adaptive dynamics of crosstalk. Blue curves represent numerically computed solutions of the adaptive dynamics, Eq (S13), for two different crosstalk scenarios. The state space consists of all pairs (p, q) in the unit square. The four corners of the square correspond to ALLD $(0,0)$, Tit-For-Tat $(1,0)$, ALLC $(1,1)$ and Anti-Tit-for-Tat $(0,1)$. The black-dotted line is the set of singular points, as given by Eq. (S11); the grey area below that line is the cooperation-rewarding zone. As the crosstalk rate γ increases from 0 to 0.75, this cooperation-rewarding zone shrinks considerably; most initial population configurations lead to a state in which everyone defects. Parameter values: population size $N = 16$, benefit $b = 10$, cost $c = 1$.
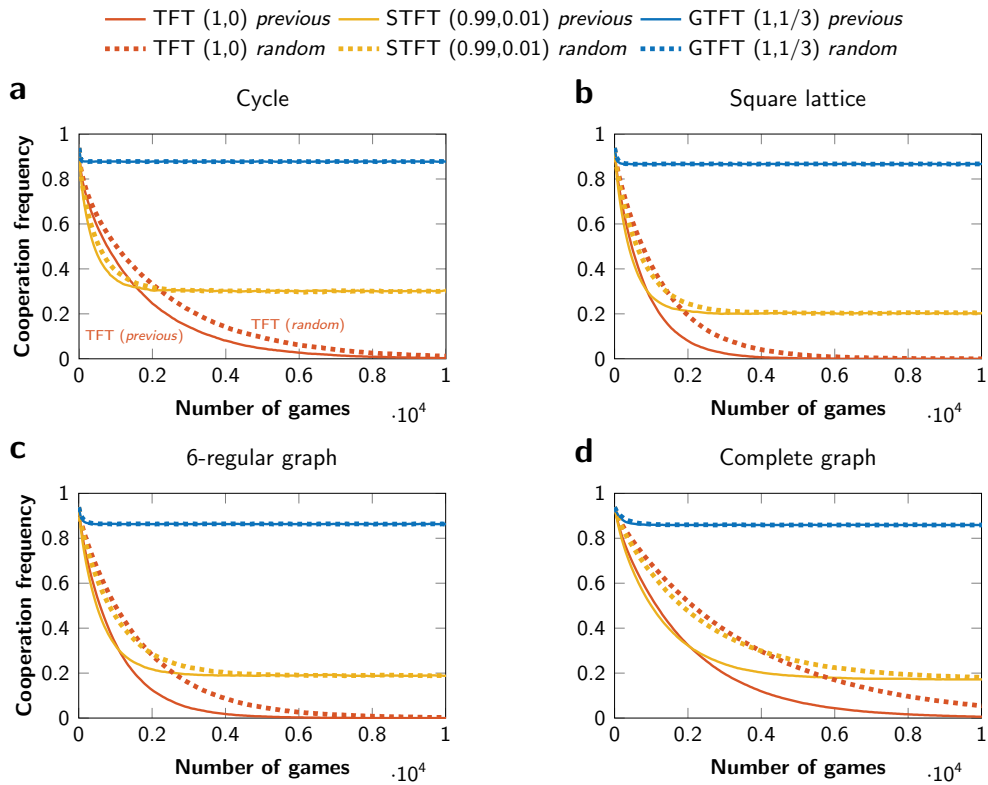
Supplementary Figure 10: Dynamics of cooperation for two different types of crosstalk. For the original model used in the main text, we have assumed that crosstalk leads a player to refer to the automaton of the *previous* interaction. Here, we compare the cooperation dynamics of this original model (see also Fig. 3) to an alternative implementation of crosstalk, according to which players refer to a *random* automaton. While the behavioral dynamics can be different under the two types of crosstalk, the stationary distributions are identical. Higher crosstalk rates, densely connected populations and previous interaction crosstalk (full lines) accelerate spread of defective behavior. The number of players is $N = 16$ (one of those is the ALLD player), and the crosstalk rate is $\gamma = 0.5$. Simulation results are averages over 10^4 realizations.
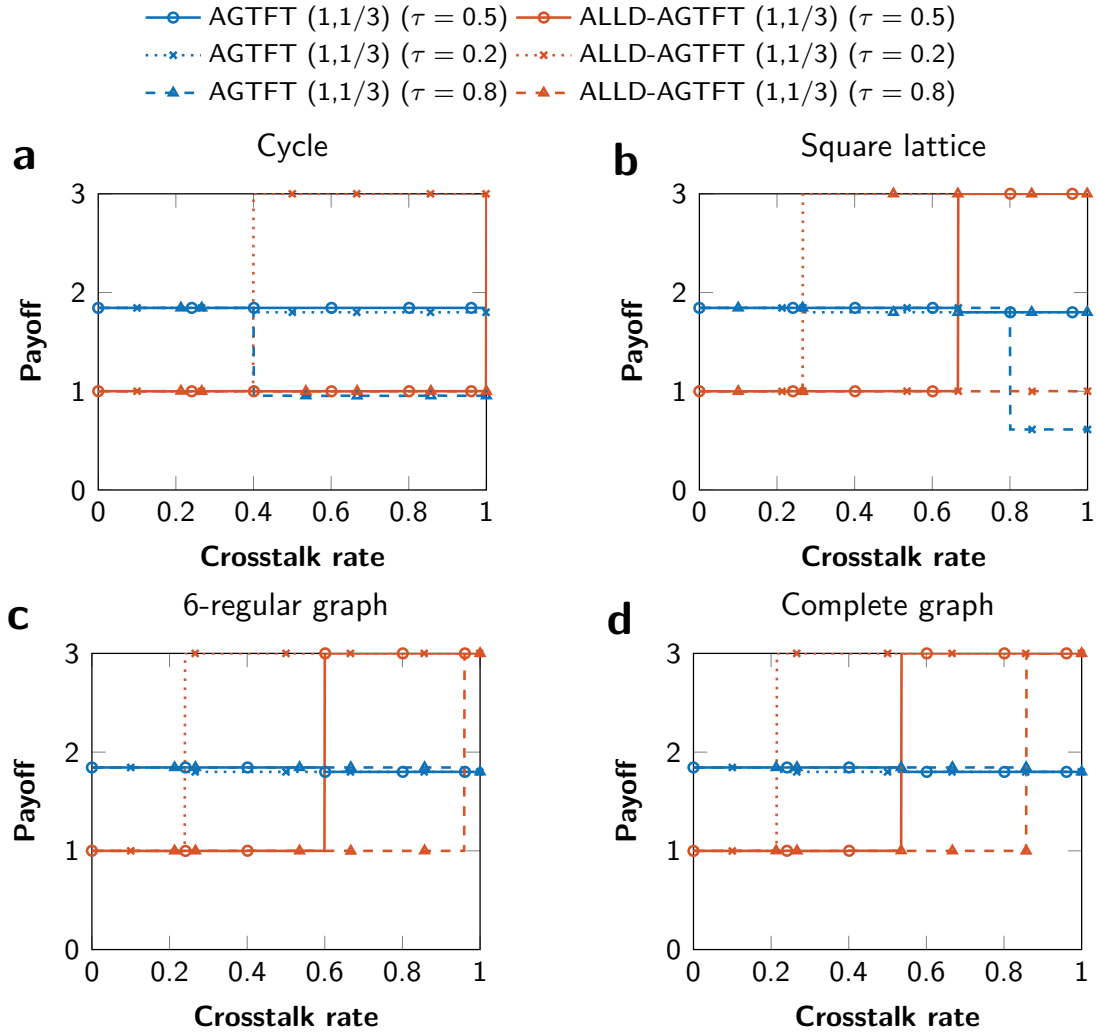
Supplementary Figure 11: Stationary payoff of Aggregate Generous Tit-for-Tat (AGTFT) and ALLD players over the crosstalk rate across different population structures. Generalizing the strategy space of reactive strategies to aggregate reactive strategies allowed us to condition the next action on the aggregate received cooperation in the previous round (see **Sec. 2.2** for details). Simulation results accurately match our analytical results (see **Supplementary Fig. 12** and **Sec. 2.2**). One ALLD player is randomly placed on the graph, among $N-1$ GTFT players. Parameter values: number of players $N = 16$, all AGTFT players ($p = 1$, $q = 1/3$; full lines: $\tau = 0.5$, dotted lines: $\tau = 0.2$; dashed lines: $\tau = 0.8$), benefit $b = 3$, and costs $c = 1$. Simulation results are averages over 10^4 realizations.
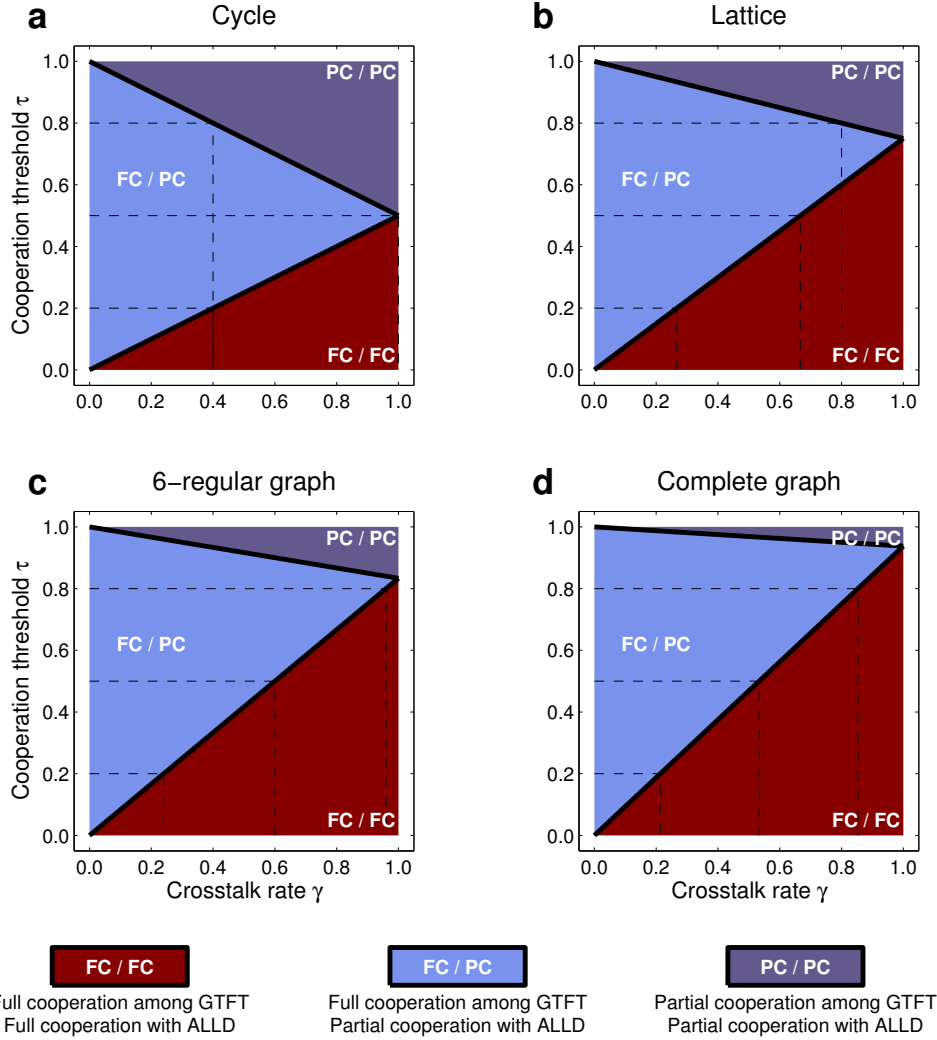
Supplementary Figure 12: Aggregate Generous Tit-for-Tat (AGTFT) requires intermediate cooperation thresholds τ to be most robust against invasion of defectors. We consider four different population structures, and as in **Supplementary Fig. 11**, we assume there is one ALLD players and $N-1$ players with strategy AGTFT. Depending on the region in the (γ, τ) parameter space, there are three different qualitative outcomes. *(i) FC/FC:* In this case, the AGTFT players cooperate with everyone. As a consequence, the defector gets a higher payoff than all residents. *(ii) FC/PC:* The AGTFT players fully cooperate among each other, but they only partially cooperate with the ALLD player. In this case AGTFT is stable against ALLD if the conditional cooperation probability q is sufficiently low. *(iii) PC/PC:* Here, the AGTFT do no longer fully cooperate among themselves. The analytically derived boundaries of the three parameter regions match the numerically found results in **Supplementary Fig. 11**. Parameter values: number of players $N = 16$.
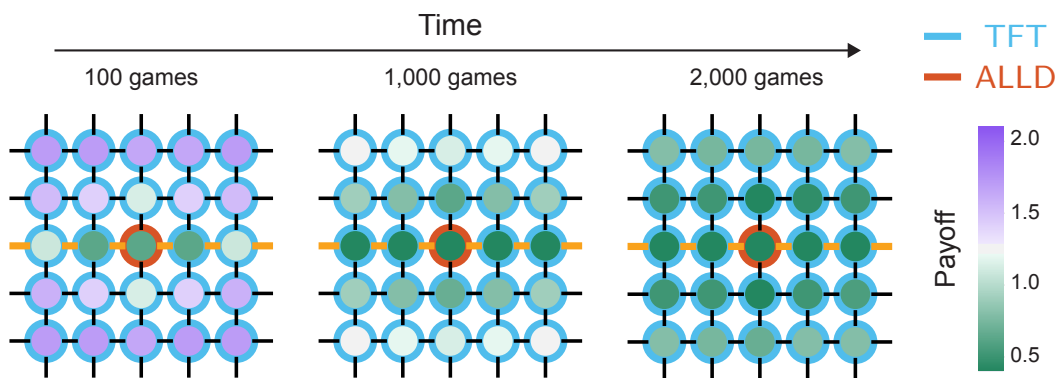
Supplementary Figure 13: Increased interaction frequencies boost effect of crosstalk. Twenty-four conditional cooperators (blue framed nodes, panels) and one ALLD (Always-Defect) player (red framed node, placed in the center) populate a 5x5 lattice. Players connected by an orange line have a 10-fold increased interaction probability. Defection spreads faster due to the increased interaction probability along the central, horizontal line of players. The fill color of the nodes depicts the expected payoff of the players after 100, 1,000 and 2,000 games. Parameter values: crosstalk rate $\gamma = 0.5$, benefit $b = 3$, and cost $c = 1$. For GTFT (defined by $p = 1$ and $0 < q < 1$), we used $q = 1/3$.

Supplementary Note 1

In Section 1, we provide further analytical results for our model of crosstalk in the special case of well-mixed populations. Specifically, we describe a more efficient algorithm to calculate steady-state payoffs when only two different strategies are present. Using this algorithm, we can calculate explicitly which strategies (p, q) are able to resist invasion by any other mutant strategy (p', q'). Moreover, the algorithm allows us to explore the adaptive dynamics of the system for any crosstalk rate.

In Section 2, we present additional results that hold for any population structure. We compute the time that a cooperative population needs to recover from an isolated defection event. Moreover, we introduce a model of crosstalk that allows players to react to the aggregate cooperation received across all their co-players. Finally, we argue that the evolutionary results presented in the main text remain unchanged if we consider a birth-death process instead of an imitation process.

1 Analytical results for well-mixed populations

1.1 Efficient calculation of payoffs in the special case of two strategies

In the main text, we have derived the following linear system to capture the players' cooperation frequencies in the steady state,

$$y_{ij} - (1 - \gamma)(p_i - q_i)y_{ji} - \gamma(p_i - q_i)y_j = q_i. \tag{S1}$$

In this equation, the unknowns y_{ij} represent the probability that player i cooperates against player j in the steady state, and (p_i, q_i) is the reactive strategy of player i. By solving this linear system, we can calculate payoffs in small and intermediate-sized populations. However, as populations become large, the computational effort increases quadratically in the population size N. We thus derive a more efficient algorithm for the complete graph, assuming that there are only two different strategies present in the population. Suppose that k individuals use strategy (p_1, q_1), whereas the remaining $N - k$ individuals use strategy (p_2, q_2). Because the population structure is fully symmetric, we can assume that players with the same strategy receive the same payoff. Hence, we set $y_{ij} = y_{i'j'}$ in Eq. (S1) whenever the strategies of player i and i' and the strategies of player j and j' coincide. This implies a drastic simplification: instead of having to consider all $N \cdot (N-1)$ possible combinations of players, we only need to consider all 4 possible combinations of strategies present in the population. That is, the linear system (S1) simplifies to the linear system $M\mathbf{y} = \mathbf{x}$,

where M is the $4{\times}4$ matrix

$$M = \begin{pmatrix} 1 - \left(1 - \frac{N-k}{N-1}\gamma\right)r_1 & -\frac{N-k}{N-1}\gamma r_1 & 0 & 0 \\ 0 & 1 & -\left(1 - \frac{N-k-1}{N-1}\gamma\right)r_1 & -\frac{N-k-1}{N-1}\gamma r_1 \\ -\frac{k-1}{N-1}\gamma r_2 & -\left(1 - \frac{k-1}{N-1}\gamma\right)r_2 & 1 & 0 \\ 0 & 0 & -\frac{k}{N-1}\gamma r_2 & 1 - \left(1 - \frac{k}{N-1}\gamma\right)r_2 \end{pmatrix}, \quad \text{(S2)}$$

with $r_i := p_i - q_i$, and $\mathbf{x} = (q_1, q_1, q_2, q_2)^T$. The solution vector $\hat{\mathbf{y}} = (\hat{y}_{11}, \hat{y}_{12}, \hat{y}_{21}, \hat{y}_{22})^T$ contains the respective steady-state frequencies $\hat{y}_{ij}$ for a player with strategy i to be in state C with respect to a co-player with strategy j. Using this vector, we can again calculate the expected payoffs of the two strategies as

$$\begin{aligned} \pi_1 &= \left((1-\gamma)\left(\frac{k-1}{N-1}\hat{y}_{11} + \frac{N-k}{N-1}\hat{y}_{21}\right) + \gamma\left(\frac{k-1}{N-1}\frac{k-1}{N-1}\hat{y}_{11} + \frac{k-1}{N-1}\frac{N-k}{N-1}\hat{y}_{12} + \frac{N-k}{N-1}\frac{k}{N-1}\hat{y}_{21} + \frac{N-k}{N-1}\frac{N-k-1}{N-1}\hat{y}_{22}\right)\right) \cdot b \\ &\quad - \left(\frac{k-1}{N-1}\hat{y}_{11} + \frac{N-k}{N-1}\hat{y}_{12}\right) \cdot c, \end{aligned}$$

$$\begin{aligned} \pi_2 &= \left((1-\gamma)\left(\frac{N-k-1}{N-1}\hat{y}_{22} + \frac{k}{N-1}\hat{y}_{12}\right) + \gamma\left(\frac{k}{N-1}\frac{k-1}{N-1}\hat{y}_{11} + \frac{k}{N-1}\frac{N-k}{N-1}\hat{y}_{12} + \frac{N-k-1}{N-1}\frac{k}{N-1}\hat{y}_{21} + \frac{N-k-1}{N-1}\frac{N-k-1}{N-1}\hat{y}_{22}\right)\right) \cdot b \\ &\quad - \left(\frac{N-k-1}{N-1}\hat{y}_{22} + \frac{k}{N-1}\hat{y}_{21}\right) \cdot c \ . \end{aligned}$$

$$\text{(S3)}$$

We note that the computation time for the payoffs is now independent of the population size.

1.2 The optimal level of generosity

Based on the above method to calculate payoffs in well-mixed populations with two strategies, we can also analytically derive the most generous strategy $(1, q_M)$ and the most robust strategy $(1, q_R)$, as defined in the main text. To this end, we consider a population in which $N-1$ individuals adopt a cooperative strategy, whereas the remaining individual plays ALLD. If we set $(p_1, q_1) := (0, 0)$, $(p_2, q_2) := (1, q)$, and $k = 1$, we can use Eq. (S3) to calculate the payoff of the single ALLD player as

$$\pi_D = bq \cdot (N-1)\frac{q(1-\gamma) + \gamma}{q(N-1-\gamma) + \gamma} \ . \quad \text{(S4)}$$

In contrast, the payoff of each cooperative player becomes

$$\pi_C = b - c - \left(b - c(1-q)\right)\frac{q(1-\gamma) + \gamma}{q(N-1-\gamma) + \gamma} \ . \quad \text{(S5)}$$

To calculate the most generous strategy that can resist invasion by ALLD we solve $\pi_D = \pi_C$, yielding

$$q_M = 1 - \frac{b + c(N-1)}{c + b(N-1)} \cdot \frac{1}{1-\gamma} \ . \quad \text{(S6)}$$

In particular, for no crosstalk and large populations ($\gamma=0$ and $N\to\infty$), we recover the well-known probability $q_M = 1-c/b$ [3, 4]. Because

$$\frac{\partial q_M}{\partial \gamma} = -\frac{b + c(N - 1)}{c + b(N - 1)} \cdot \frac{1}{(1 - \gamma)^2} < 0, \tag{S7}$$

the maximum level of generosity is monotonically decreasing in γ. Thus, the more crosstalk, the less generous cooperative players need to be to still prevent the invasion of ALLD. The value of q_M becomes zero when

$$\gamma^* = \frac{(b - c)(N - 2)}{c + b(N - 1)} \leq 1 - c/b < 1 . \tag{S8}$$

In particular, only if the crosstalk rate satisfies $\gamma < \gamma^*$, we can hope for full cooperation to evolve in the complete graph.

Similarly, we can also calculate the most robust cooperative strategy, defined as the strategy $(1, q)$ that has the highest relative payoff advantage compared to a single ALLD mutant. By setting $\frac{\partial}{\partial q}(\pi_C - \pi_D) = 0$, we yield

$$q_R = -\frac{\gamma}{N - 1 - \gamma} + \sqrt{\frac{(N - 2)\gamma\big((b - c)(N - 1) - bN\gamma\big)}{\big(c + b(N - 1)\big)(1 - \gamma)(N - 1 - \gamma)^2}} . \tag{S9}$$

We note that q_R is zero for $\gamma = 0$ and for $\gamma = \gamma^*$, with γ^* as defined by Eq. (S8). In between, for $0 < \gamma < \gamma^*$, the value of q_R is positive. This means that as the crosstalk goes to zero, $\gamma\to 0$, we get $q_R \to 0$ and the strategy most robust against invasion by ALLD approaches TFT $= (1, 0)$. For positive γ, the most robust level of generosity is non-monotononic (as shown in **Fig. 3d**). For small crosstalk rates, the most robust response to an increase in γ is to slightly increase q. A small increase of q is often sufficient to prevent the spread of defection across the network without being too generous towards the single defector. But once the crosstalk rate has passed a certain threshold, robustness requires players to become less generous with increasing γ. In that case, a certain spread of defection can no longer be prevented, and players instead have to minimize the payoff of the defector by decreasing q.

1.3 A general invasion analysis

When a cooperative resident strategy $(1, q)$ satisfies $q < q_M$, the above results only guarantee that residents can resist invasion by ALLD. However, in the following we show that if $q < q_M$ holds, residents are in fact able to resist *all* possible mutants with a reactive strategy. To this end, suppose a single mutant employs the strategy (p_1, q_1) whereas the remaining residents use strategy (p_2, q_2). Again, we can use Eq. (S3) to calculate the payoff π_1 of the mutant, as well as the payoff π_2 of each

resident. This yields the following payoff difference

$$\pi_1 - \pi_2 = \frac{(1-\gamma)\big(c + b(N-1)\big) \cdot \big(q_1(1-p_2) - q_2(1-p_1)\big) \cdot (r_2 - r_M)}{(N-1)(1-r_2)(1-r_1 r_2) + \gamma\Big((1-r_1)r_2 + (N-1)r_1(1-r_2)r_2\Big)} \ . \tag{S10}$$

Here, $r_1 := p_1 - q_1$ and $r_2 := p_2 - q_2$, whereas

$$r_M := \frac{b + c(N-1)}{c + b(N-1)} \cdot \frac{1}{1-\gamma} \ . \tag{S11}$$

For the resident strategy (p_2, q_2) to be resistant against invasion, we require $\pi_1 - \pi_2 \leq 0$ for all mutant strategies (p_1, q_1). We can distinguish three cases:

Case 1: $r_2 > r_M$. In this case, Eq. (S10) implies for every $p_2 < 1$ that the mutant strategy ALLC with $(p_1, q_1) = (1, 1)$ can invade. Hence, resident strategies can only resist invasion if $p_2 = 1$. Conversely, if $p_2 = 1$, it follows from Eq. (S10) that $\pi_1 - \pi_2 \leq 0$ for all mutants, as required.

Case 2: $r_2 < r_M$. Analogously to before, Eq. (S10) implies for every $q_2 > 0$ that the mutant strategy ALLD with $(p_1, q_1) = (0, 0)$ can invade. Hence, resident strategies resist invasion if and only if $q_2 = 0$.

Case 3: $r_2 = r_M$. In that case, Eq. (S10) immediately implies $\pi_1 = \pi_2$, irrespective of the mutant strategy.

This analysis suggests there are three different sets of strategies that can resist invasion by single mutants. The first case corresponds to the case of cooperative strategies $(1, q)$ such that $1 - q > r_M$ (or, equivalently, $q < q_M$ as defined by Eq. (S6)). The second case corresponds to the case of defective strategies $(p, 0)$ such that $p < r_M$. Finally, the last case corresponds to all strategies (p, q) that satisfy the linear relationship $p - q = r_M$.

1.4 Adaptive dynamics for well-mixed populations

Based on the above static results, we can also derive a simple deterministic model to describe how the players' strategies evolve over time, the so-called adaptive dynamics of the system [5]. We consider a well-mixed population of size N. The population is monomorphic and applies the resident strategy (p_2, q_2). This population is then invaded by a single mutant with strategy (p_1, q_1). We define the mutant's invasion fitness as $F := \pi_1 - \pi_2$, as given by Eq. (S10). Adaptive dynamics posits that evolutionary trajectories point towards the mutant with the highest invasion fitness,

$$\dot{p} = \left.\frac{\partial F}{\partial p_1}\right|_{p_1 = p_2 =: p, \ q_1 = q_2 =: q} \qquad \text{and} \qquad \dot{q} = \left.\frac{\partial F}{\partial q_1}\right|_{p_1 = p_2 =: p, \ q_1 = q_2 =: q} \ . \tag{S12}$$

Plugging Eq. (S10) into Eq. (S12) yields the following two-dimensional dynamical system,

$$\dot{p} = \frac{q}{1-r} \cdot h(r) \quad \text{and} \quad \dot{q} = \frac{1-p}{1-r} \cdot h(r), \quad (S13)$$

where

$$h(r) = \frac{(1-\gamma)r\big(c + b(N-1)\big) - \big(b + c(N-1)\big)}{(N-1)(1-r^2) + r\big(1 + (N-1)r\big)\gamma}. \quad (S14)$$

Eq. (S13) implies that $\dot{p}$ and $\dot{q}$ always have the same sign. Since $h(r) = 0$ if and only if $r = r_M$, with r_M as defined in Eq. (S11), we obtain the analogous three cases as in the previous section. For initial populations (p, q) with $p - q > r_M$, both $\dot{p}$ and $\dot{q}$ are positive, and populations evolve towards higher cooperation probabilities. The 2-dimensional area in the (p, q)-space for which $p - q > r_M$ is thus called the *cooperation rewarding zone* [6]. In contrast, for initial populations with $p - q < r_M$, both $\dot{p}$ and $\dot{q}$ are negative, and we speak of the *defection rewarding zone*.

Provided that $r_M < 1$, the system is thus bistable (**Supplementary Fig. 9** shows phase portraits for two different crosstalk rates). Orbits either converge to a fully cooperative population $(1, q)$ with $q < 1 - r_M$, to a fully defective population $(p, 0)$ with $p < r_M$, or to the line of interior singular points $p - q = r_M$. In the limiting case of no crosstalk (**Supplementary Fig. 9a**) this recovers previous results on the adaptive dynamics of reciprocity in finite populations [7]. However, as the crosstalk rate γ increases, it follows from Eq. (S11) that r_M increases. Geometrically, this means that the line of fixed points is shifted to the right and the cooperation rewarding zone shrinks (**Supplementary Fig. 9b**). As γ exceeds the value of γ^* as defined by Eq. (S8), this zone vanishes altogether. Higher rates of crosstalk thus impede the evolution of cooperation, as they diminish the set of initial population that converge towards fully cooperative states.

The above results consider evolution as a deterministic process: if the initial population is in the defection rewarding zone, then the population will not employ a cooperative strategy $(1, q)$ in subsequent generations. In the main text, we have thus contrasted this deterministic model of adaptive dynamics with a stochastic imitation process. According to the imitation process, an ALLD population may be invaded by a cooperative mutant, even if this mutant is initially at a disadvantage in a population of defectors. To explore which mutants are particularly likely to invade, **Supplementary Fig. 7** represents the success of all possible mutant strategies if the resident population either employs a noisy variant of ALLD, $(0.001, 0.001)$, or a noisy variant of GTFT, $(0.999, 0.333)$. When crosstalk is rare, ALLD populations are less robust against mutant invasions. On average, it only takes 41 successive mutant invasions until the first mutant fixes. Moreover, successful mutants typically exhibit TFT-like behavior, and are thus often in the cooperation-rewarding zone. In contrast, if residents employ GTFT, it takes 697 mutants until the first mutant fixes, and successful mutants are highly cooperative themselves. However, ALLD outperforms GTFT when crosstalk is frequent. For $\gamma = 0.5$, we observe that it typically takes 116 mutants until an ALLD population is successfully replaced (again, TFT-like strategies are most likely to fix in an ALLD population).

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In contrast, GTFT is already invaded after 105 mutant strategies, and successful mutants are no longer similar to GTFT. These simulation results again highlight that high crosstalk rates undermine the evolutionary robustness of cooperation. For large values of γ, cooperative strategies become unstable, and defective strategies prevail.

1.5 The evolutionary relevance of extortionate strategies under crosstalk

When the population only consists of $N = 2$ individuals with respective strategies (p_1, q_1) and (p_2, q_2), their respective payoffs according to Eq. (S3) become

$$
\begin{aligned}
\pi_1 &= \frac{(q_2 + q_1 r_2)b - (q_1 + q_2 r_1)c}{1 - r_1 r_2}, \\
\pi_2 &= \frac{(q_1 + q_2 r_1)b - (q_2 + q_1 r_2)c}{1 - r_1 r_2} \ .
\end{aligned}
\tag{S15}
$$

These two payoffs satisfy the linear relationship

$$
\pi_1 = \frac{br_2 - c}{b - cr_2} \cdot \pi_2 + \frac{(b - c)(b + c)q_2}{b - cr_2} \ .
\tag{S16}
$$

In particular, by choosing a strategy of the form $(p_2, 0)$, player 2 can enforce the relation

$$
\pi_1 = \frac{bp_2 - c}{b - cp_2} \cdot \pi_2 \ .
\tag{S17}
$$

Since $c < b$ and $0 \le p_2 \le 1$, it follows that $\pi_2 \ge \pi_1$, irrespective of player 1's strategy (for $p_2 < 1$, equality only holds if both players get the mutual defection payoff 0). Moreover, by choosing $p_2 > c/b$, player 2 makes sure that the two payoffs π_1 and π_2 are positively related. In that case, if the co-player 1 aims to maximize her own payoff, she automatically maximizes player 2's payoff as well. Strategies of the set

$$
E = \left\{ (p, q) \in [0, 1]^2 \ \middle| \ c/b < p < 1, \ q = 0 \right\}
\tag{S18}
$$

have thus been termed extortionate [8]. With an extortionate strategy, players can ensure that they almost always outperform the opponent. At the same time, it is in the opponent's best interest to be unconditionally cooperative.

Here, we aim to explore when such extortionate strategies are stable in populations of size N in the presence of crosstalk. Case 2 in Section 1.3 implies that extortionate strategies need to satisfy

$$
\frac{c}{b} < p < \frac{b + c(N - 1)}{c + b(N - 1)} \cdot \frac{1}{1 - \gamma} \ .
\tag{S19}
$$

to resist invasion by all mutant strategies. We note that this condition is automatically satisfied

if $N = 2$, recovering previous results that extortion can succeed in small populations [1, 2]. But while generic models of direct reciprocity (with $\gamma = 0$) predict that extortionate strategies become unstable in large populations, condition (S19) suggests that crosstalk can stabilize extortion. In particular, once $\gamma > \gamma^*$ (as defined in Eq. (S8)), *every* extortionate strategy $(p, 0)$ is resistant against mutant invasions. At the same time, however, it should be noted that by becoming stable, extortionate strategies lose their most appealing property when crosstalk rates are high. For high values of γ, the best response in a population of extortioners is no longer to give in and to cooperate unconditionally. The best response is to be extortionate as well.

In **Supplementary Fig. 8**, we show simulations using the stochastic imitation process considered in the main text. We consider a resident population that employs a given extortionate strategy $(p, 0) \in E$. For this resident population, we calculate the fixation probability for all possible reactive mutant strategies, as well as the average time it takes until a random mutant replaces the resident. These simulations support the above analytical findings. For moderate population sizes and no crosstalk, the extortionate strategy is quickly invaded by more cooperative strategies (**Supplementary Fig. 8a**). As the crosstalk rate γ increases, the extortionate strategy become more robust against mutant invasions, and successful mutants typically show the characteristics of extortionate strategies themselves (**Supplementary Fig. 8b**). We have also explored the evolutionary relevance of extortionate strategies by measuring how often the evolving population visits a δ-neighborhood of E. The respective fraction of time increases substantially as the crosstalk rate γ increases (**Supplementary Fig. 8c**). We conclude that under crosstalk, extortionate strategies are able to persist even in larger populations.

1.6 Stochastic evolutionary dynamics for a birth-death process

In the main text, we have considered a cultural evolution setup to describe how strategies in a population change over time. We have assumed that strategies that perform well are more likely to be imitated by other players. Similarly, we can also study the dynamics when strategies spread by inheritance, and not by imitation. To this end, let us consider a Moran process. As in the main text, we consider a population of individuals that engage in repeated games subject to crosstalk. Each individual i acts according to a fixed strategy (p_i, q_i) that is now genetically determined. The payoff π_i of individual i again is determined by Eq. (3) of the main text. This payoff translates into an individual fitness $f_i = \exp(s\pi_i)$, with $s \geq 0$ being again the strength of selection (the exponential fitness mapping ensures that the players' fitness is always positive). We assume that in each evolutionary time step one individual is chosen for reproduction (proportional to its fitness), and that its offspring replaces a randomly chosen individual. The offspring inherits the parent's strategy with probability $1 - \mu$, and it adopts a new reactive strategy with probability μ, where μ is the mutation rate. For this Moran process, the fixation probability of a single mutant in a

well-mixed population of $N-1$ residents is given by Ref. [9]:

$$\rho_F = \left(1 + \sum_{i=1}^{N-1} \prod_{j=1}^{i} \exp\left[-s\big(\pi_M(j) - \pi_R(j)\big)\right]\right)^{-1}. \tag{S20}$$

Here, $\pi_M(j)$ and $\pi_R(j)$ are the mutant's and the resident's payoff in a population with j mutants, respectively. This fixation probability coincides with the respective fixation probability for the pairwise imitation process [10]. In particular, all corresponding evolutionary results for the imitation process (**Fig. 4c,d**) considered in the main text equally apply to the Moran process discussed here.

2   Further results for arbitrary population structures

2.1   Expected recovery time after errors

So far we have been concerned with the effects of crosstalk on the stationary cooperation rates and payoffs in a population. In particular, we have seen that crosstalk can lead to a spread of defection across a network. Herein we are interested in the respective timescale. How long does it take until an isolated defection event (e.g. due to an error) is "forgotten" in a generally cooperative population?

To this end, we consider a population of size N on a regular network with degree k. All players apply the strategy $(1,q)$, and all players are in state C initially. Suppose that due to an error in the very first game, one of the players defects and that in all subsequent rounds no more errors occur and players act according to their strategies. We are interested in the recovery time, in other words, the time it takes until all players are in state C again.

In the limiting case of no crosstalk, this recovery time can be calculated analytically. Since $\gamma = 0$, an error only affects the edge between the pair of players that has interacted in the very first game. Moreover, within this pair there is always at most one player who is in the D state (because in each round, at least one of the players cooperates and players have $p = 1$). As the probability that a specific edge of the regular graph is chosen is $2/(N \cdot k)$, we can calculate the probability that the population recovers after exactly t rounds as follows:

	Probability	Explanation
Recovery after 1 round	q	Player 2 immediately forgives defecting player 1.
Recovery after 2 rounds	$(1-q)\frac{2q}{N \cdot k}$	Player 2 does not forgive immediately, but the same edge is chosen in the second round, player 2 defects and player 1 forgives player 2.
$\vdots$	$\vdots$	$\vdots$
Recovery after t rounds	$(1-q)\left(1-\frac{2q}{N \cdot k}\right)^{t-2}\frac{2q}{N \cdot k}$	No recovery in first $t-1$ rounds, but in the t-th round the respective edge is chosen and the co-player of the defector forgives.

Therefore, the expected recovery time T_γ for $\gamma = 0$ is

$$T_0 = q + (1-q)\frac{2q}{Nk}\sum_{t=2}^{\infty} t\left(1-\frac{2q}{Nk}\right)^{t-2} = 1 + \frac{Nk(1-q)}{2q} \ . \tag{S21}$$

In particular $q=1$ implies $T_0=1$. The expected recovery time T_0 has the following two properties:

1. For any given q, the recovery time is monotonically increasing in k (i.e., recovery always takes longer in the complete graph than in the circle).

2. For any given k, the recovery time is monotonically decreasing in q (i.e., recovery always occurs faster when players are more forgiving).

These two properties hold in fact for any crosstalk rate, as further simulations show (**Supplementary Fig. 6**). Moreover, these simulations also show the recovery time is a decreasing function of γ. Intuitively, under crosstalk each player's automaton is more likely to be updated during a single interaction. Given that the residents have $p=1$ and $q>0$, these updating events on average increase the cooperation level in a population: a player's D state is more likely to be overridden by a C than the other way around.

2.2 Crosstalk based on aggregate experience

In the so far explored models of crosstalk, a player who needs to decide whether to cooperate or not only considered single experiences (either with the present co-player, or with the previous co-player). Instead one may also consider a model where decisions are based on a player's aggregate experience in previous games. In the following, we sketch a simple model for that case.

Again, we consider a population of size N, and each player holds a two-state automaton for each of her co-players. This automaton is in state C if the respective co-player has cooperated in the previous round, and it is in state D otherwise. To encode the present state of a player's automaton at time t, we use the variable x_{ij}^t. The value of this variable is $x_{ij}^t = 1$ if in the last interaction between i and j prior to round t, player j cooperated. Otherwise, we set $x_{ij}^t = 0$. Suppose now that in round t, players i and j interact. We assume that prior to her decision which action to choose, player i considers a weighted average score across all her co-players' previous decisions,

$$\bar{x}_{ij}^t(\gamma) = (1 - \gamma) \cdot x_{ij} + \gamma \sum_{k=1}^N \frac{w_{ik}}{\bar{w}_i} x_{ik}^t. \tag{S22}$$

As before, we interpret γ as the model's crosstalk rate. In the limiting case $\gamma = 0$, there is no crosstalk and only the direct co-player's previous action is taken into account. In the other limiting case $\gamma = 1$, there is full crosstalk and player i simply considers the average cooperation rate across all her co-players. Given the average score $\bar{x}_{ij}^t(\gamma)$, we assume that player i with strategy (p_i, q_i) cooperates with probability p_i if $\bar{x}_{ij}^t(\gamma) \geq \tau$, and otherwise cooperates with probability q_i. The parameter τ_i denotes an exogenous cooperation threshold. In the special case $\gamma = 0$, the above model is equivalent to the standard model of reactive strategies of direct reciprocity [3, 6] for any $0 < \tau < 1$. However, for positive values of γ, players do not only respond to their direct co-player, but they are also affected by outside experiences with previous co-players.

First, we explore the above model using computer simulations. To this end, we consider players using the strategy $(1, 1/3, \tau)$, to which we refer to as *Aggregate Generous Tit-for-Tat* (AGTFT). For four different population structures (cycle, lattice, 6-regular graph and complete graph), we study the cooperation dynamics that arise in a population in which one player applies ALLD and all other players apply AGTFT. In **Supplementary Fig. 11**, we show the resulting payoffs for three different values of the cooperation threshold $\tau \in \{0.2, 0.5, 0.8\}$ and for different crosstalk rates $0 \leq \gamma \leq 1$. As expected, in all population structures the GTFT players gain a higher payoff than the ALLD player in the absence of crosstalk. However, as the crosstalk rate increases, the ranking of strategies can change once γ exceeds a certain threshold. There are two qualitative changes that can occur. When τ is relatively low compared to γ, AGTFT players start to fully cooperate with the ALLD player (in **Supplementary Fig. 11**, the red curve jumps from $\pi_D = 1$ to $\pi_D = 3$). On the other hand, when τ is high compared to γ, already a single defector in the population can prevent AGTFT players to fully cooperate with other AGTFT players (in **Supplementary Fig. 11a,b**, this happens when the blue curve for $\tau = 0.8$ jumps from $\pi_A \approx 2$ to $\pi_A < 1$).

To understand these discontinuous transitions in the players' payoffs, we calculated when *AGTFT* players fully cooperate among themselves, and when they fully cooperate with the ALLD player. This yields three different cases:

1. *AGTFT players fully cooperate with everyone.* This case applies if the average cooperation

rate $\bar{x}_{ij}^t$ is always above the threshold τ, even if the respective co-player is a defector. By Eq. (S22), this yields the condition

$$\gamma \cdot \frac{N-2}{N-1} \geq \tau \ . \tag{S23}$$

2. *AGTFT players are fully cooperative among themselves, but they only cooperate against the defector with probability q.* This case applies if $\bar{x}_{ij}^t \geq \tau$ in case the co-player uses AGTFT, whereas $\bar{x}_{ij}^t < \tau$ if the co-player used ALLD. By Eq. (S22), this yields the following condition,

$$\gamma \cdot \frac{N-2}{N-1} < \tau \leq (1-\gamma) + \gamma \frac{N-2}{N-1} \ . \tag{S24}$$

3. *AGTFT players are no longer fully cooperative among themselves.* This case applies if $\bar{x}_{ij}^t < \tau$ even if the co-player adopts AGTFT and even if all AGTFT players have cooperated in the previous round. This yields

$$(1-\gamma) + \gamma \frac{N-2}{N-1} < \tau \ . \tag{S25}$$

In **Supplementary Fig. 12**, we show the parameter regions (γ, τ) that satisfy the three inequalities (S23), S24, and (S25). For all population structures, we find that if τ is too small, the AGTFT population cooperates with everyone. On the other hand, if τ is too large, AGTFT do not even fully cooperate among themselves. Only when τ is intermediate, the AGTFT players succeed in keeping the defector's payoff low, while still maintaining full cooperation among themselves. Surprisingly, we find that this region in the (γ, τ)-space always has an area of 1/2. Independent of the population structure, half of the parameter combinations are amenable to AGTFT to be stable against defectors. However, as in our original model, we find that, all other parameters kept constant, it is easier for AGTFT to succeed against ALLD if γ is small (**Supplementary Fig. 12**).

Supplementary References

[1] C. Hilbe, M. A. Nowak, and K. Sigmund. The evolution of extortion in iterated prisoner's dilemma games. *Proceedings of the National Academy of Sciences USA*, 110:6913–6918, 2013.

[2] A. J. Stewart and J. B. Plotkin. From extortion to generosity, evolution in the iterated prisoner's dilemma. *Proceedings of the National Academy of Sciences USA*, 110(38):15348–15353, 2013.

[3] M. A. Nowak and K. Sigmund. Tit for tat in heterogeneous populations. *Nature*, 355(6357):250–253, 1992.

[4] P. Molander. The optimal level of generosity in a selfish, uncertain environment. *Journal of Conflict Resolution*, 29:611–618, 1985.

[5] J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge, UK, 1998.

[6] K. Sigmund. *The Calculus of Selfishness*. Princeton Univ. Press, 2010.

[7] L. A. Imhof and M. A. Nowak. Stochastic evolutionary dynamics of direct reciprocity. *Proceedings of the Royal Society B*, 277:463–468, 2010.

[8] W. H. Press and F. D. Dyson. Iterated prisoner's dilemma contains strategies that dominate any evolutionary opponent. *Proceedings of the National Academy of Sciences USA*, 109:10409–10413, 2012.

[9] A. Traulsen and C. Hauert. Stochastic evolutionary game dynamics. In Heinz Georg Schuster, editor, *Reviews of Nonlinear Dynamics and Complexity*, volume II, pages 25–61. Wiley-VCH, Weinheim, 2009.

[10] Bin Wu, Benedikt Bauer, Tobias Galla, and Arne Traulsen. Fitness-based models and pairwise comparison models of evolutionary games are typically different—even in unstructured populations. *New Journal of Physics*, 17:023043, 2015.