Evolutionary games and spatial chaos

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MUCH attention has been given to the Prisoners' Dilemma as a metaphor for the problems surrounding the evolution of cooperative behaviour[1–6]. This work has dealt with the relative merits of various strategies (such as tit-for-tat) when players who recognize each other meet repeatedly, and more recently with ensembles of strategies and with the effects of occasional errors. Here we neglect all strategical niceties or memories of past encounters, considering only two simple kinds of players: those who always cooperate and those who always defect. We explore the consequences of placing these players in a two-dimensional spatial array: in each round, every individual 'plays the game' with the immediate neighbours; after this, each site is occupied either by its original owner or by one of the neighbours, depending on who scores the highest total in that round; and so to the next round of the game. This simple, and purely deterministic, spatial version of the Prisoners' Dilemma, with no memories among players and no strategical elaboration, can generate chaotically changing spatial patterns, in which cooperators and defectors both persist indefinitely (in fluctuating proportions about predictable long-term averages). If the starting configurations are sufficiently symmetrical, these ever-changing sequences of spatial patterns—dynamic fractals—can be extraordinarily beautiful, and have interesting mathematical properties. There are potential implications for the dynamics of a wide variety of spatially extended systems in physics and biology.

Although it has a long history, the paradox of the Prisoners' Dilemma has recently been much studied for the light it may shed on the evolution of altruistic or cooperative behaviour[1,2]. In its standard form, the Prisoners' Dilemma is a game played by two players, each of whom may choose either to cooperate, C, or defect, D, in any one encounter. If both players choose C, both get a pay-off of magnitude R; if one defects while the other cooperates, D gets the game's biggest pay-off, T, while C gets S; if both defect, both get P. With $T > R > P > S$, the paradox is evident. In any one round, the strategy D is unbeatable (being better than C whether the opponent chooses C or D). But by playing D in a sequence of encounters, both players end up scoring less than they would by cooperating (because $R > P$). Following Axelrod and Hamilton's pioneering work[1], many authors have sought to understand which strategies do best when the game is played many times between players who remember past encounters. These theoretical analyses, computer tournaments, and laboratory experiments continue, with the answers depending on the extent to which future pay-offs are discounted, on the ensemble of strategies present in the group of players, on the degree to which strategies are deterministic or error-prone (for example, imperfect memories of opponents or of past events), and so on[2–6].

In this paper, we consider only two kinds of players: those who always cooperate, C, and those who always defect, D. No explicit attention is given to past or likely future encounters, so no memory is required and no complicated strategies arise. Interesting results emerge when we place these 'players'—who may be individuals or organized groups—on a two-dimensional, $n \times n$ square lattice of 'patches': each lattice-site is thus occupied either by a C or a D. In each round of our game (or at each time step, or each generation), each patch-owner plays the game with its immediate neighbours. The score for each player is the sum of the pay-offs in these encounters with neighbours. At the start of the next generation, each lattice-site is occupied by the player with the highest score among the previous owner and the immediate neighbours. The rules of this simple game among n^2 players on an $n \times n$ lattice are thus completely deterministic. (In ref. 2 spatial arrays were briefly explored, but with a focus on the interplay among tit-for-tat and other explicitly memory-laden strategies in iterated encounters; the interest was in spatial generalizations of earlier results, such as "if a [strategy] is collectively stable, it is territorially stable".)

Specifically (but preserving the essentials of the Prisoners' Dilemma), we chose the pay-offs of the Dilemma's matrix to have the values $R = 1$, $T = b (b > 1)$, $S = P = 0$. That is, mutual cooperators each score 1, mutual defectors 0, and D scores b (which exceeds unity) against C (who scores 0 in such an encounter). The parameter b, which characterizes the advantage of defectors against cooperators, is thus the only parameter in our model; none of our findings are qualitatively altered if we instead set $P = \varepsilon$, with ε positive but significantly below unity (so that $T > R > P > S$ is strictly satisfied). In the illustrations below, we assume the boundaries of the $n \times n$ matrix are fixed, so that players at the boundaries simply have fewer neighbours; the qualitative character of our results is unchanged if we instead choose periodic boundary conditions (so that the lattice is really a torus). The illustrations are for the case when the game is played with the eight neighbouring sites (the cells corresponding to the chess king's move), and with one's own site (which is reasonable if the players are thought of as organized groups occupying territory). As amplified below, the essential conclusions remain true if players interact only with the four orthogonal neighbours in square lattices, or with six neighbours in hexagonal lattices; the results also hold whether or not self-interactions are included.

Using an efficient computer program in which each lattice-site is represented as a pixel of the screen, we have explored the asymptotic behaviour of this system for various values of b, and with various initial proportions of C and D arranged randomly or regularly on an $n \times n$ lattice ($n = 20$ and more). The dynamical behaviour of the system depends on the parameter b; the discrete nature of the possible pay-off totals means that there will be a series of discrete transition-values of b that lead from one dynamical regime to another. These transition-values and the corresponding patterns are described in detail elsewhere[7]. The essentials, however, can be summarized in broad terms. If $b > 1.8$, a 2×2 or larger cluster of D will continue to grow at the corners (although not necessarily along the edges, for large squares); for $b < 1.8$, big D clusters shrink. Conversely, if $b < 2$, a 2×2 or larger cluster of C will continue to grow; for $b > 2$, C clusters do not grow. The most interesting regime is therefore $2 > b > 1.8$, where C clusters can grow in regions of D and also D clusters can grow in regions of C. As intuition might suggest, in this interesting regime we find chaotically varying spatial arrays, in which C and D both persist in shifting patterns. Although the detailed patterns change from generation to generation—as both C clusters and D clusters expand, collide, and fragment—the asymptotic overall fraction of sites occupied by C, f_C, fluctuates around 0.318 for almost all starting proportions and configurations.

Figure 1 illustrates typical asymptotic patterns for two different regimes of b values. The colour coding is as follows: blue represents a C site that was C in the preceding generation; red, a D site following a D: yellow, D following a C; and green, C following a D. Thus a purely red and blue pattern would necessarily be static. The amount of yellow and green in a picture indicates how many sites are changing from one generation to the next. Figure 1*a*, for $1.75 < b < 1.8$, is typical of the irregular and relatively static network of 'D lines' against a background of C which arises for these b values; one gets less connected fragments of D lines or 'D blinkers' for lower b values. Figure 1*b* is for the interesting regime $2 > b > 1.8$, and shows the typical patterns of dynamic chaos found for almost all starting conditions in this regime. Figure 2*a* adds a temporal dimension to Fig. 1*b*, showing the proportion of sites occupied by C in successive time-steps (starting with 10% D). The asymptotic

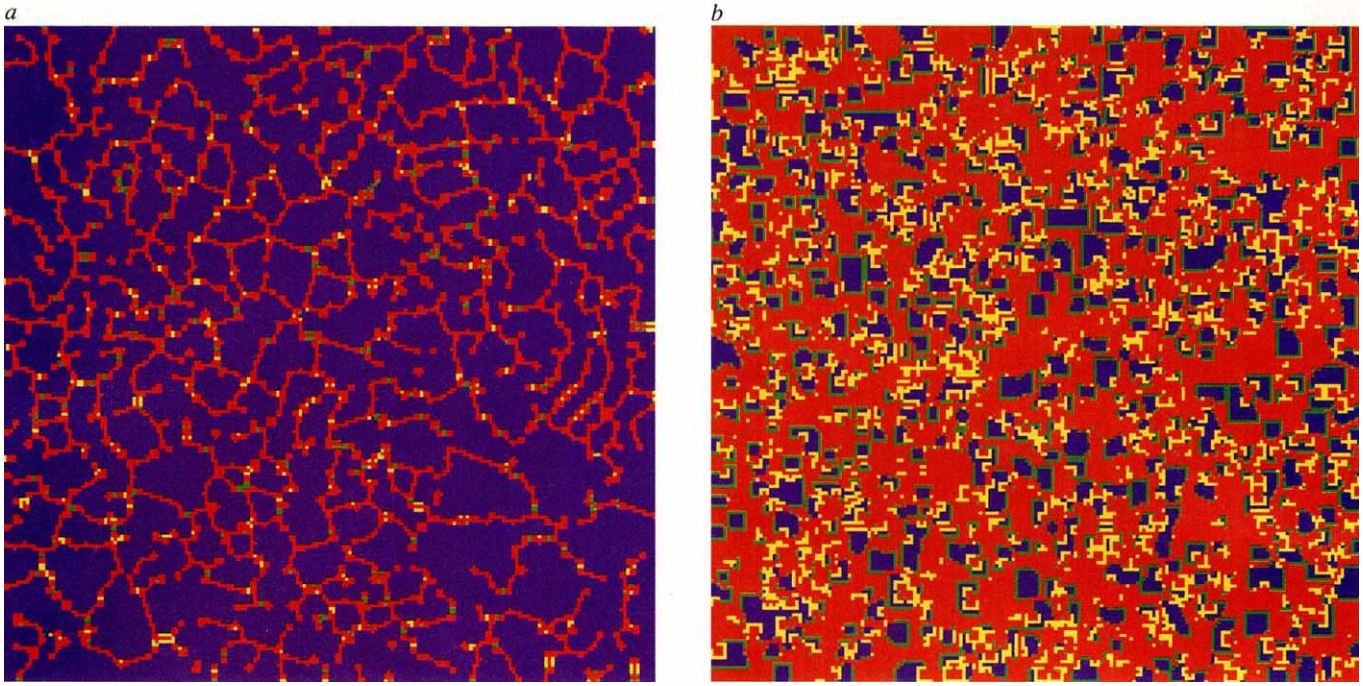

FIG. 1 The spatial Prisoners' Dilemma can generate a large variety of qualitatively different patterns, depending on the magnitude of the parameter, *b*, which represents the advantage for defectors. This figure shows two examples. Both simulations are performed on a 200×200 square lattice with fixed boundary conditions, and start with the same random initial configuration with 10% defectors (and 90% cooperators). The asymptotic pattern after 200 generations is shown. The colour coding is as follows: blue represents a cooperator (C) that was already a C in the preceding generation; red is a defector (D) following a D; yellow a D following a C; green a C following a D. *a*, An irregular, but static pattern (mainly of interlaced networks) emerges if $1.75 < b < 1.8$. The equilibrium frequency of C depends on the initial conditions, but is usually between 0.7 and 0.95. For lower *b* values (provided $b > \frac{9}{8}$), D persists as line fragments less connected than shown here, or as scattered small oscillators ('D-blinkers'). *b*, Spatial chaos characterizes the region $1.8 < b < 2$. The large proportion of yellow and green indicates many changes from one generation to the next. Here, as outlined in the text, 2×2 or bigger C clusters can invade D regions, and vice versa. C and D coexist indefinitely in a chaotically shifting balance, with the frequency of C being (almost) completely independent of the initial conditions at ~0.318.

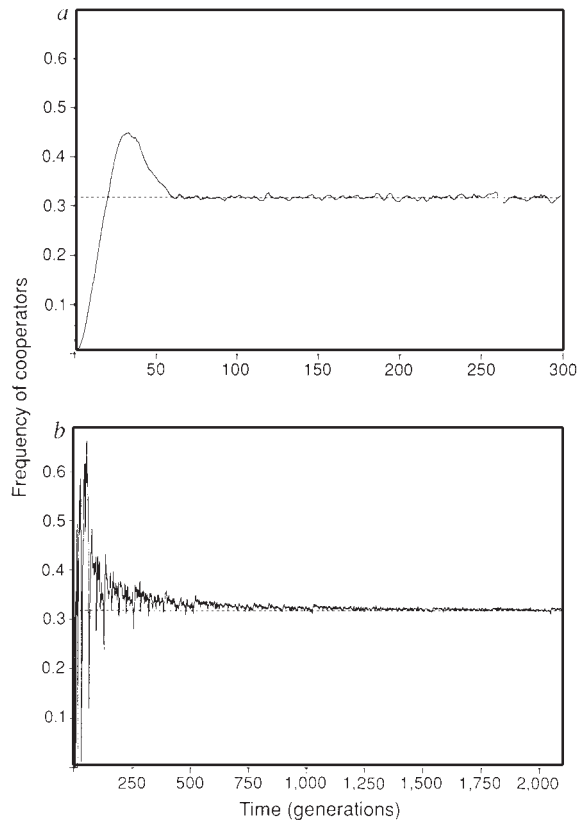

FIG. 2 The frequency of cooperators in simulations with random or symmetrical initial conditions, within the interesting region $1.8 < b < 2$. *a*, The frequency of cooperators, $f_C(t)$, for 300 generations, starting with a random initial configuration of $f_C(0) = 0.6$. The simulation is performed on a 400×400 square lattice with fixed boundary conditions, and each player interacts with 9 neighbours (including self). The dashed line represents $f_C = 12 \log 2 - 8$ (see *b*). *b*, The frequency of C within the dynamic fractal generated by a single D invading an infinite array of C. At generation *t*, the width for the growing D structure is $2t+1$, and the frequency of C, $f_C(t)$ within the square of size $(2t+1)^2$ centred on the initial D site is shown as a function of *t*. This curve has interesting properties, which can be partly understood by referring to the geometry of the D structure. The D structures are closed-boundary squares in generations that are powers of 2, $t = 2^n$; hence $f_C(t)$ has minima at generations that are powers of 2. These squares now expand at the corners and erode along the sides, returning to square shape after another doubling of total generations. On this basis, a crude approximation suggests that, *i* time steps going from *t* to $2t$, there will be roughly $4(2i)(2t+1-2i)$ C sites within the D structure of size $(2t+1+2i)^2$; hence the asymptotic C fraction, f_C, for very large such symmetrical patterns is $f_C = 4 \int_0^1 s(1-s)/(1+s)^2 \, ds = 12 \log 2 - 8 = 0.318 \ldots$. As discussed in the text, this approximation agrees with the numerical results surprisingly well in both parts *a* and *b* of the figure.

fraction, f_C, shown in Fig. 2*a* is found for essentially all starting proportions and configurations for these *b* values.

Figure 3 is perhaps more in the realm of aesthetics than biology. Again $2 > b > 1.8$, but now we begin ($t = 0$) with a single D at the centre of a 99×99 lattice of Cs. Figure 3*a* shows the consequent symmetrical pattern 30 time-steps later, and Fig. 3*b*, *c* and *d* shows three successive patterns at $t = 217$, 219 and 221 after the pattern has reached the boundary (which happens at $t = 49$). These patterns, each of which can be characterized in fractal terms, continue to change from step to step, unfolding a remarkable sequence, dynamic fractals. The patterns show every lace doily, rose window or Persian carpet you can imagine. As Fig. 2*b* shows, the asymptotic fraction of C is as for the chaotic pattern typified by Figs 1*b* and 2*a*. Many of the dynamic features of the symmetric patterns illustrated in Fig. 3 can be understood analytically. In particular, we can make a crude estimate of the asymptotic C fraction, f_C, for such very large symmetrical patterns. This approximation is shown by the dashed horizontal line in Fig. 2*b*, and it agrees with the numerical results significantly better than we would have expected. Why the approximation also works for the irregular, spatially chaotic patterns (Fig. 2*a*) we do not know.

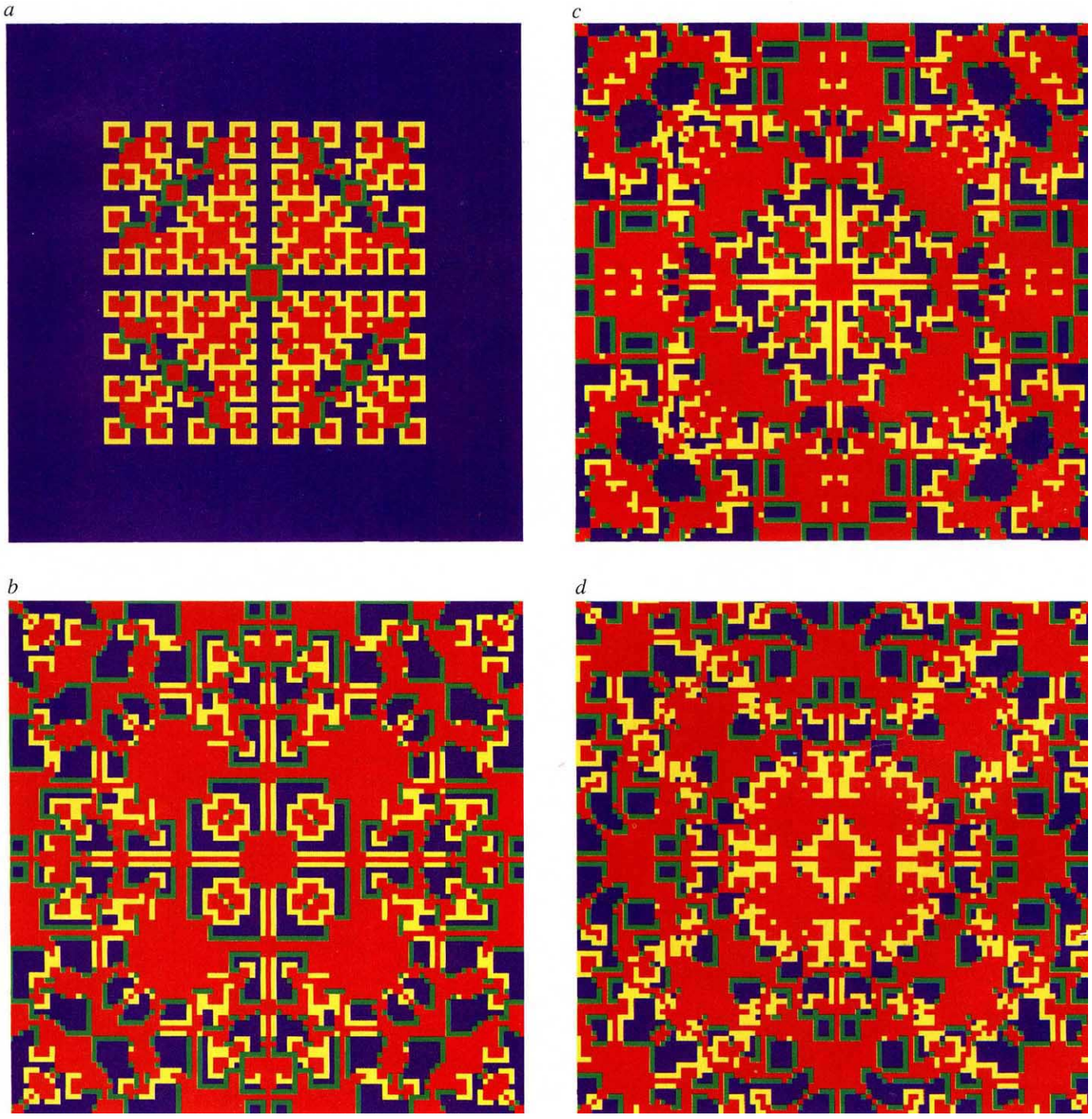

FIG. 3 Spatial games can generate an 'evolutionary kaleidoscope'. This simulation is started with a single D at the centre of a 99×99 square-lattice world of C with fixed boundary conditions. Again $1.8 < b < 2$. This generates an (almost) infinite sequence of different patterns. The initial symmetry is always maintained, because the rules of the game are symmetrical. The frequency of C oscillates (chaotically) around a time average of 12 log 2–8 (of course). *a*, Generation $t = 30$; *b*, $t = 217$; *c*, $t = 219$; *d*, $t = 221$.

Our 'spatial dilemmas' game obviously invites comparison with more familiar cellular automata, such as Conway's 'Game of Life'[8-11]. There are, however, qualitative differences. First, what happens to a site or cell in our lattice depends on the neighbours' scores, and thence on the state of the neighbours' neighbours. Thus, in the terminology of cellular automata, 25 cells are relevant to specifying the change in a given cell: the transition matrix has 2^{25}rules (this contrasts with Life, when 9 cells specify a cell's fate). That is, the motivating biological metaphor of the Prisoners' Dilemma generates a transition rule that is simple, but it would look horrendous if expressed in canonical cellular automata terms. Second, the patterns shown in Figs 1 and 3 have a combination of complexity and underlying regularity (exemplified by the asymptotic $f_C = 0.318$) unlike any cellular automata with which we are familiar. Third, we do also have a rich zoo of specific objects (rotators, gliders, blinkers, and an expanding jaw-like configuration of C cells that eats up a universe of D, leaving only structured strings of D ('eaters')) reminiscent of, but different from, those in Conway's Life[8,9]. The taxonomy of this zoo is described elsewhere[7].

Results similar to these are found if we exclude self-interaction, and consider interactions only with the eight nearest neighbours; here the 'interesting' region is $\frac{5}{3} > b > \frac{8}{5}$. The symmetrical patterns analogous to Fig. 3 are similarly kaleidoscopic, though different. The asymptotic C fraction, f_C, is now ~ 0.299 for both symmetric and random starting conditions. For interactions only with the four orthogonal neighbours, again the same qualitative regimes are found (here the interesting regime is $2 > b > \frac{5}{3}$ if self-interaction is included, and $\frac{3}{2} > b > \frac{4}{3}$ if not). Numerical studies suggest that f_C is around 0.374. Hexagonal arrays give complex patterns, but show less of the lacy, fractal character seen above, unless we weight the pay-offs from self-interactions somewhat more heavily than from neighbours (which is biologically plausible). In short, the above results seem robust[7].

More generally, we have explored other evolutionary games played with neighbours in spatial lattices along the basic lines laid down above. They have features, particularly chaotic polymorphisms, similar to those seen for the spatial Prisoners' Dilemma. The hawk-dove game[12] gives notably beautiful patterns when begun from one hawk (or dove) invading an infinite array of doves (or hawks).

The Prisoners' Dilemma is an interesting metaphor for the fundamental biological problem of how cooperative behaviour may evolve and be maintained; alternative approaches involve, for example, studies of how the patchiness that can be created by limited dispersal or population 'viscosity' might favour the evolution of altruism through the elevation of inclusive fitness within kin groups[13-15]. Essentially all previous studies of the Prisoners' Dilemma are confined to individuals or organized groups who can remember past encounters, who have high probabilities of future encounters (with little discounting of future pay-offs), and who use these facts to underpin more-or-less elaborate strategies of cooperation or defection. The range of real organisms obeying these constraints is limited (although there is evidence suggesting 'tit-for-tat' strategies among some fish, birds, bats and monkeys[5,6,16-18]). In contrast, our models involve no memory and no strategies: the players are pure C or pure D. Deterministic interaction with immediate neighbours in a two-dimensional spatial lattice, with success (site, territory) going each generation to the local winner, is sufficient to generate astonishingly complex and spatially chaotic patterns in which cooperation and defection persist indefinitely. The details of the patterns depend on the magnitude of the advantage accruing to defectors (the value of b), but a wide range of values leads to chaotic patterns, whose nature is almost always independent of the initial proportions of C and D. We believe that deterministically generated spatial structure within populations may often be crucial for the evolution of cooperation, whether it be among molecules, cells or organisms[13-15,19-21]. Other evolutionary games (hawk-dove, and so on) which recognize such chaotic or patterned spatial structure may be more robust and widely applicable than those that do not. More generally, such self-generated and complex spatial structures may be relevant to the dynamics of a wide variety of spatially extended systems: Turing models, 2-state Ising models, and possibly pre-biotic evolution[19-21] (where it seems increasingly likely that chemical reactions took place on surfaces, rather than in solutions).

Although the motive for this work is primarily biological, we emphasize that 'spatial dilemmas' generate patterns of extreme richness and beauty. These have an aesthetic and mathematical (explaining, for example, why $12 \log 2 - 8$ in Fig. 2 works unexpectedly well) interest of their own. □

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Connectivity of chemosensory neurons is controlled by the gene *poxn* in *Drosophila*

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THE function of the nervous system depends on the formation of a net of appropriate connections, but little is known of the genetic program underlying this process. In *Drosophila* two genes that specify different types of sense organs have been identified: *cut* (*ct*)[1,2], which specifies the formation of external sense organs as opposed to chordotonal organs, and *pox-neuro* (*poxn*)[3], which specifies the formation of poly-innervated (chemosensory) organs as opposed to mono-innervated (mechanosensory) organs. Whether these genes are also involved in specifying the connectivity of the corresponding neurons is not known. The larval sense organs are unsuitable for analysis of the axonal pathway and connections and so we have investigated the effect of *poxn* on the adult. Here we show that overexpression of *poxn* induces the morphological transformation of mechanosensory into chemosensory bristles on the legs and that the neurons innervating the morphologically transformed bristles follow pathways and establish connections that are appropriate for chemosensory bristles.