Journal club

'TIT-FOR-TAT' IN CELL BIOLOGY

Although my colleagues (and, hopefully, readers) value the importance of evolutionary theory in biology, many of us fail to incorporate it into our research. Therefore, I am going to tell you about a paper that influenced me long ago.

In 1981, Axelrod and Hamilton asked how cooperation evolves; the prevailing notion was that this occurs when individuals are sufficiently genetically identical that altruism serves to promote genome replication, regardless of whose genome is replicating. They explored the game theory construct of the 'prisoner's dilemma', in which two criminals are caught and questioned separately. If each gives up the other (defection), both will get long sentences. If neither defects, both will serve minor sentences. If one defects, this person will go free and the other will serve a full sentence. Even though cooperation (no defection) gives a net benefit, the

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only 'winning' strategy is to try defection. The authors asked, what happens if the game is played repeatedly? The winning strategy is simple: cooperate in the first round, and, in subsequent meetings, do what the other did last time. This 'tit-for-tat' strategy beats all others, and Axelrod and colleagues subsequently showed (Riolo *et al.*, 2001) that cooperation evolves even when recognition is only for a 'marker' that may be shared among divergent individuals.

But why discuss this here? The tit-for-tat strategy is found throughout nature and human society. My research focuses on physiological cell death, which can be viewed as altruism in the 'society of cells' that constitutes an organism. Thinking about cellular cooperation in the immune system and tumour suppression, and being influenced by these papers (among others), led me to investigate cell death when I founded my laboratory in the 1980s. Although cooperation between cells in a multicellular organism is generally viewed as a given, the idea that cells compete for niches and

resources has helped to frame our thinking about the evolution of development. Recent studies on stem cell competition inform us about cancer and related pathologies (discussed in Green, 2010) and Axelrod and colleagues have speculated about cooperation in oncogenesis (Axelrod *et al.*, 2006). Personally, I'm not done thinking about tit-for-tat and its consequences for cell biology, and such theoretical work might lead to novel avenues in readers' own research.

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ORIGINAL RESEARCH PAPERS Axelrod, R., & Hamilton, W. D. The evolution of cooperation. *Science* **211**, 1390–1396 (1981) | Riolo, R., Cohen, M. D. & Axelrod R. Evolution of cooperation without reciprocity. *Nature* **414**, 441–443 (2001) | Axelrod, R., Axelrod D. E. & Pienta, K. J. Evolution of cooperation among tumor cells. *Proc. Natl Acad. Sci. USA* **103**, 13474–13479 (2006)
FURTHER READING Green, D. R. Cell competition: pirates on the tangled bank. *Cell Stem Cell* **6**, 287–288 (2010)