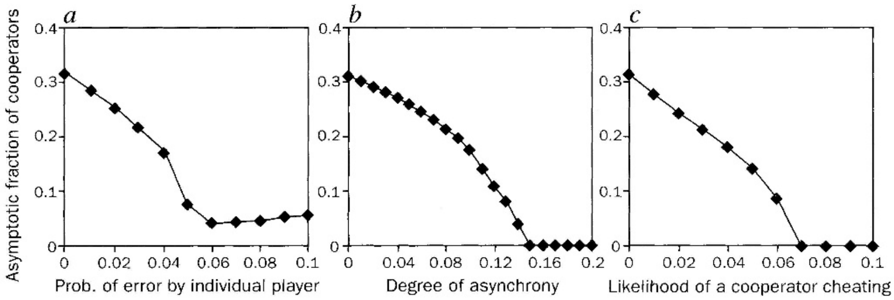

FIG. 1 Simulations were performed on a 100×100 lattice, for 500 periods starting with a random initial configuration with 10% defectors (and 90% cooperators) and pay-offs $T = 1.85$, $R = 1$, $P = S = 0$. *a*, The asymptotic fraction of cooperators, f_C, decreases rapidly with small increases in the error factor ϵ (the probability with which each player errs and chooses evenly between *C* and *D*). As ϵ approaches 0.06, some isolated cooperators remain, but they are too few and too dispersed to form clusters of cooperation. With further increases in ϵ, the number of cooperators increases, because $\epsilon/2$ of the population will randomly choose to cooperate. However, no clusters of cooperation were observed. *b*, A high degree of synchronization is required to maintain cooperation. Each player was allowed to skip updating its strategy during a period with a small independent probability, θ. With $\theta = 0$ (100% synchronization), $f_C \approx 0.318$. When θ was increased to 0.1, f_C dropped by half. Cooperation is eliminated when θ reaches 0.15. Thus, a relatively small percentage (~15%) of the population not being synchronized, as opposed to the condition of complete asynchrony[6], is sufficient to eliminate cooperation. *c*, Cooperation is rapidly reduced if each cooperator has a small independent probability, ϕ, of cheating after following the Nowak and May update rule. The fraction of cooperators, f_C, quickly decreases as ϕ increases. Clusters of cooperation are wiped out when about 7% of the cooperators cheat.

defectors. Clusters of cooperators and defectors grow and diminish, producing a variety of spatial patterns. The asymptotic behaviour shows small, tightly knit clusters of cooperators gliding around in a world of defectors. However, even one member of a cluster of cooperators changing to defection can eliminate or shrink the cluster. For cooperation to persist in the spatial Prisoner's Dilemma, a high degree of synchronization with no errors is required, a condition that is unlikely in most natural and social systems.

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NOWAK *ET AL.* REPLY — Mukherji *et al.* investigate the question of whether cooperation can survive in the spatial Prisoner's Dilemma in the presence of noise. They perform computer simulations of three different types of stochastic perturbation: (1) a fraction of sites is occupied at random by cooperators or defectors; (2) a fraction of sites is not updated, but remains with the current strategy; and (3) a fraction of cooperators turns spontaneously into defectors (this third assumption is well chosen for attempting to eliminate cooperators). All their simulations are restricted to the particular parameter region $2 > T > 1.8$.

We have explored Mukherji *et al.*'s extensions of our model, but for the wider range of parameters outlined in our original papers. For the particular region considered by Mukherji *et al.*, we of course confirm their results, but the spatial Prisoner's Dilemma has nine different parameter regions for $2 > T > 1$ (see refs 3, 4, 7–9). For the other parameter regions, we find in all three cases that cooperators can persist despite significant amounts of noise (see Fig. 2). In model (1) the baseline level of cooperators is $\epsilon/2$ (because of the random assignment of a fraction ϵ of sites). We find that in parameter regions 1–5, cooperators exist at abundances well above baseline for noise levels up to 25%, and in parameter regions 1–3, for noise levels up to 50% and more. In model (2) the degree of asynchrony has essentially no effect on the asymptotic abundance of cooperators in parameter regions 1–8. In model (3), survival of cooperators is possible in parameter regions 1–6 for noise levels of about 13% and in regions 1–3 for noise levels of about 26 %.

The main conclusion in our original papers[3,7–9] was that spatial structures can facilitate the survival of cooperators. It is clear that any kind of noise that tends to destroy spatial structures will work against the survival of cooperators. But, even in the region $2 > T > 1.8$, our original results for the deterministic case remain valid at low noise levels and are lost only when the noise exceeds a threshold magnitude. Our present simulations (and previous work[7,8,10]) also show that the spatial Prisoner's Dilemma — if seen in the whole range of parameter regions — is, in fact, robust against significant amounts of stochastic perturbations, as well as several other complications[8].

In contrast with Mukherji *et al.*'s final conclusion, we contend that cooperation persists in the spatial Prisoner's Dilemma even in the face of reasonably high levels of noise.

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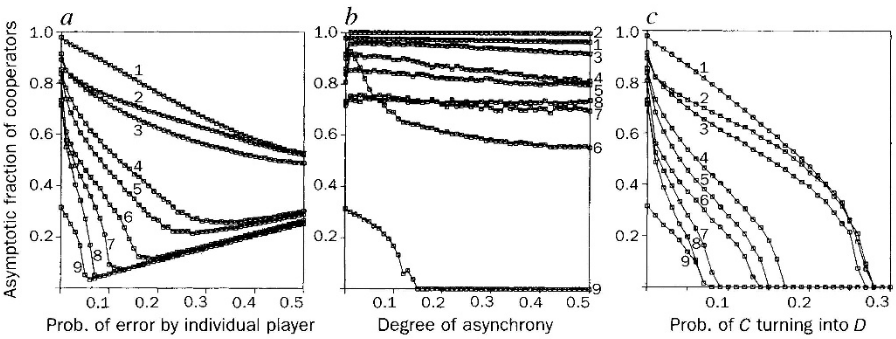

FIG. 2 Computer simulations for the spatial Prisoner's Dilemma with three different types of stochastic perturbations as proposed by Mukherji *et al.*, but for all 9 relevant parameter regions of the game[7,8] represented by the *T* values 1.05, 1.13, 1.16, 1.35, 1.42, 1.55, 1.71, 1.77 and 1.9 (corresponding to labels 1–9 in the figure). Mukherji *et al.* show results for the ninth parameter region $2 > T > 1.8$. The *x*-axis denotes: *a*, the fraction of sites given randomly to cooperators or defectors in each generation; *b*, the fraction of sites that are not updated in every generation; *c*, the fraction of cooperators that are changed into defectors in every generation. The *y*-axis is the asymptotic fraction of cooperators in a 100×100 array after 500 generations with an initial condition of 90% cooperators.

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Scientific Correspondence

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