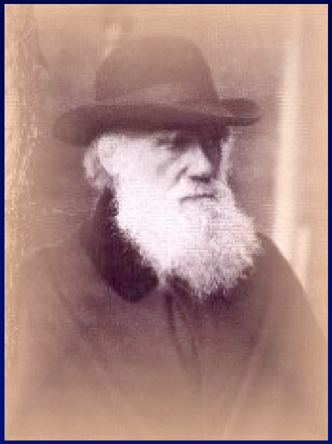
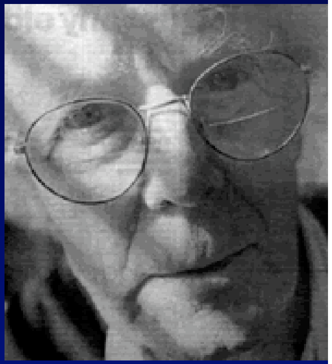
Evolutionary Dynamics



Martin Nowak
Harvard University

Evolution

Mutation

Selection

Sequence space

Fitness landscapes

Evolutionary game dynamics

Cooperation

Fairness

Evolution: major events

?	Origin of life
3500	Bacteria
1500	Eukaryotic cells
600	Multicellular organisms
1	Human language

(million years ago)

Evolution needs populations of reproducing individuals.

Evolutionary change occurs by mutation and selection.

Mutation

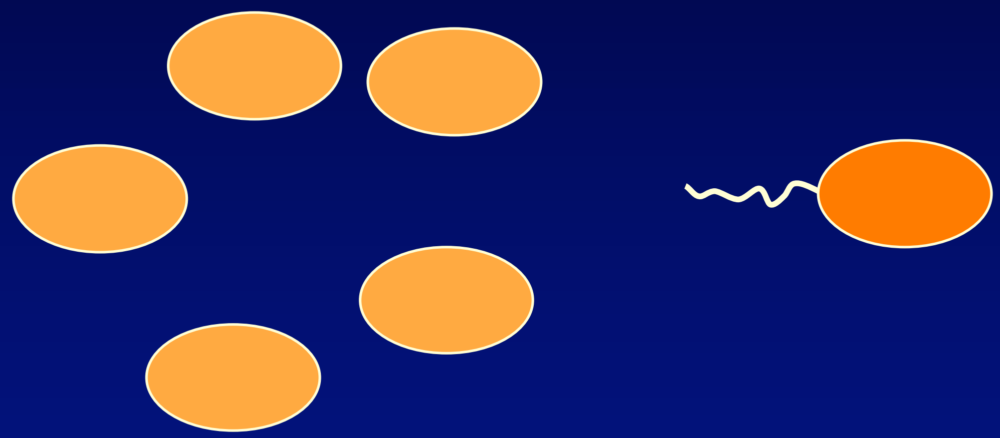
Genome:

….ACTATACGCCGGCATTACCTTATTATGG…

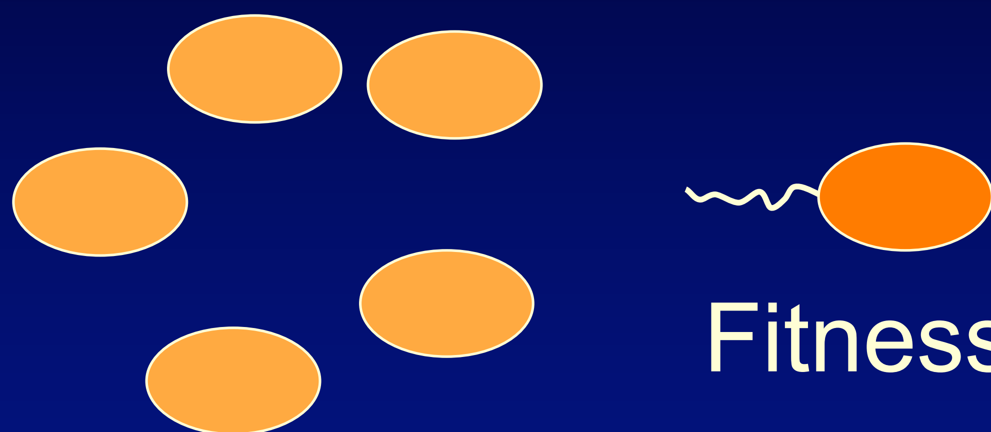
↓ Replication

….ACTATACGCGGGCATTACCTTATTATGG…

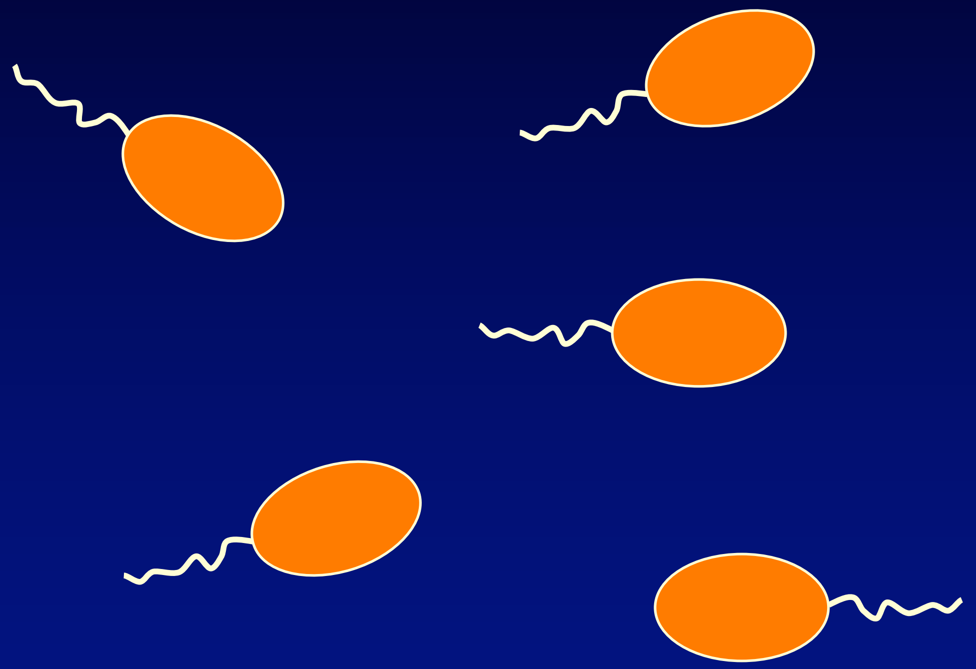
Selection



Selection



Selection



B out-competes A

Genomes live in sequence space

…ACTATACGCCGGCATTACCTTATTATGG…

Length, L

Arrange all sequences such that nearest neighbors differ by one point mutation.

You will need L dimensions.

Genomes live in sequence space

…ACTATACGCCGGCATTACCTTATTATGG…

Length, L

a small virus	L= 10000
a bacterium	L= 4 million
humans	L= 3.5 billion
newts	L= 19 billion

Genomes live in sequence space

…ACTATACGCCGGCATTACCTTATTATGG…

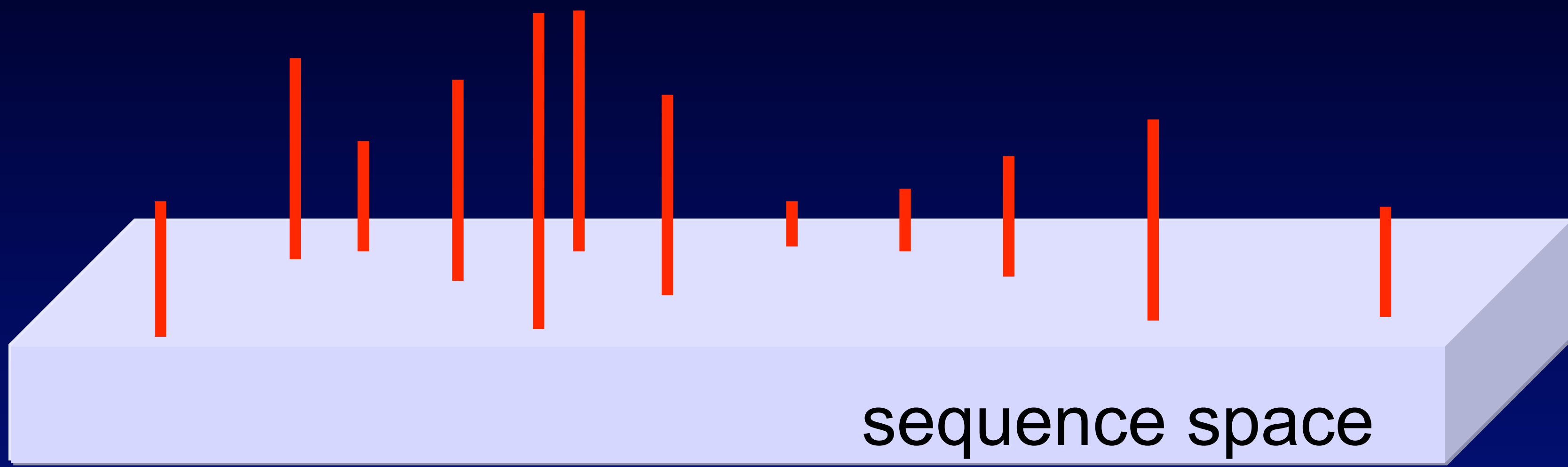
Length, L

a small virus L= 10000
a bacterium L= 4 million
humans L= 3.5 billion
newts L= 19 billion

4^{10000} is about 10^{6000}

There are only 10^{80} protons in the universe.

Populations of genomes explore fitness landscapes



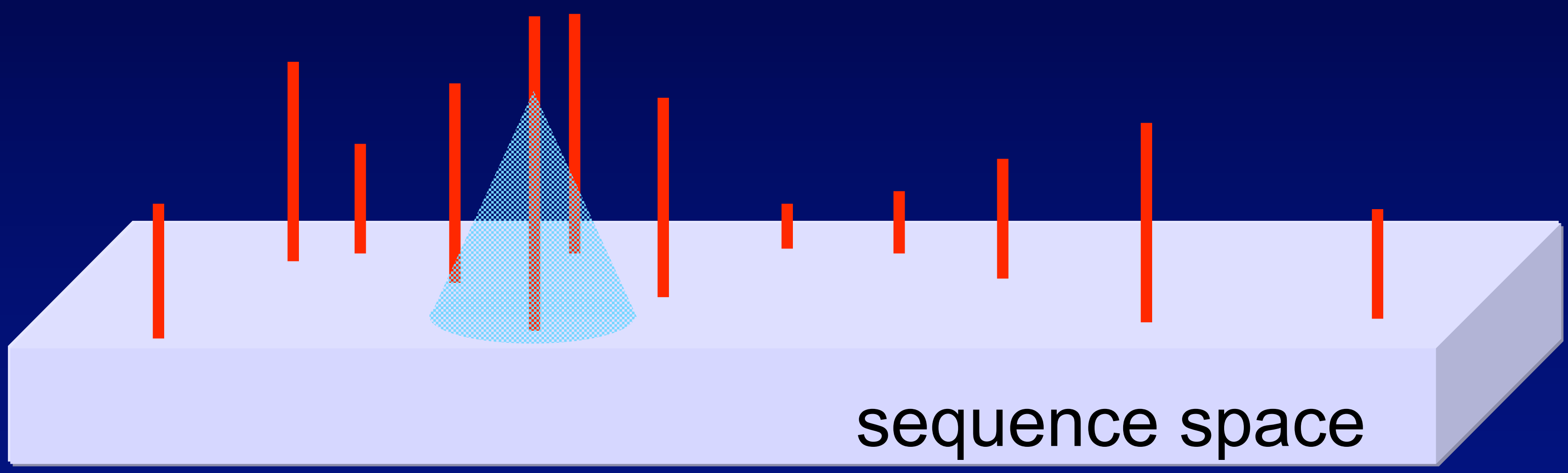
each genome has a reproductive rate (=fitness)

Evolutionary dynamics are given by the quasispecies equation:

$$\dot{x}_i = \sum_j x_j f_j Q_{ji} - \bar{f} x_i$$

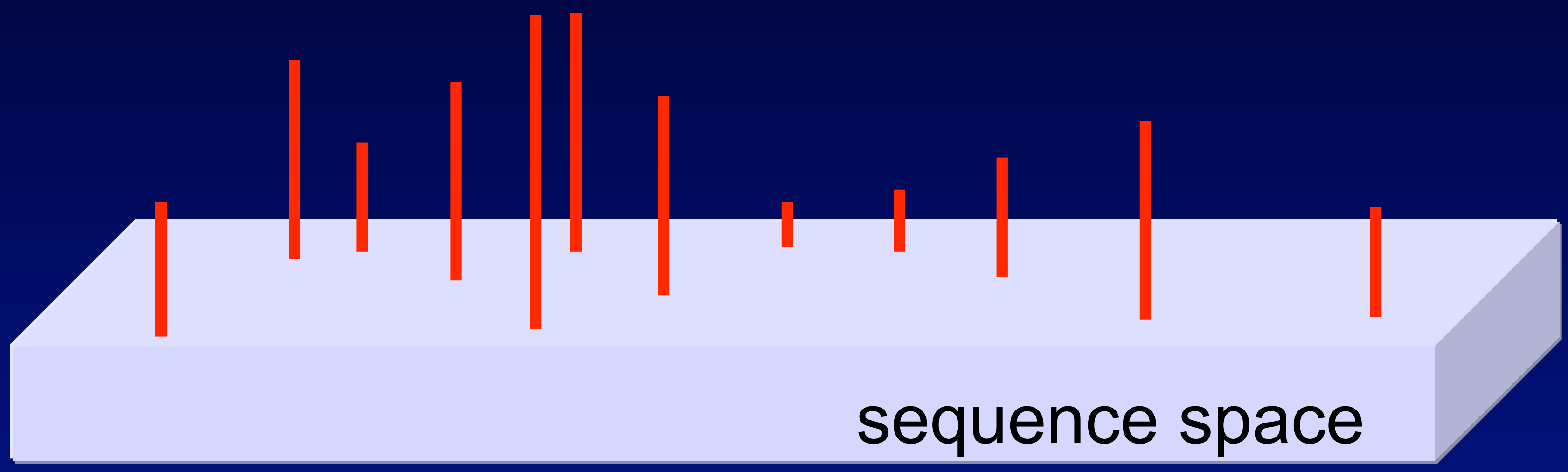
Error threshold

Mutation rate (per base) < 1 / Genome length

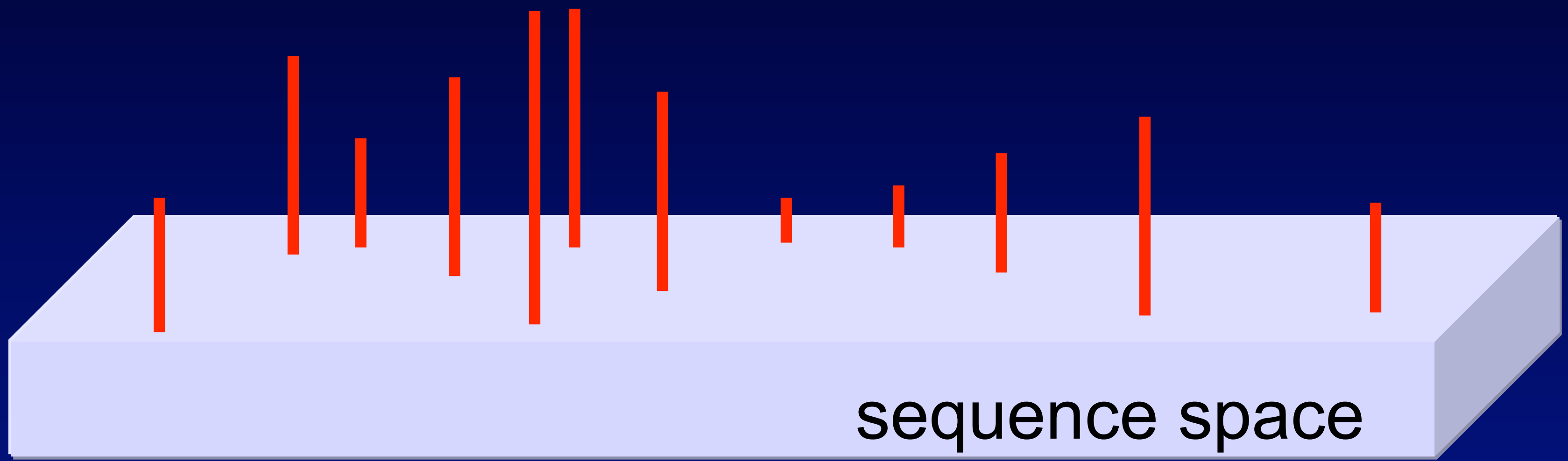


necessary for adaptation
(=finding peaks in fitness landscape)

A special case:
the fitness landscape is constant



In general, the fitness landscape changes as the population moves across



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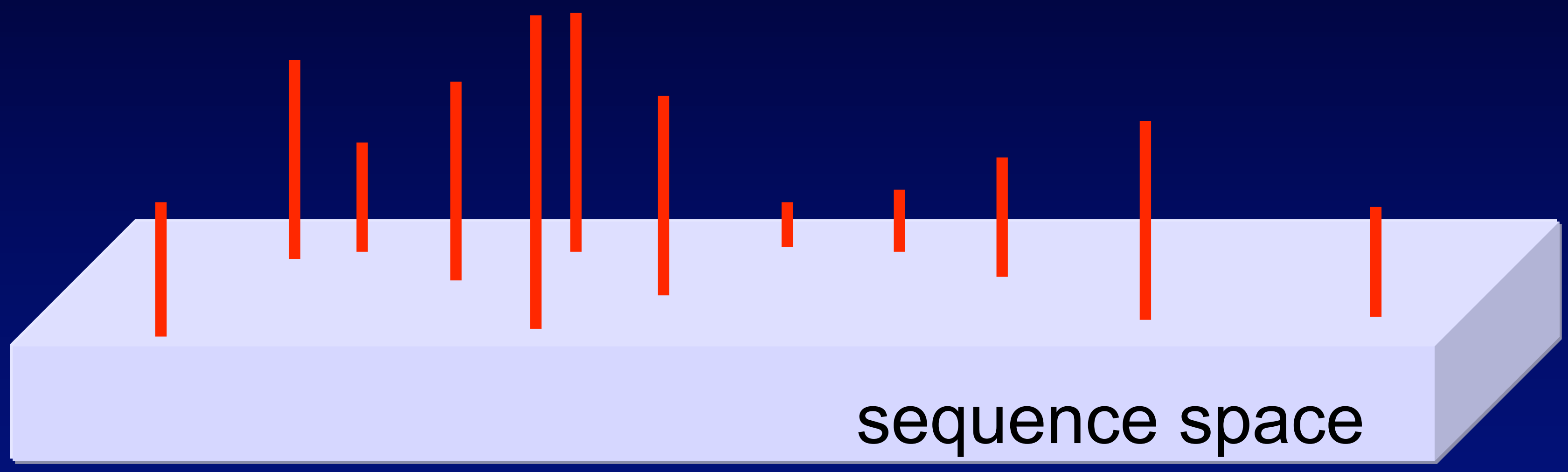


= evolutionary game theory

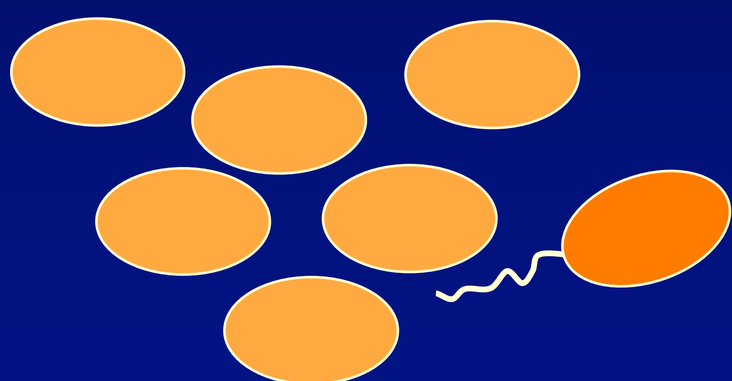
Constant selection

Fitness of type A = 1

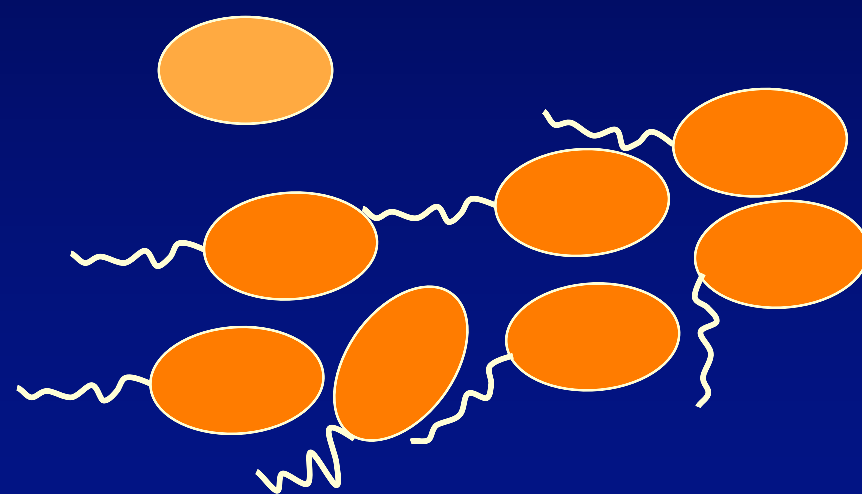
Fitness of type B = 1.1

Evolutionary game theory

Fitness depends on the relative abundance of different types.

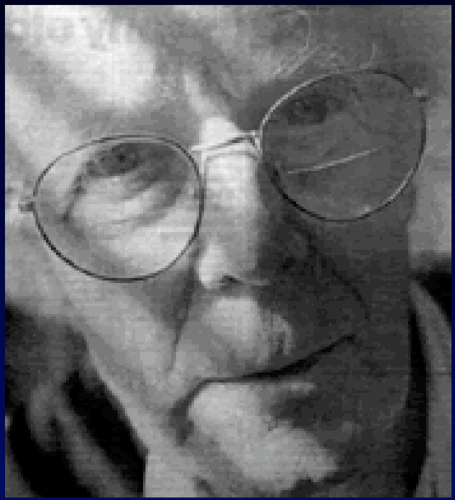


Fitness of type A = 1
Fitness of type B = 1.1



Fitness of type A = 1
Fitness of type B = 0.9

Evolutionary Game Theory



John Maynard Smith

Game Theory

John von Neumann   Oskar Morgenstern

Evolutionarily stable strategy

If every individual of a population adopts the evolutionarily stable strategy, then no mutant can invade.

Nash equilibrium

Replicator dynamics

Successful strategies spread by natural selection.
Payoff = fitness.

$$\dot{x}_i = x_i[f_i(\vec{x}) - \bar{f}(\vec{x})] \qquad i = 1,..,n$$

Replicator dynamics

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$$\dot{x}_i = x_i[f_i(\vec{x}) - \bar{f}(\vec{x})] \qquad i = 1,..,n$$

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$$\bar{f}(\vec{x}) = \sum_i x_i f_i(\vec{x})$$

$$f_i(\vec{x}) = \sum_j a_{ij} x_j$$

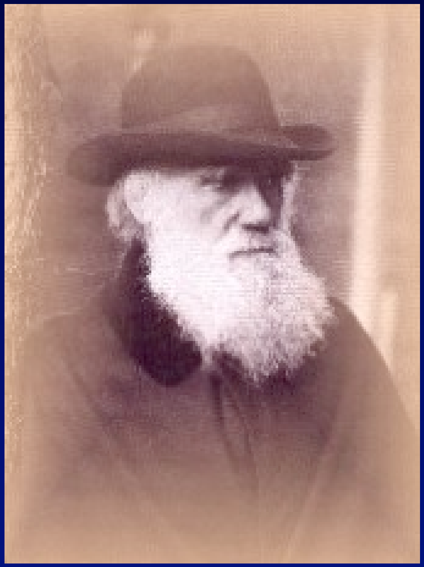
= Lotka Volterra equation of ecology

Social insects

- Workers do not reproduce, but raise the offspring of another individual, the queen.
- How can evolution design such altruistic behavior ?

Evolution of cooperation

Natural selection is based on competition. How can natural selection lead to cooperation?



Charles Darwin

Cooperation between relatives

Hamilton's rule

$$r > c / b$$

William Hamilton

r … coefficient of relatedness

c … cost of cooperation

b … benefit of cooperation

Cooperation between relatives

‘I will jump into the river to save
2 brothers or 8 cousins’

J.B.S Haldane

How to get cooperation between non-relatives ?

Prisoner's Dilemma

cooperate: C **defect: D**

C - C	3 : 3	C - D	0 : 5
D - C	5 : 0	D - D	1 : 1

Rational players choose defection

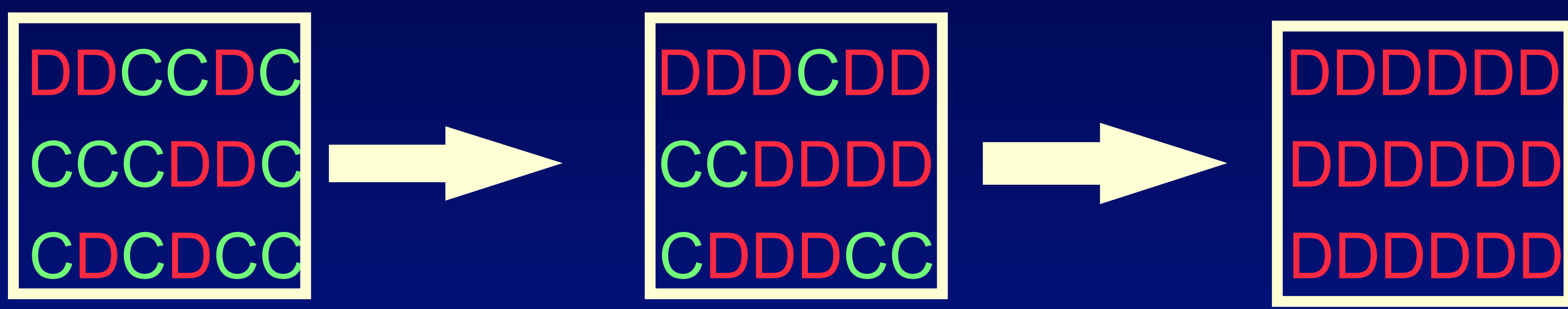
D - D 1 : 1

but cooperation would have been better for both:

C - C 3 : 3

Cooperation is ‘irrational’.

Natural selection chooses defection



D wins against C

3 possibilities for the evolution of cooperation

- Direct reciprocity
- Indirect reciprocity
- Spatial reciprocity

Direct reciprocity

I help you,

but I expect we will meet again.

Then you can help me.

Repeated Prisoner's Dilemma

Player 1 : C D C D C C C ….

Player 2 : D C D D C C C ….

Repeated Prisoner's Dilemma

Player 1 : C D C D C C C ….

Player 2 : D C D D C C C ….

What is a good strategy for the repeated Prisoner's Dilemma?

Robert Axelrod

Tit-for-tat

- If you cooperate, then I will cooperate.
- If you defect, then I will defect.

Anatol Rapaport

Tit-for-tat is too unforgiving

Errors destroy cooperation

Tit-for-tat : CCCCDCDCDCDDDDDD….

Tit-for-tat : CCCDCDCDCDDDDDDD….

Let natural selection design a strategy

Random

Let natural selection design a strategy

Always defect

↑

Random

Let natural selection design a strategy

Tit-for-tat

Always defect

Random

Let natural selection design a strategy

Tit-for-tat → Generous Tit-for-tat

Always defect

Random

Generous Tit-for-tat

- If you cooperate, then I will cooperate.
- If you defect, then I will cooperate with probability 1/3.

Never forget a good move.
Sometimes forgive a bad move.

Let natural selection design a strategy

Tit-for-tat → Generous Tit-for-tat

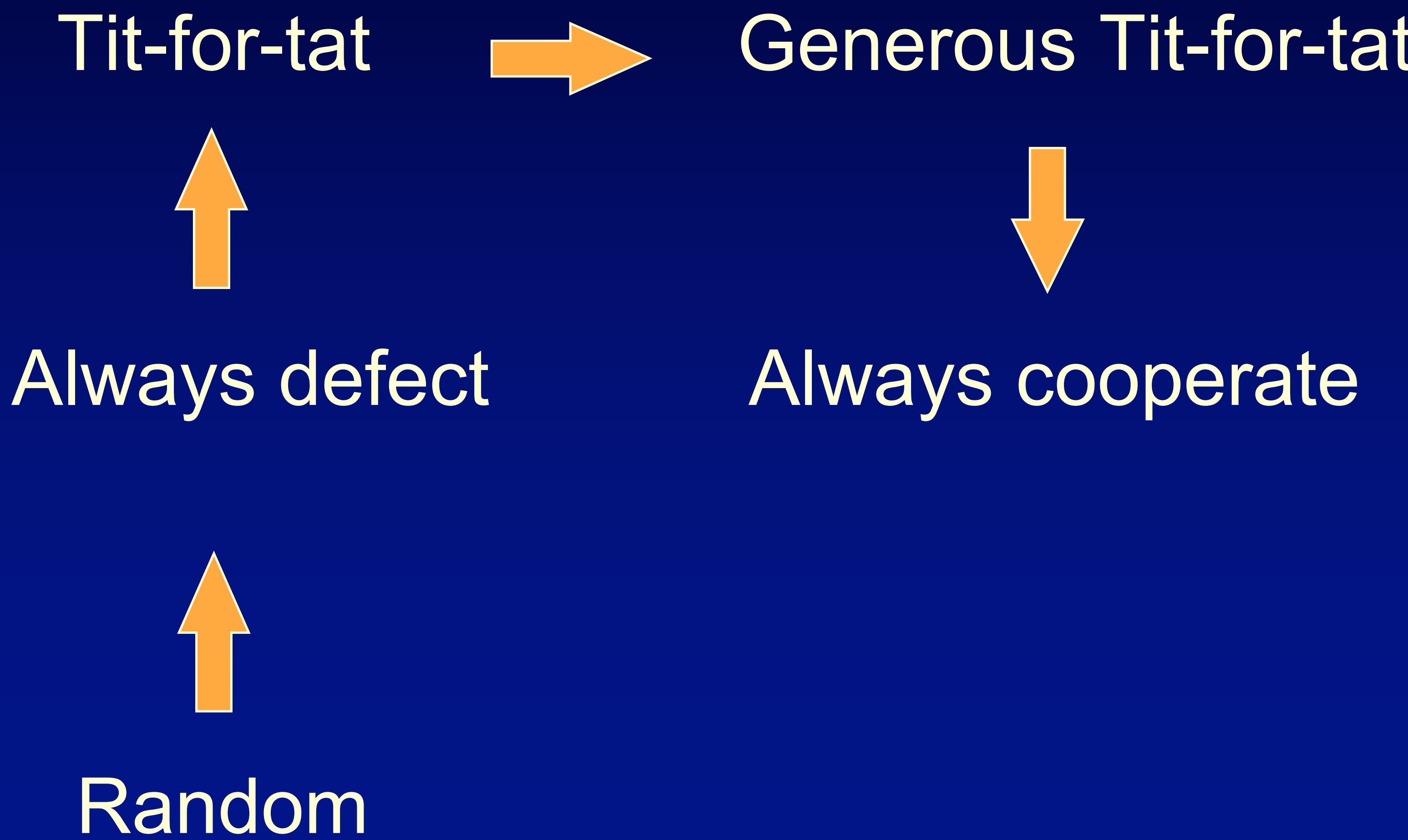
↑

Always defect

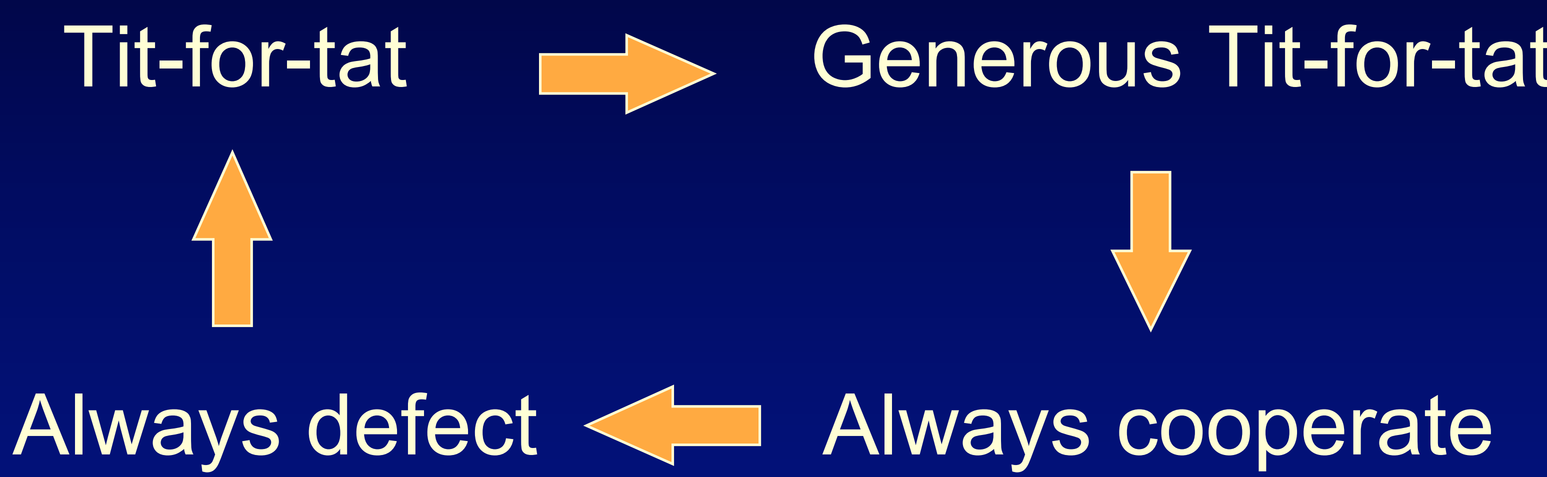
↑

Random

Let natural selection design a strategy

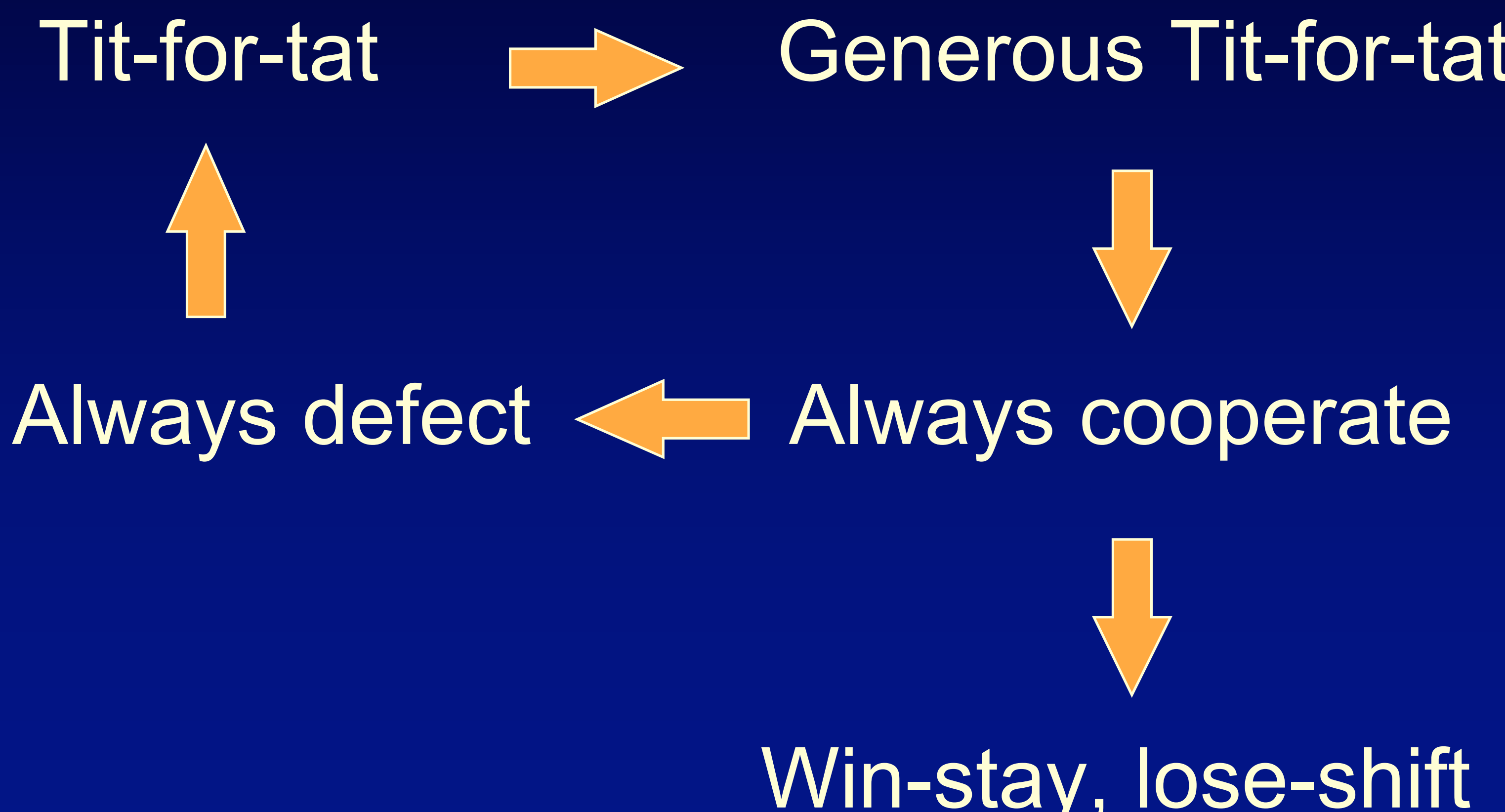


Let natural selection design a strategy



War and peace

Let natural selection design a strategy



Win-stay, lose-shift

Win - stay :

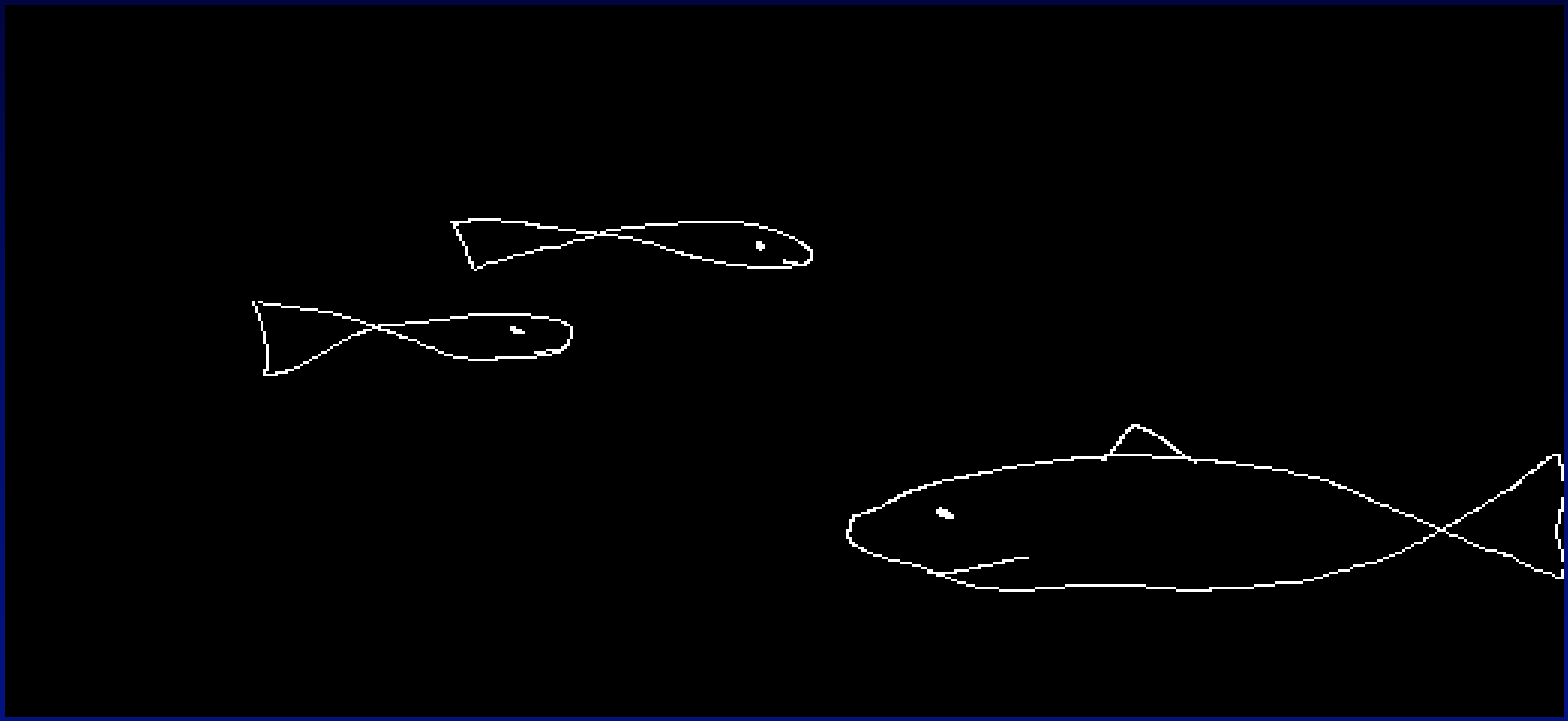
C (3) C   D (5) .... D
C   C

Lose - shift :

C (0) .... D   D (1) .... C (probabilistic)
D   D

Fudenberg & Maskin

Experimental observations



Manfred Milinski

Direct reciprocity

‘I help you, you help me.’

Indirect reciprocity

'I help you, somebody else helps me.'

Indirect reciprocity

	donor	recipient	donor's reputation
cooperate	-c	+b	+1
defect	0	0	-1

Natural selection chooses

strategies that base their decision to cooperate on the reputation of the recipient: ‘help those who have helped others’

Give and you shall receive.

A rule for indirect reciprocity

$$q > c / b$$

q … probability to know someone's reputation

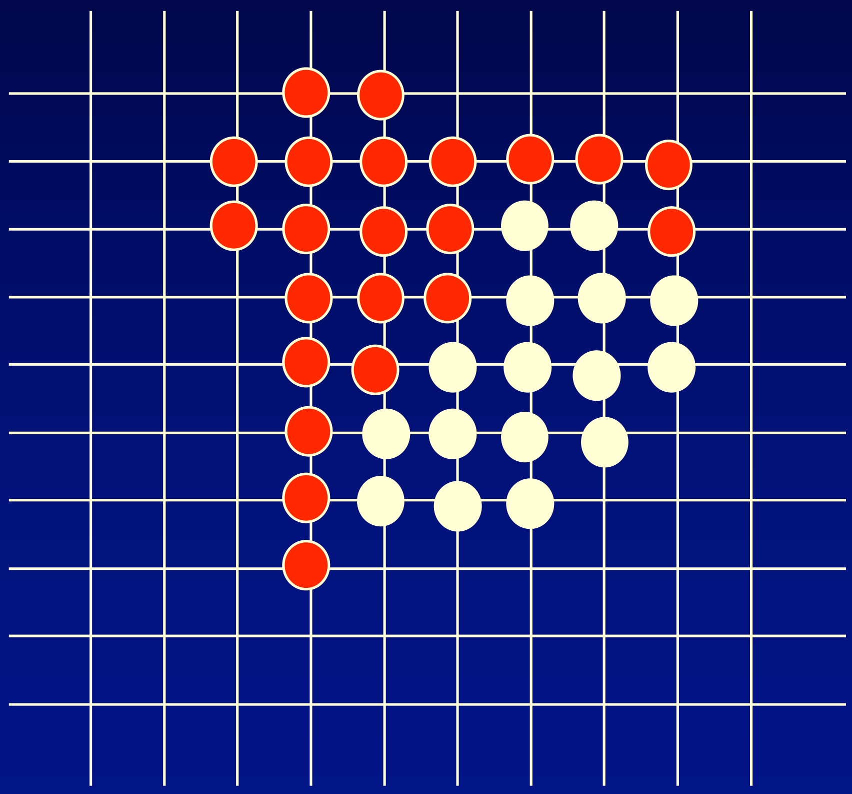
c … cost of cooperation

b … benefit of cooperation

A universal constant of nature

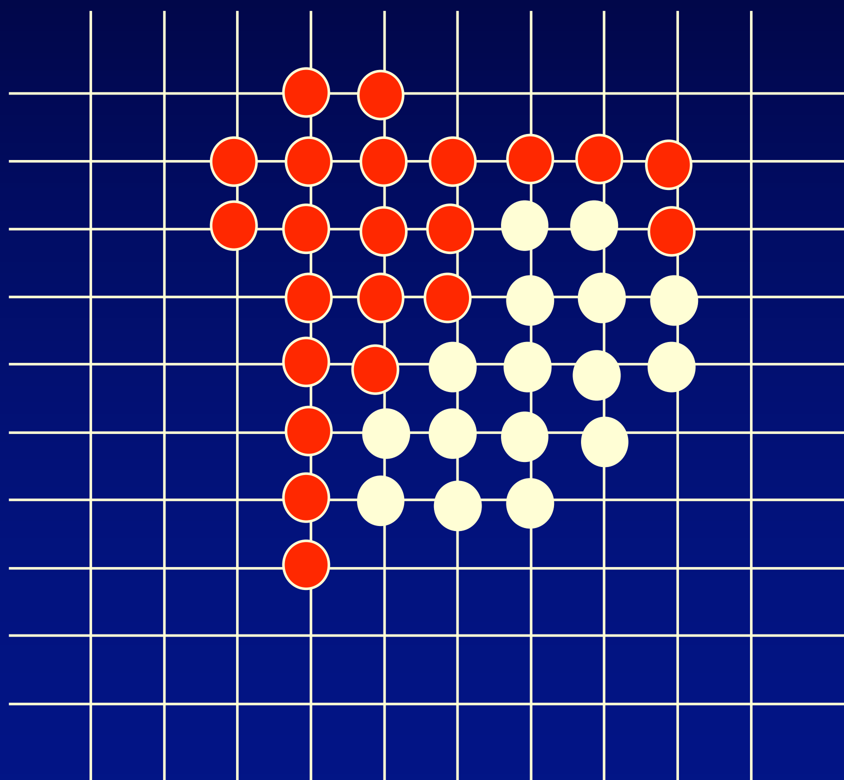
- 0.7380294688… is the maximum fraction of people who can be bad in the beginning such that everyone will be good in the end

Spatial reciprocity



Cooperators
Defectors

Spatial reciprocity



Cooperators
Defectors

Von Neumann invented both
game theory and cellular automata

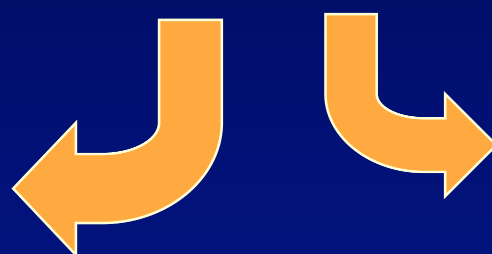
Fairness

Ultimatum Game

Proposer
makes an offer.

Ultimatum Game

$1,000,000



Proposer
makes an offer.

Responder
says yes or no.

Ultimatum Game

Proposer
makes an offer.

Responder
says yes or no.

What does game theory suggest?

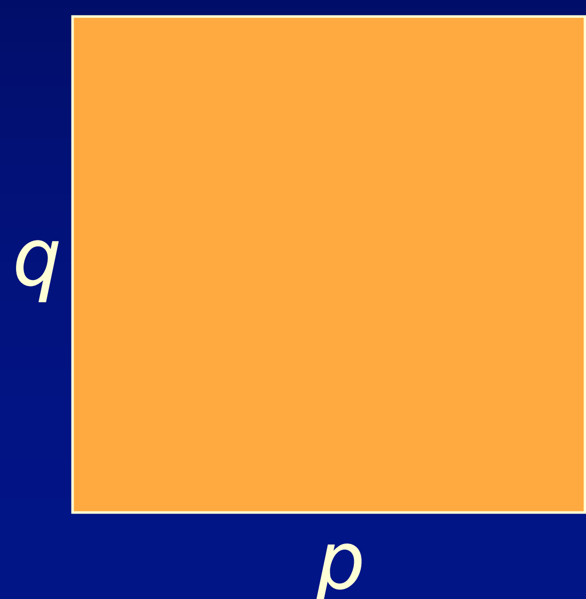
- A ‘rational’ responder should prefer $1 to $0.
- Therefore, a ‘rational’ proposer should offer $1 and keep almost the whole sum.

What do the experiments show?

- People are not ‘rational’.
- Most proposers offer 30-50%.
- Most responders reject offers below 30%.

Evolutionary ultimatum

Strategies *S(p,q)*
p…offer when proposer
q…minimum acceptance level when responder



Evolutionary ultimatum

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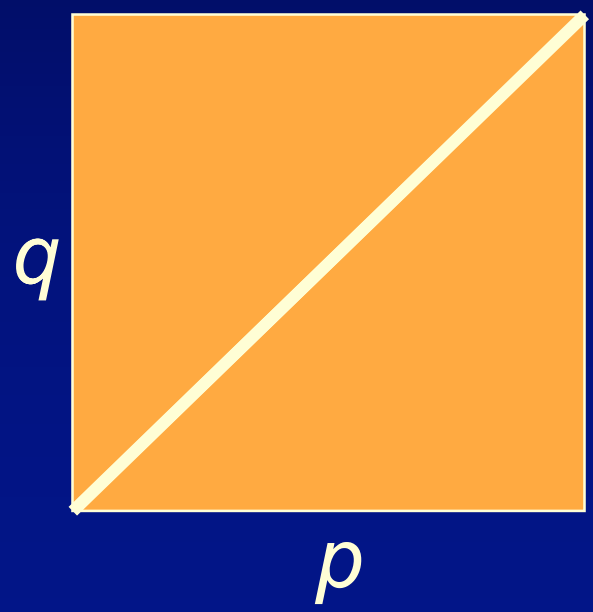

Evolutionary ultimatum

Strategies *S(p,q)*
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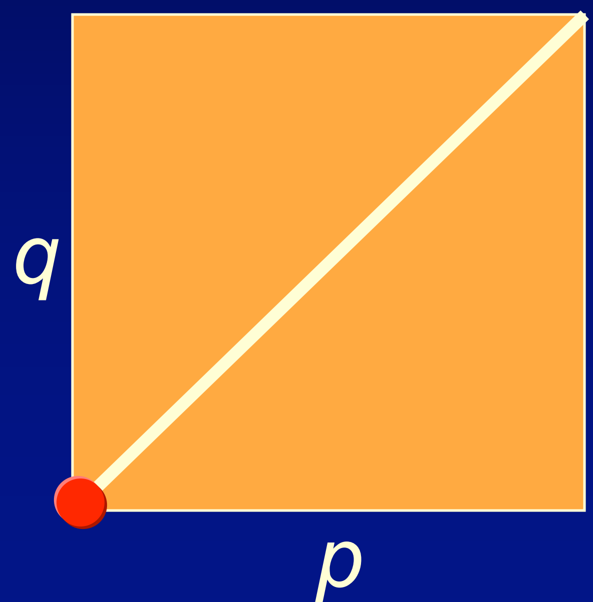
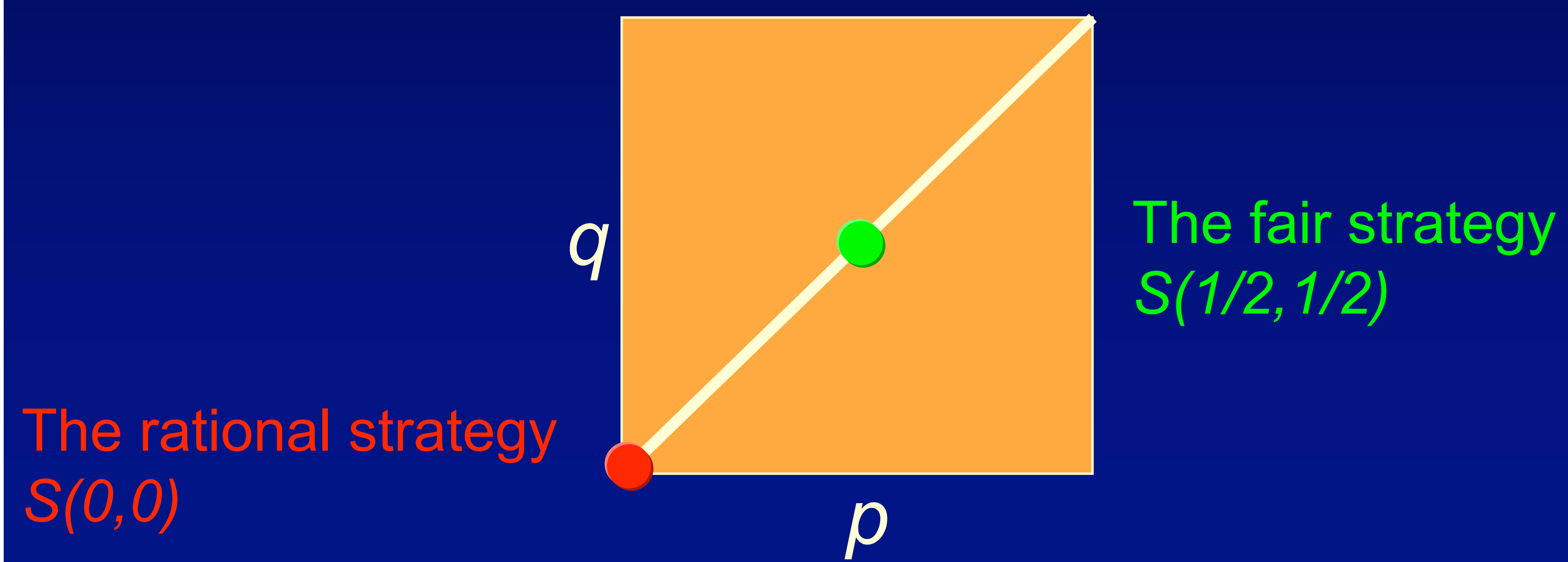


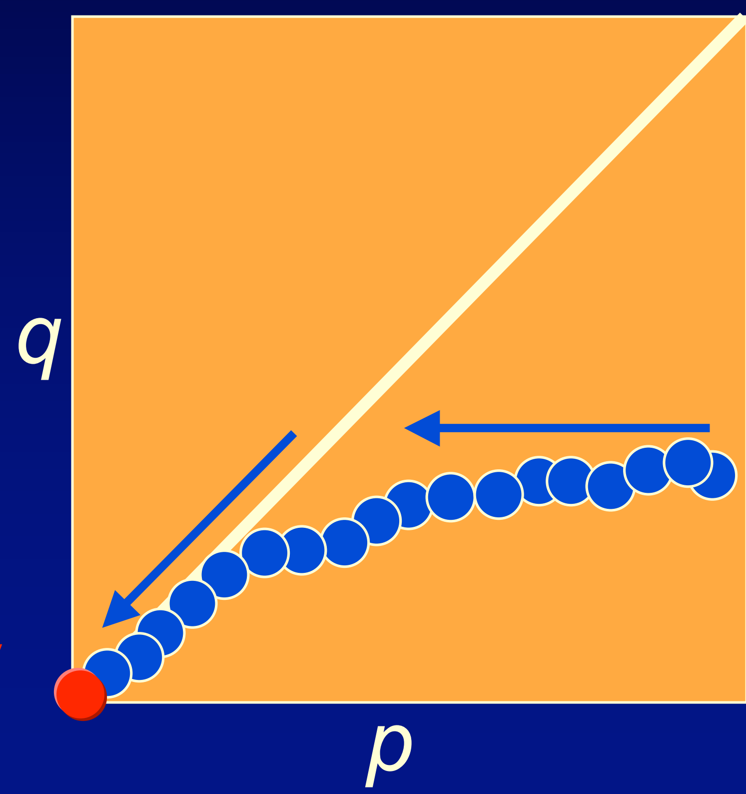
The rational strategy
S(0,0)

Evolutionary ultimatum

Strategies *S(p,q)*
p…offer when proposer
q…minimum acceptance level when responder



Evolutionary dynamics



Natural selection chooses

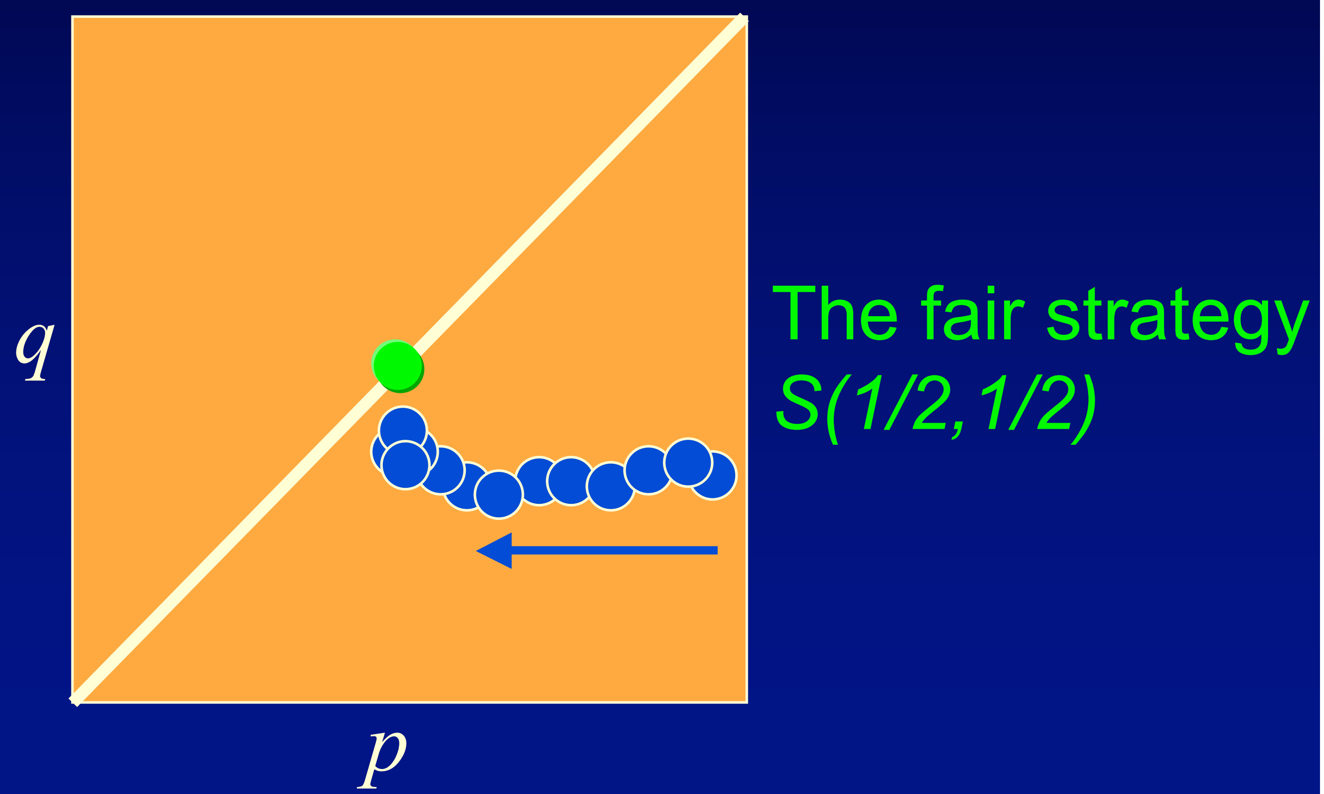
- … low offers, low demands.
- It costs to reject offers, therefore low acceptance levels are favored.
- If acceptance levels decline, then offers will decline too.

How can we explain the evolution of fairness?

Reputation

- Suppose there is a chance that it will become known what offer a person has accepted.
- Accepting low offers increases the probability of receiving reduced offers in the future.
- Rejecting low offers is costly, but buys the reputation of being someone who demands a fair share.

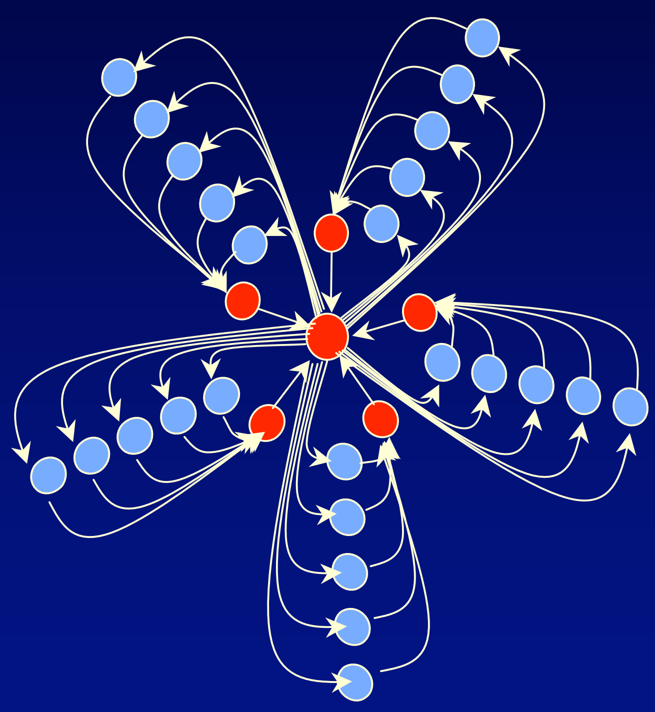
Evolutionary dynamics



The most fascinating game that evolution plays...

… is human language.

Program for Evolutionary dynamics



Games in finite populations
Evolutionary graph theory
Evolution of language
Learning
Somatic evolution of cancer
Evolution of infectious agents
Phenotypic error-thresholds
Evolution of multi-cellularity
…