évolution de la coopération, chez l'Homme

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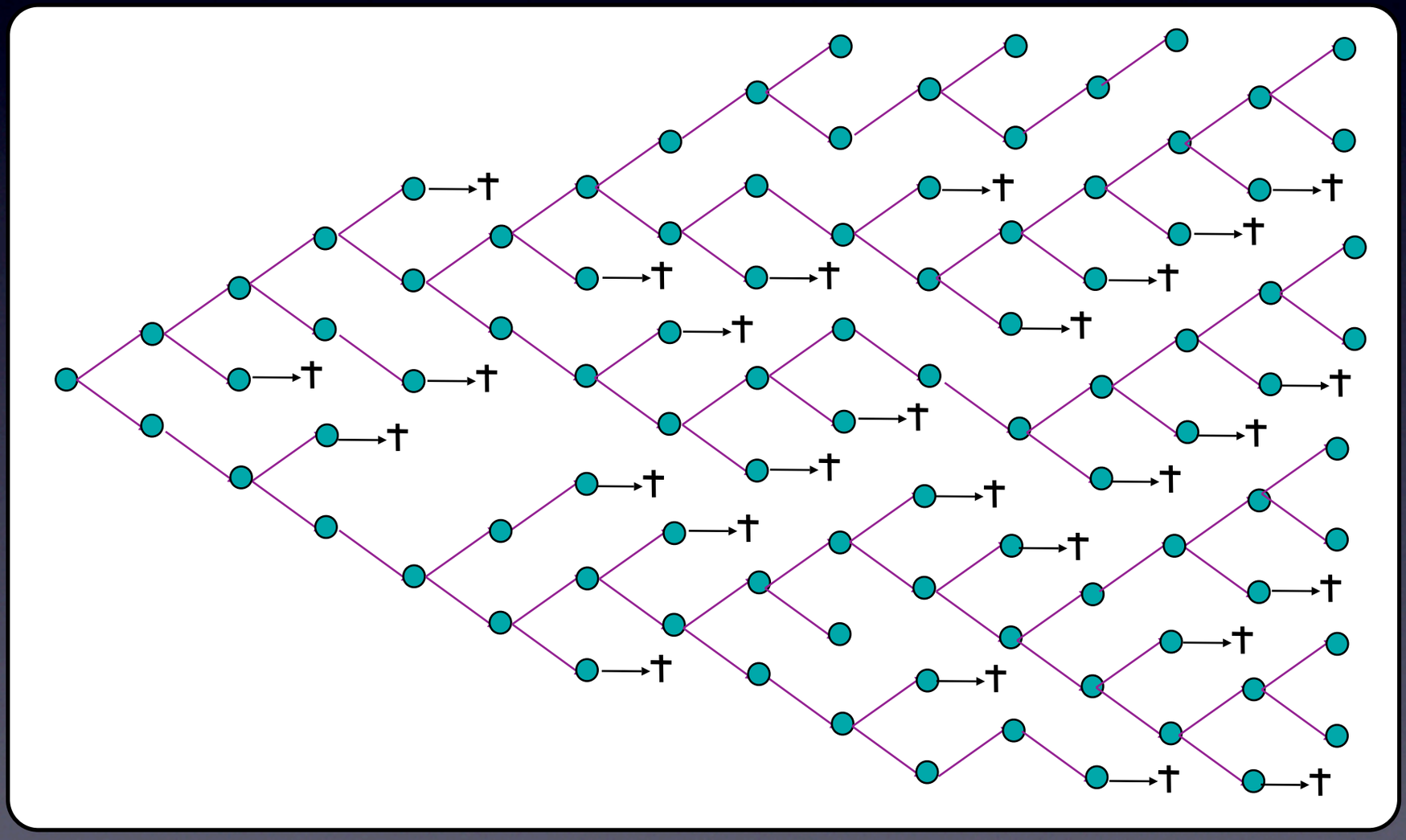
le problème de l'adaptation

Si vous trouvez une montre, vous ne doutez pas qu'elle a été fabriquée par un horloger. De même, si vous considérez un organisme un peu complexe, avec l'évidente finalité de tous ses organes, comment ne pas conclure qu'il a été produit par la volonté d'un Créateur ? Car il serait simplement absurde de supposer que l'œil d'un mammifère, par exemple, avec la précision de son optique et sa géométrie, aurait pu se former par pur hasard

François Jacob

l'argument téléologique ou "argument from design"
développé par William Paley

la biologie est une science historique



les êtres vivants actuels
ne sont pas
tirés au hasard

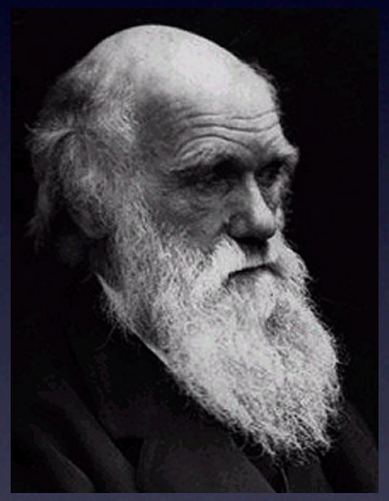
biologie évolutionnaire

- les structures vivantes sont produites par l'évolution
- on peut donc les étudier comme des adaptations
- principe de l'ingénierie inverse

psychologie

- une branche de la biologie
- qui étudie un objet particulier : le cerveau humain
- dont la fonction est de produire des comportements

psychologie évolutionnaire



Psychology will be based on a new foundation

psychologie évolutionnaire

- le cerveau produit des comportements “appropriés”...
- ... à la reproduction de l’organisme

making the natural seem strange

Of course we smile, of course our heart palpitates at the sight of the crowd, of course we love the maiden, that beautiful soul clad in that perfect form, so palpably and flagrantly made for all eternity to be loved!

And so, probably, does each animal feel about the particular things it tends to do in the presence of particular objects. ... To the lion it is the lioness which is made to be loved. To the broody hen the notion would probably seem monstrous that there should be a creature in the world to whom a nestful of eggs was not the utterly fascinating and precious and never-to-be-too-much-sat-upon object which it is to her."

(William James, 1890)

instinct blindness

- les processus cognitifs qui arrivent à la conscience ne sont que la partie émergée de l'iceberg
- nos processus cognitifs nous donnent l'impression d'être plus simples qu'ils ne sont réellement (p. ex. la vision en 3D)
- ce sont ces processus que la psychologie évolutionnaire cherche à comprendre

ex. reconnaisance des émotions

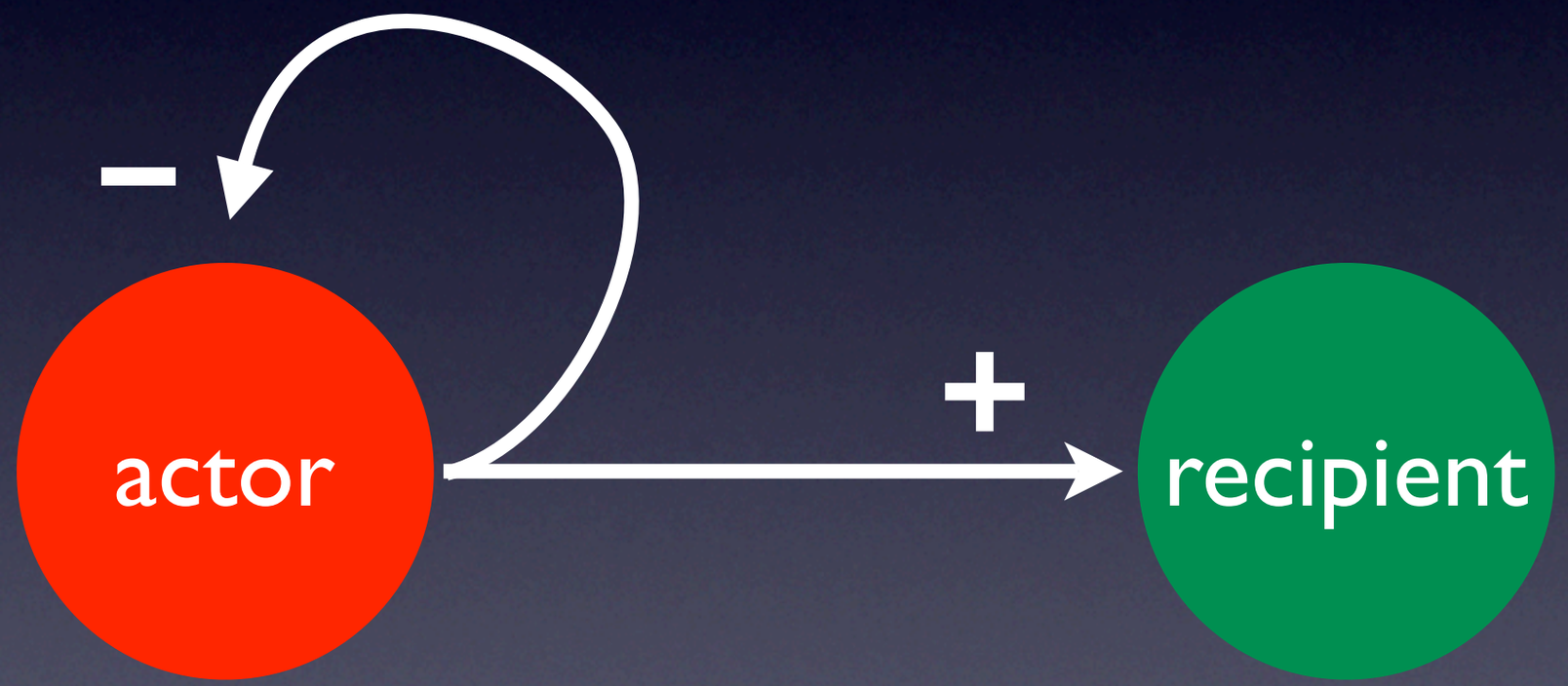
évolution de la coopération - théorie

cooperation and altruism

cooperation (or helping)

West et al. (2007) Social semantics, *j. evol. biol.* ***20***

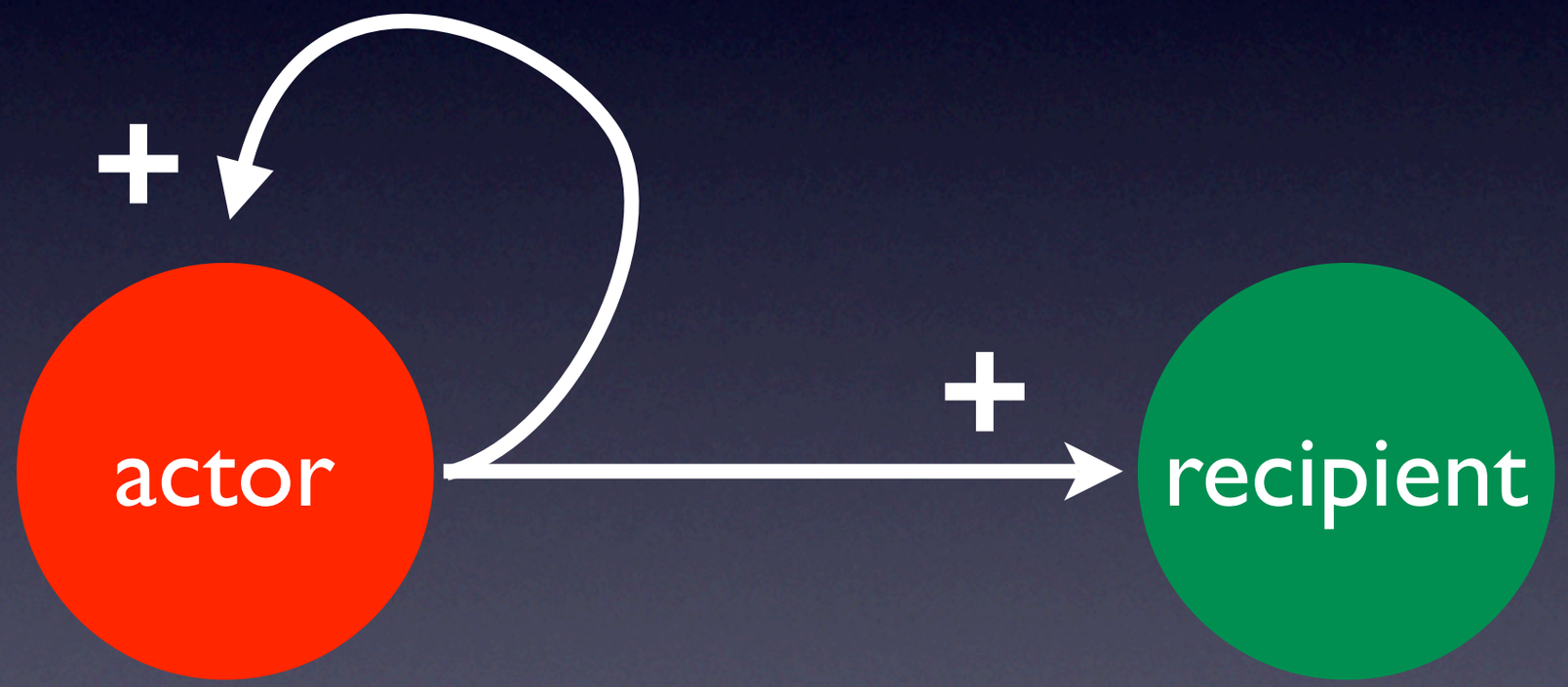
cooperation and altruism



altruism *stricto sensu*

West et al. (2007) Social semantics, *j. evol. biol.* ***20***

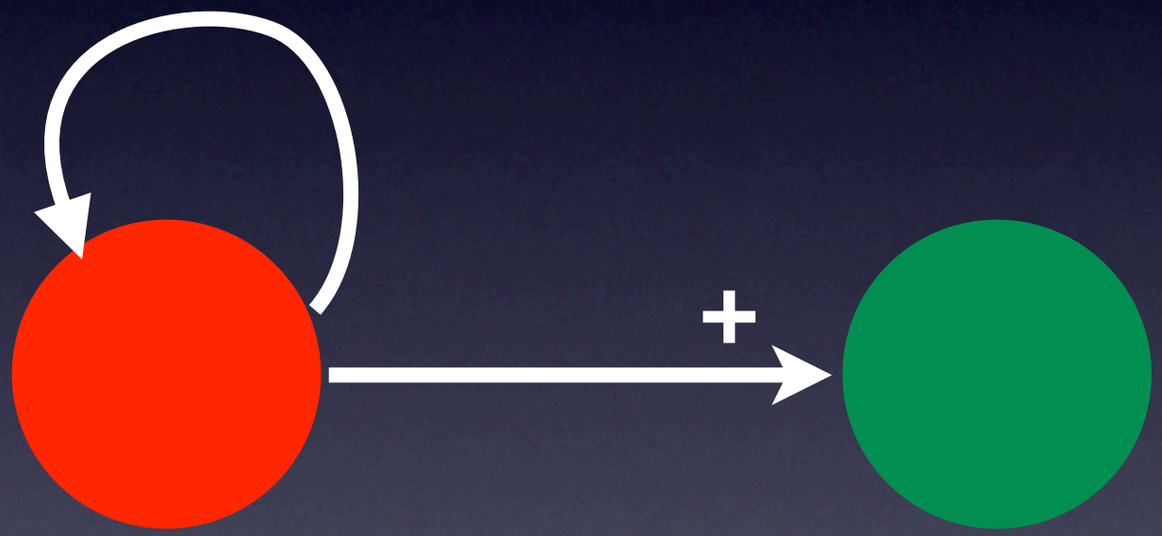
cooperation and altruism



mutualism

West et al. (2007) Social semantics, *j. evol. biol.* ***20***

evolution of cooperation



altruism is *costly* to the actor

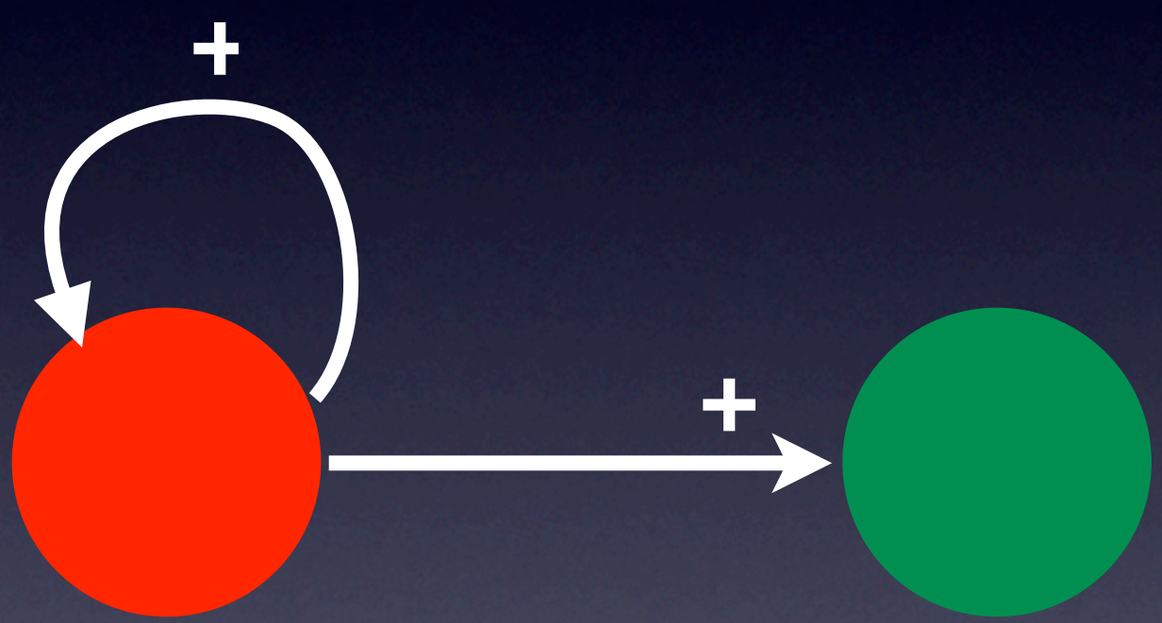
it can evolve through *indirect* fitness benefits

= kin selection

West et al. (2007) Social semantics, *j. evol. biol.* ***20***

evolution of cooperation

mutualism is *beneficial* to the actor



it can evolve through *direct* fitness benefits

= by-product mutualism, reciprocity

West et al. (2007) Social semantics, *j. evol. biol.* ***20***

evolution of mutualism

Cooperation benefits the recipient,
the benefits to the actor can be

immediate and automatic:

- by-product benefits
- investment in by-product benefits
- pseudo-reciprocity

West et al. (2007) ; Connor (2005) ; Leimar & Hammerstein (2010)

evolution of mutualism

Cooperation benefits the recipient,
the benefits to the actor can be

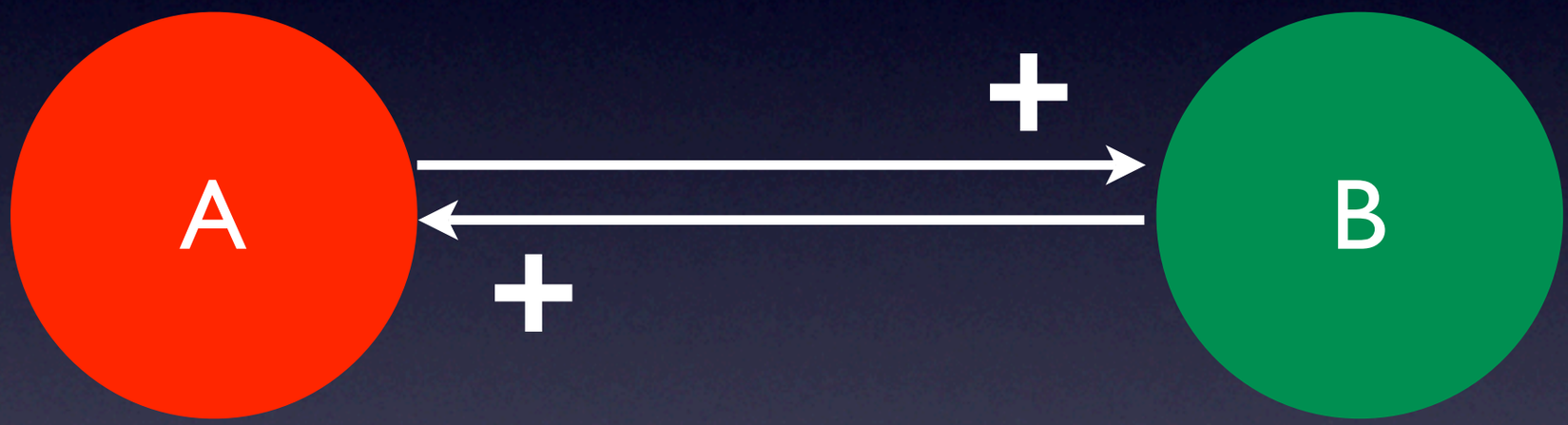
delayed and contingent:

- reciprocity
- indirect reciprocity (reputation)
- punishment (retribution)

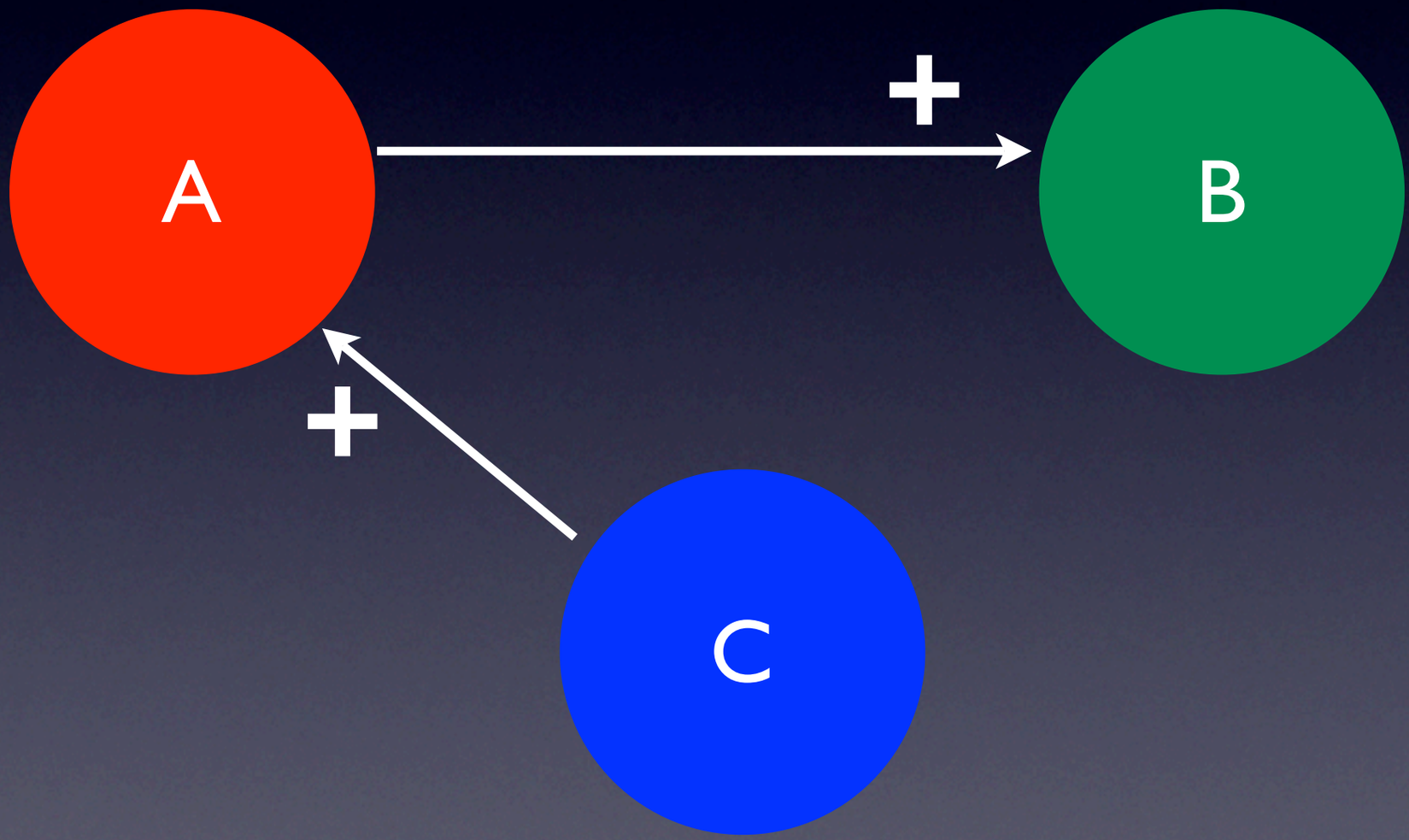
"the three Rs"

Trivers 1971; Leimar & Hammerstein 2001; Boyd and Richerson 1992

reciprocity

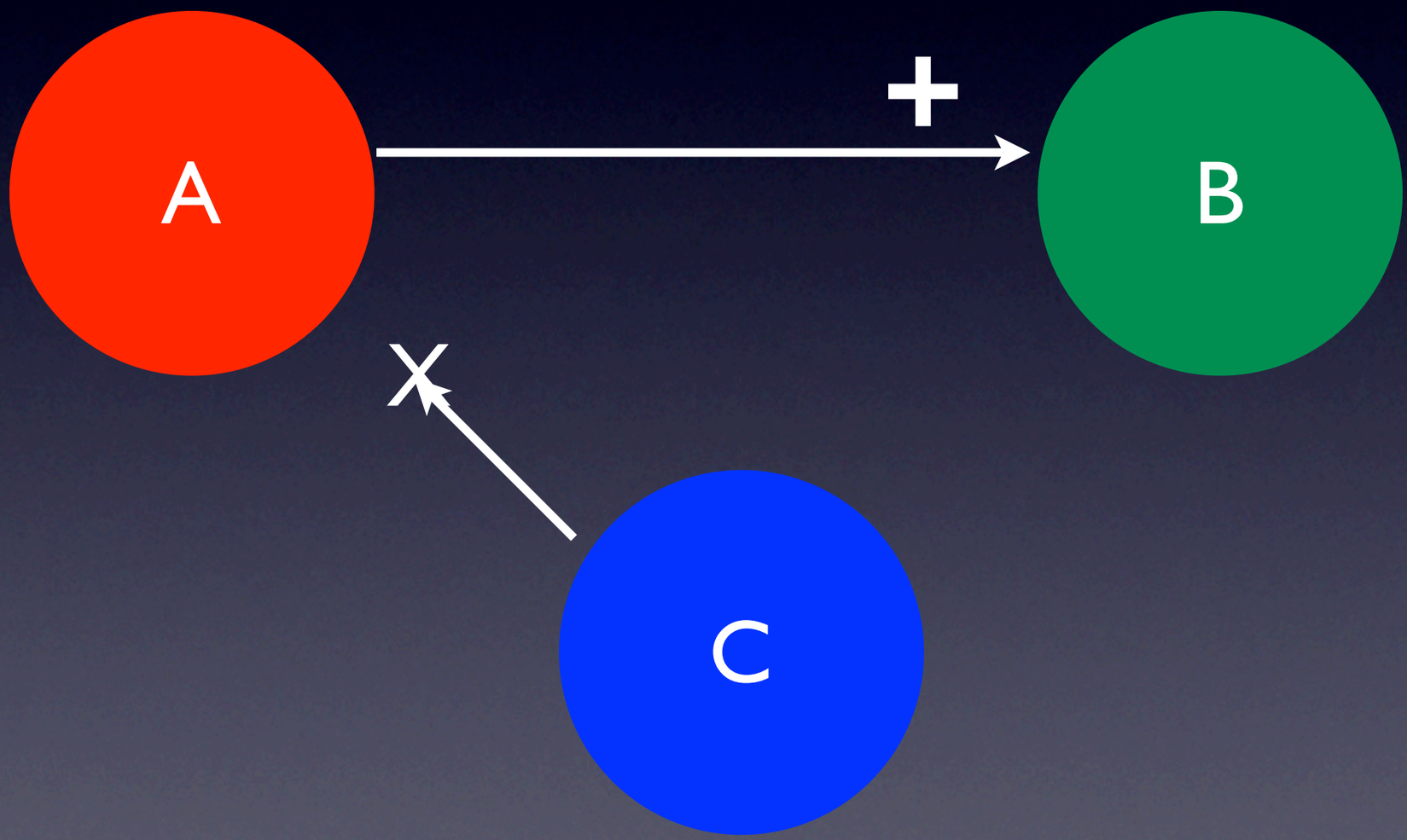


reputation



indirect reciprocity

retribution



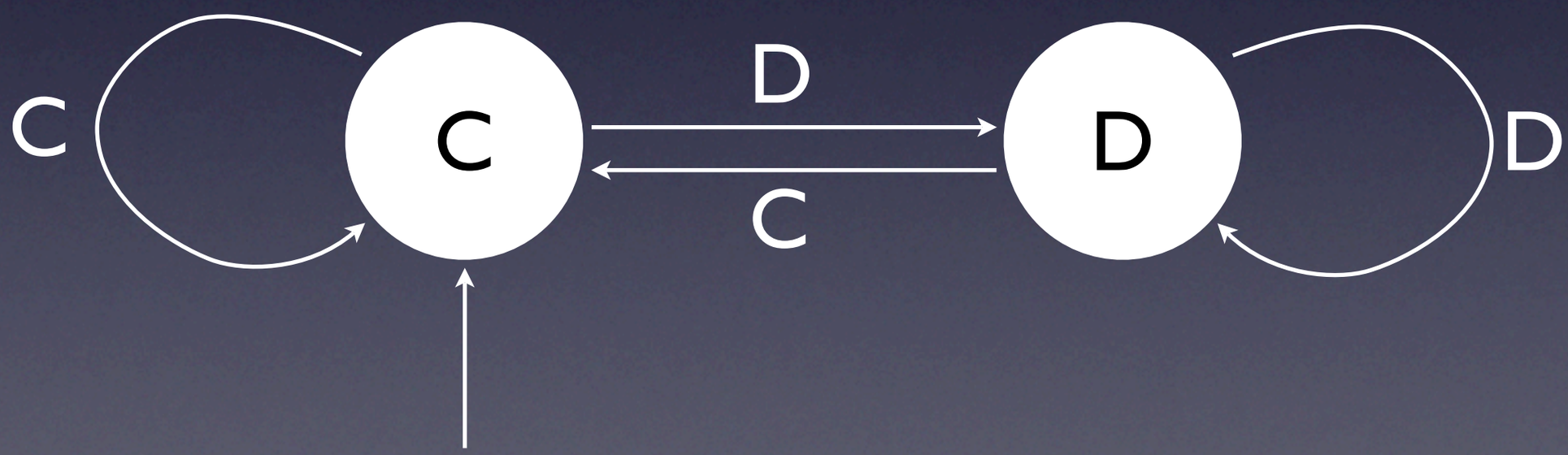
the evolution of reciprocity

Basic paradigm: the prisoner's dilemma

	C	D
C	b - c	-c
D	b	0

Tit-for-tat

- cooperate first
- then do like your partner



Trivers 1971 ; Axelrod and Hamilton 1981

finite repetition

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finite repetition

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finite repetition

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finite repetition

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infinite repetition

- TFT is Nash equilibrium and NSS
- but TFT is not good after a defection

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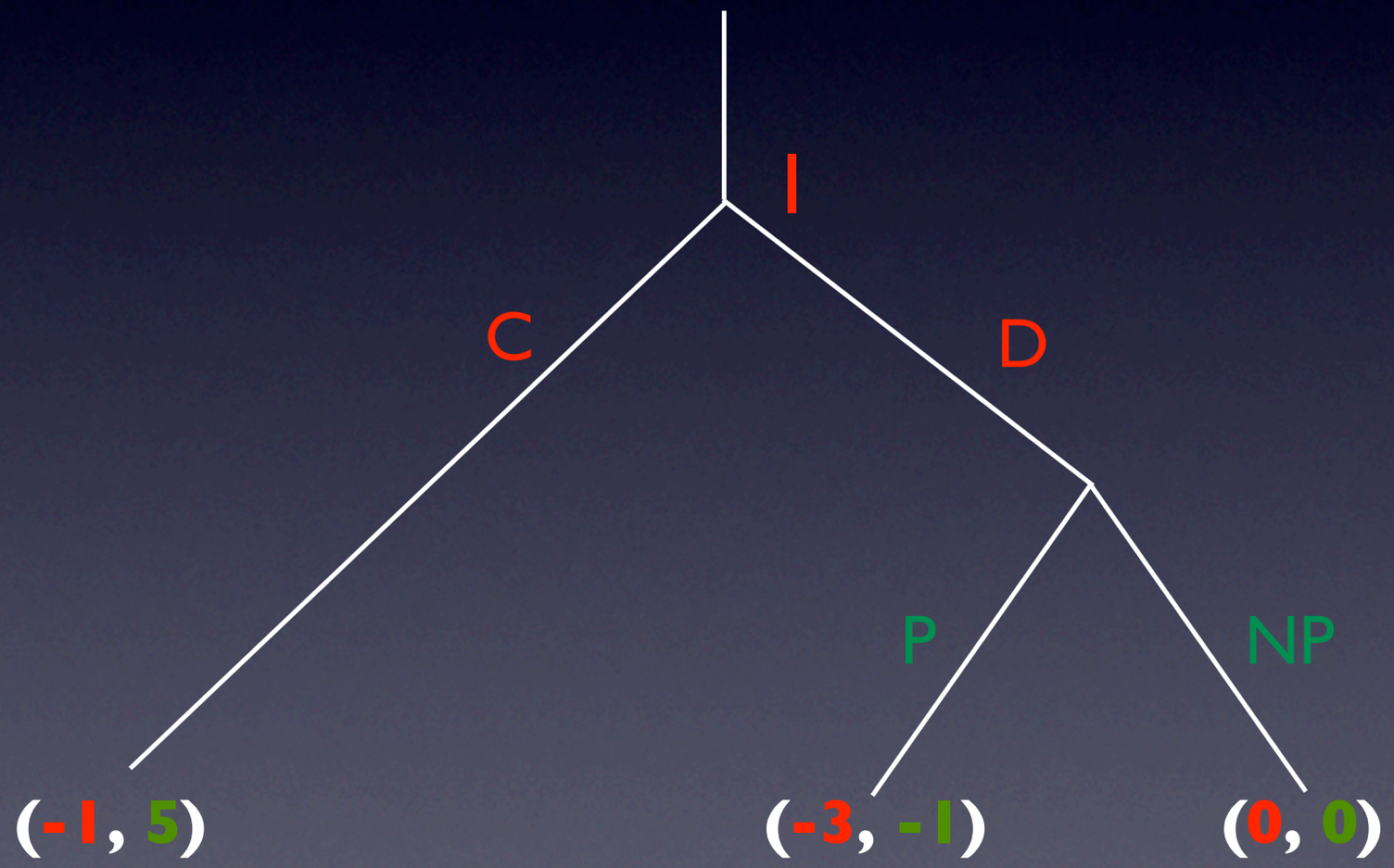
TFT is not **subgame perfect**

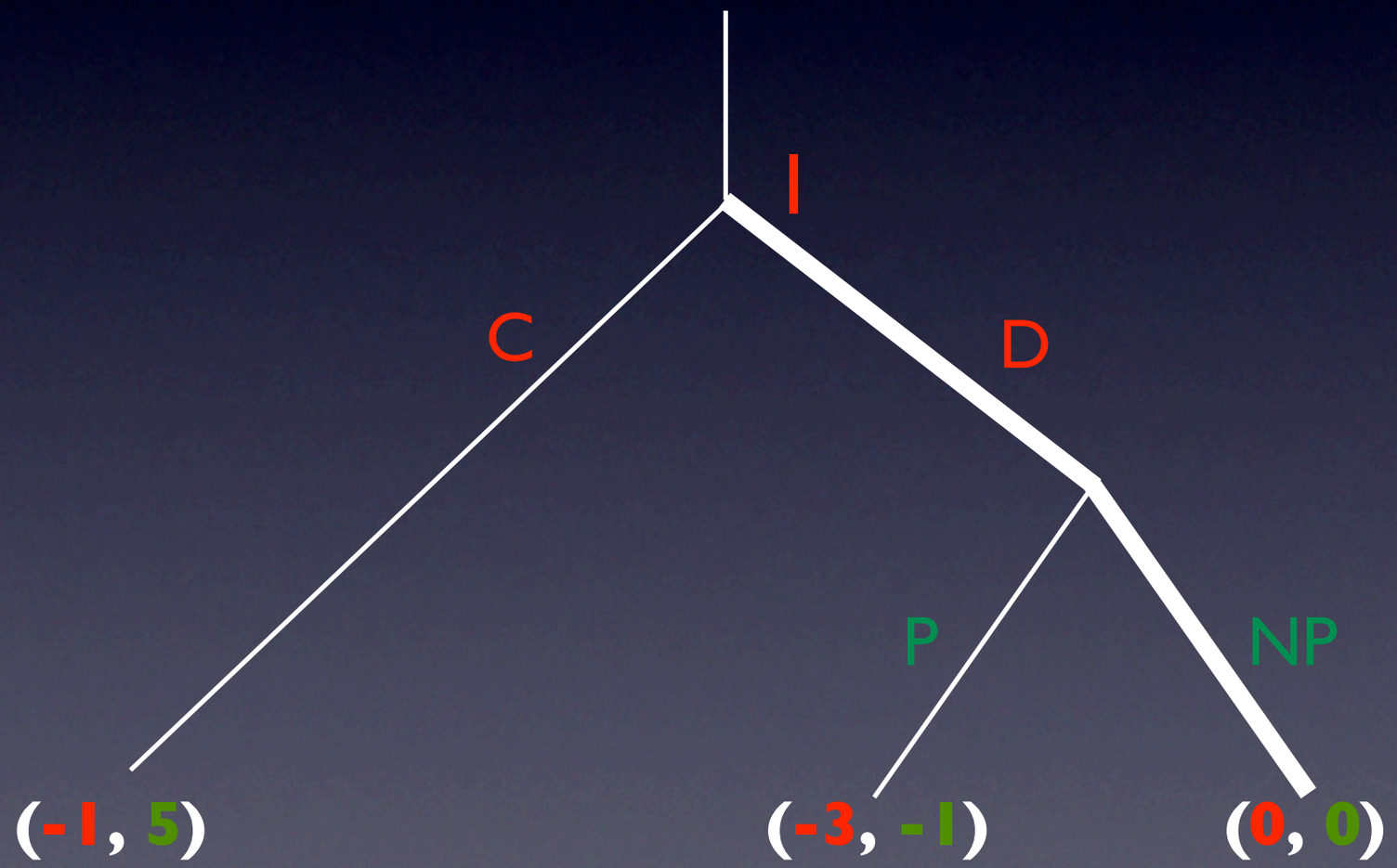
Subgame perfection

- Example: cooperate and punish



Subgame perfection

- Example: cooperate and punish

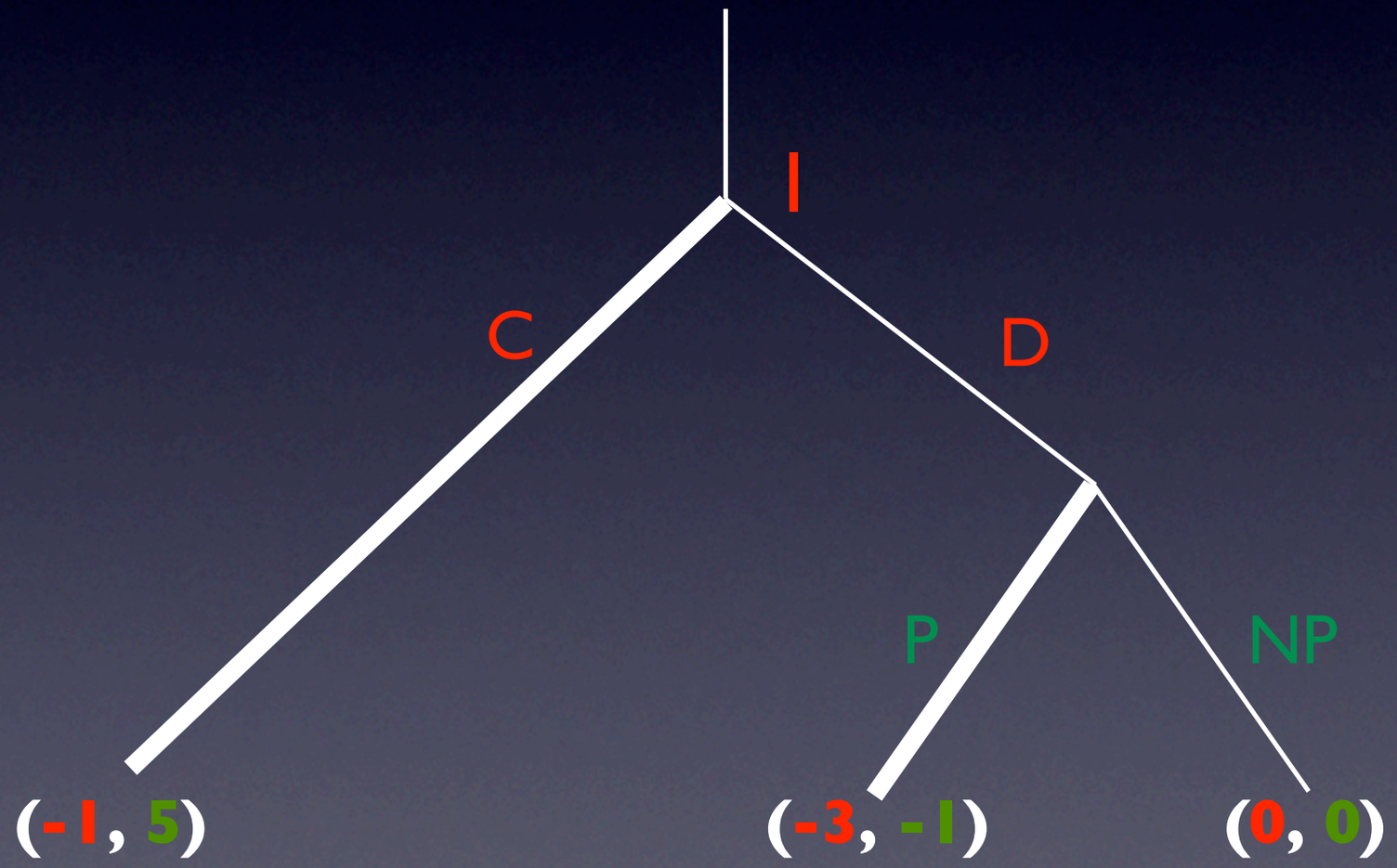


First Nash:

D, NP

Subgame perfection

- Example: cooperate and punish

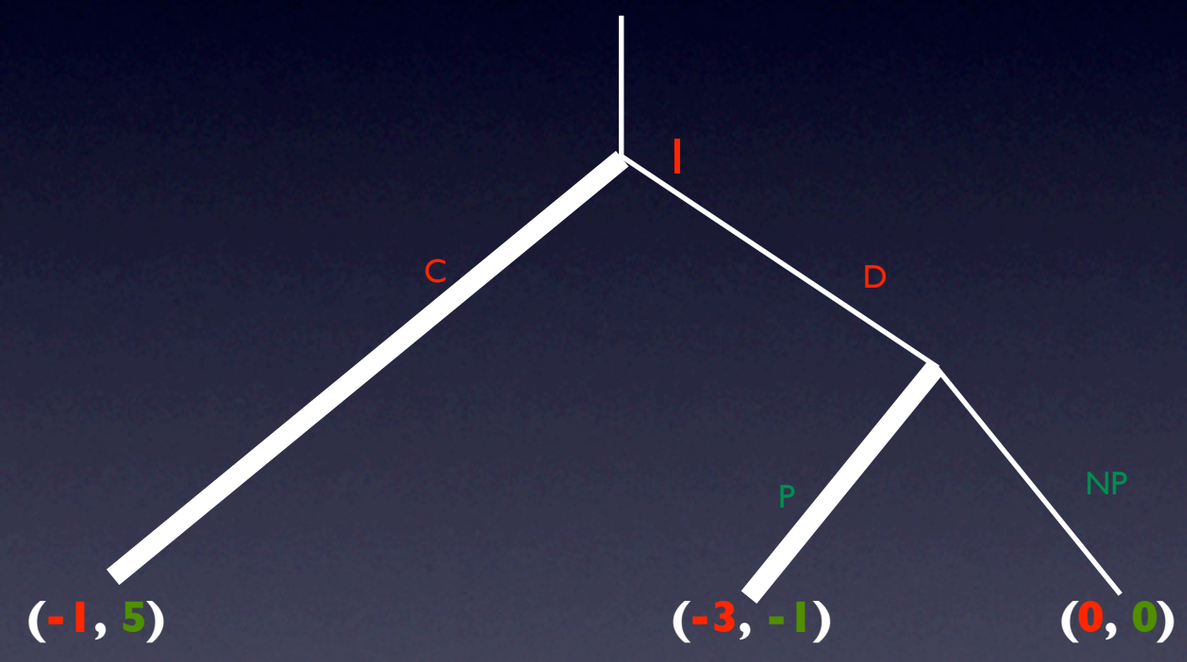


Second Nash:

C, P

Subgame perfection

- Example: cooperate and punish



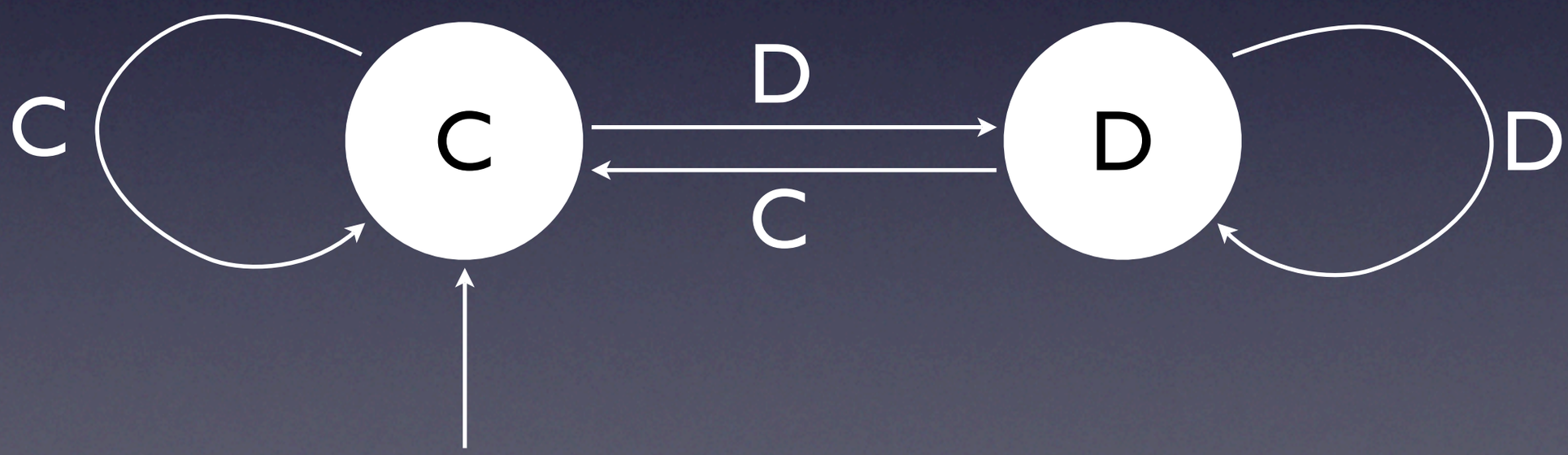
cooperation is adaptive
because punishment *would* occur

yet, punishment is adaptive
only because it *never* occurs

(C, P) is Nash
but not subgame perfect

Grim

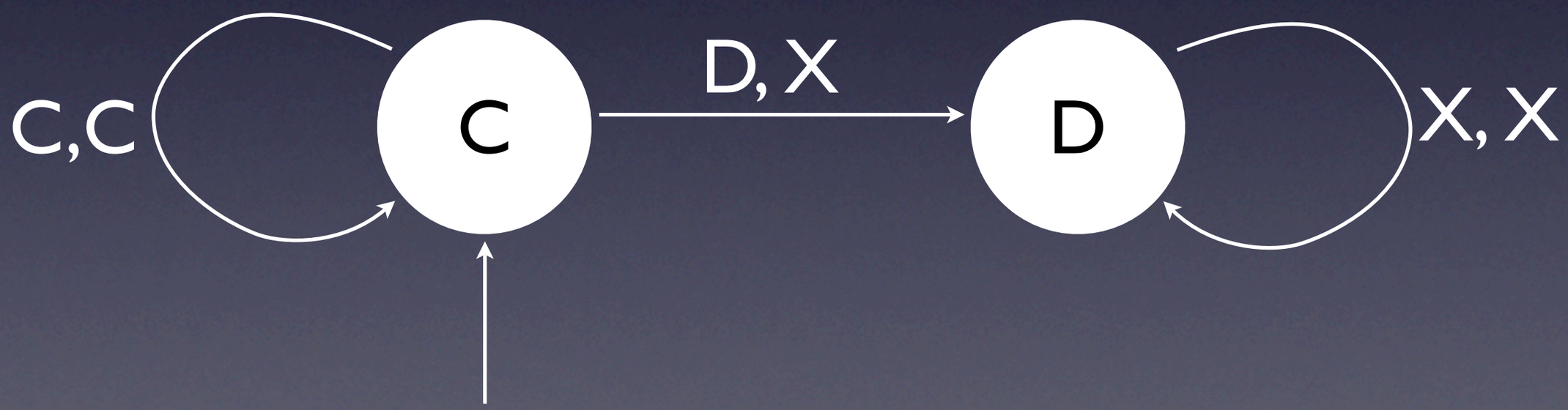
always cooperate unless one of the two players has defected in the past



Trivers 1971 ; Axelrod and Hamilton 1981

Grim

always cooperate unless one of the two players has defected in the past



Trivers 1971 ; Axelrod and Hamilton 1981

Grim

- Grim is Nash equilibrium and NSS
- Grim is subgame perfect
- Stabilized by an infinite loop of retaliation

cooperation is *possible* with reciprocity

... but is not certain

- cooperation can be stabilised by reciprocity
- but anything else can also be stabilised
  (this is called the folk theorem)

the multiplicity of equilibria

an example: **Grim**

always cooperate
unless oneself or one's partner has defected in the past

the multiplicity of equilibria

an example: **Grim**

always cooperate
unless oneself or one's partner has defected in the past

C C C C C C C C C C C C C C C C C C C C

Grim stipulates maximal and fair cooperation

the multiplicity of equilibria

but other strategies can be stable,
differing with regard to

(i) the intensity of cooperation

(ii) the fairness of cooperation

the amount of cooperation

here is an other example: **pair-Grim**

*always cooperate on **pair** days*

*unless someone has defected in the past on a **pair** day*

C D C D C D C D C D C D C D C D
C D C D C D C D C D C D C D C D

pair-Grim is a Nash equilibrium, a neutrally stable strategy,
a Subgame perfect equilibrium, a limit ESS.

the amount of cooperation

impair-Grim

D C D C D C D C D C D C D C D C D C
D C D C D C D C D C D C D C D C D C

impair-Grim is a Nash equilibrium, a neutrally stable strategy,
a Subgame perfect equilibrium, a limit ESS.

the amount of cooperation

monday-Grim

C D D D D D D C D D D D D D C D
C D D D D D D C D D D D D D C D

monday-Grim is a Nash equilibrium, a neutrally stable strategy,
a Subgame perfect equilibrium, a limit ESS.

the amount of cooperation

never-Grim (aka AllD)

D D D D D D D D D D D D D D D D
D D D D D D D D D D D D D D D D

AllD is a Nash equilibrium, a neutrally stable strategy,
a Subgame perfect equilibrium, a limit ESS.

the fairness of cooperation

- in all real life cases partners differ,
  if only with regard to an arbitrary variable
- this makes still other strategies possible

the fairness of cooperation

asymmetric-Grim-1

C C C C C C C C C C C C C C C C
C D C D C D C D C D C D C D C D

asymmetric-Grim-1 is a Nash equilibrium, a neutrally stable strategy,
a Subgame perfect equilibrium, a limit ESS.

the fairness of cooperation

asymmetric-Grim-2

C D D C D D C D D C D D C D D C
C C C C C C C C C C C C C C C C

asymmetric-Grim-2 is a Nash equilibrium, a neutrally stable strategy,
a Subgame perfect equilibrium, a limit ESS.

Folk theorem

Any *individually rational* feasible payoff profile can be reached in a subgame perfect equilibrium

Reciprocity is under-determined
(punishment as well)

see e.g. Aumann and Shapley 1976

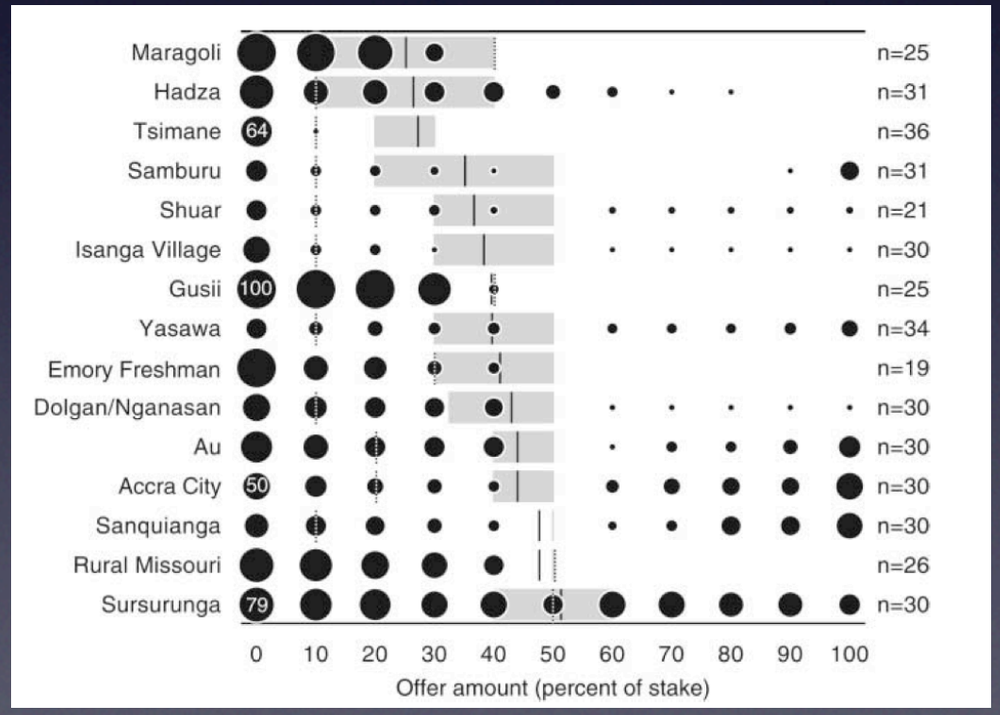
other forms of reciprocity

- generalized reciprocity
- image scoring and standing strategies
- biological markets
- punishment

coopération - quelques données

théorie des jeux expérimentale

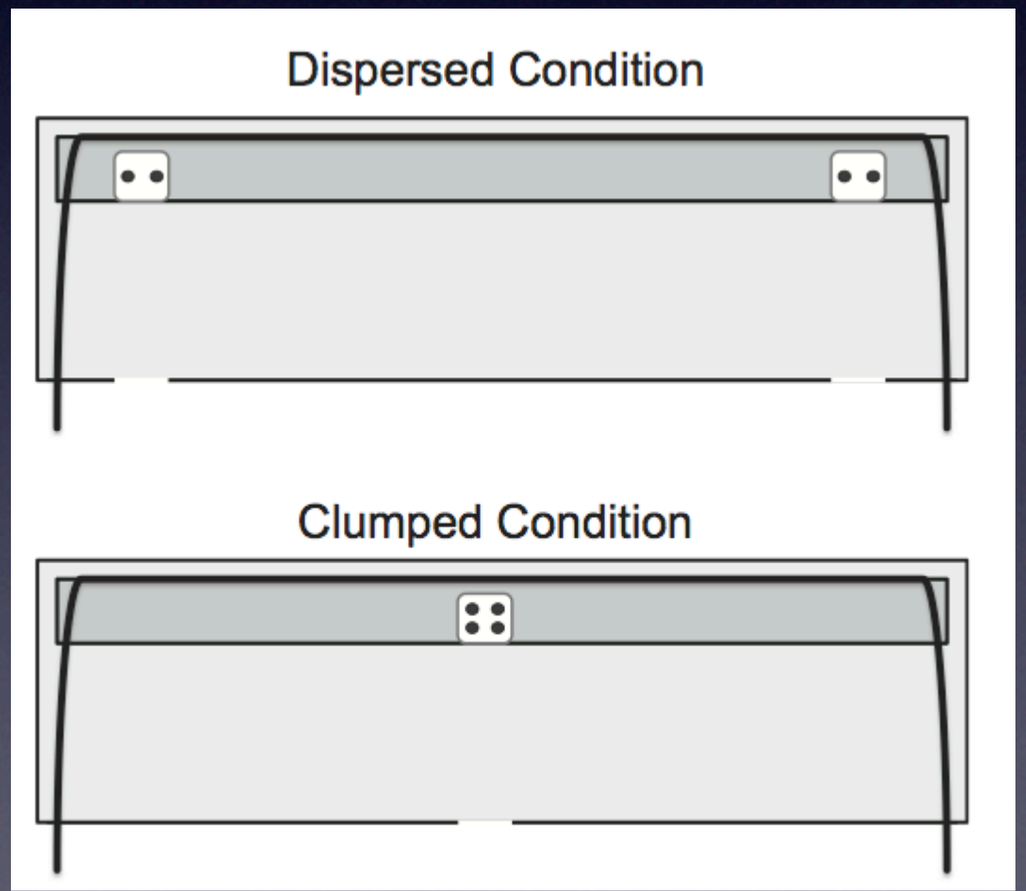
- jeu de l'ultimatum et du dictateur
- Résultats de Joseph Henrich

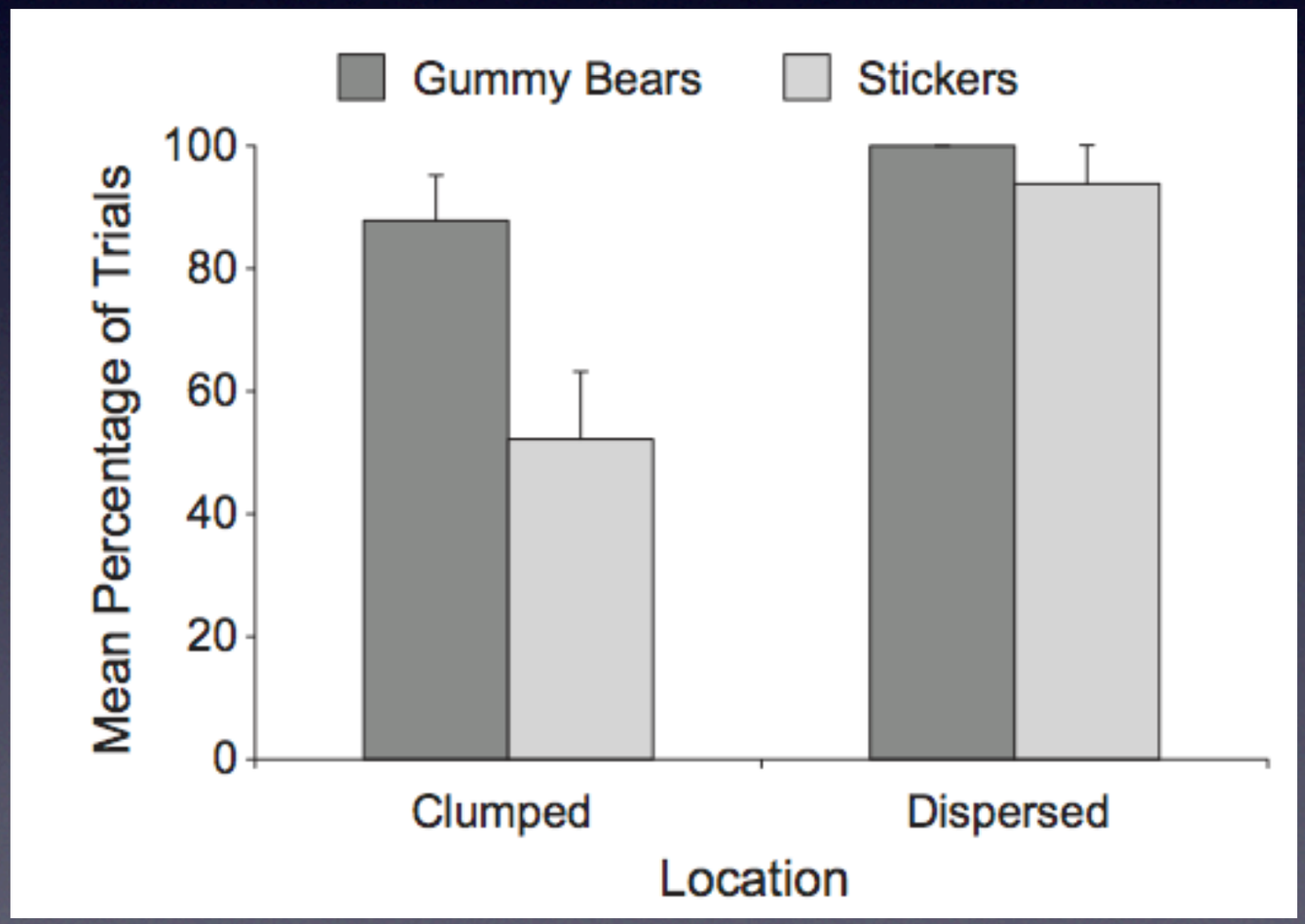


psychologie du développement

Young Children Share the Spoils After Collaboration

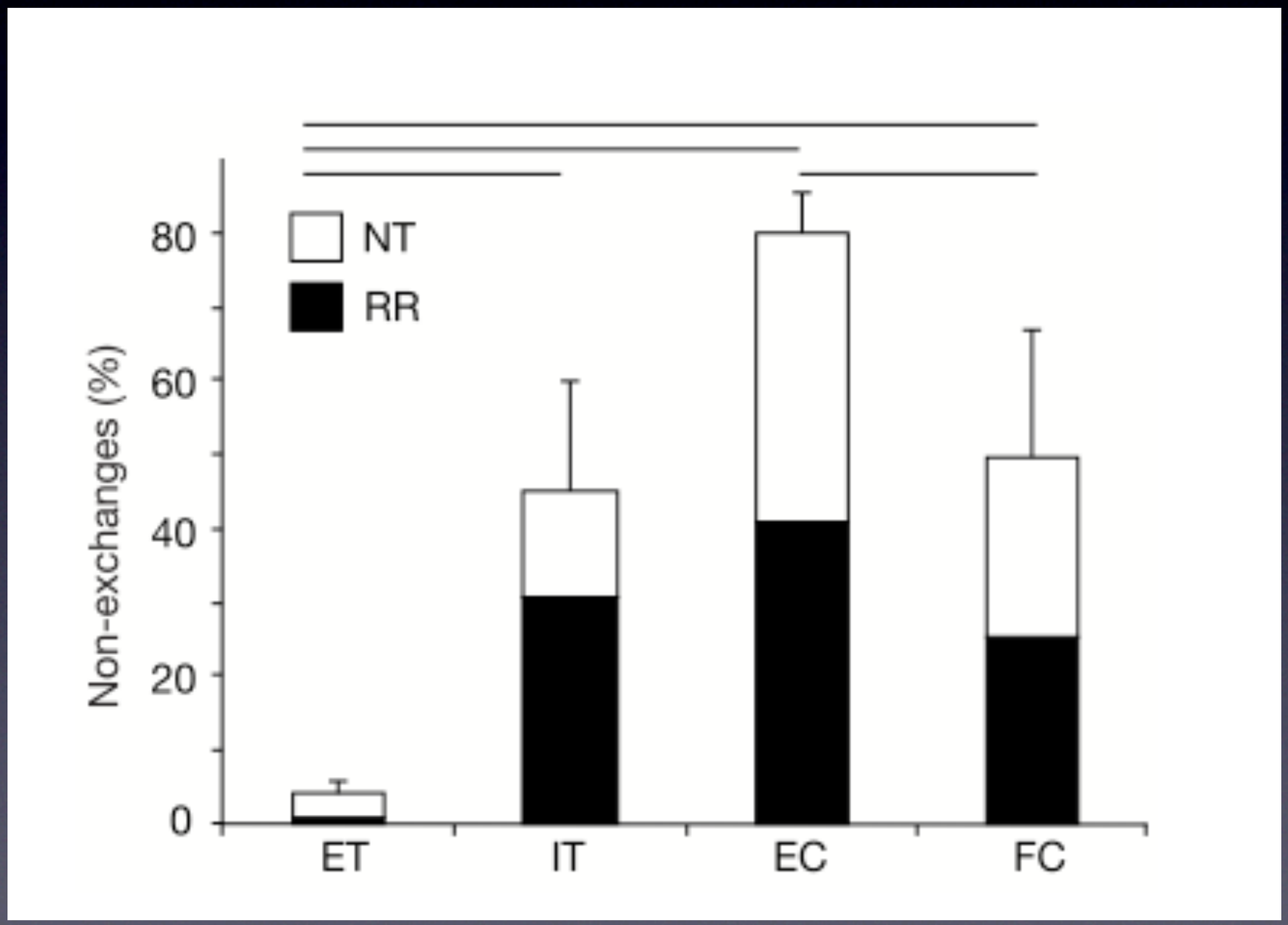
Warneken, Lohse, Melis & Tomasello, *Psychological Science*, 2010





Monkeys reject unequal pay

Sarah F. Brosnan & Frans B. M. de Waal



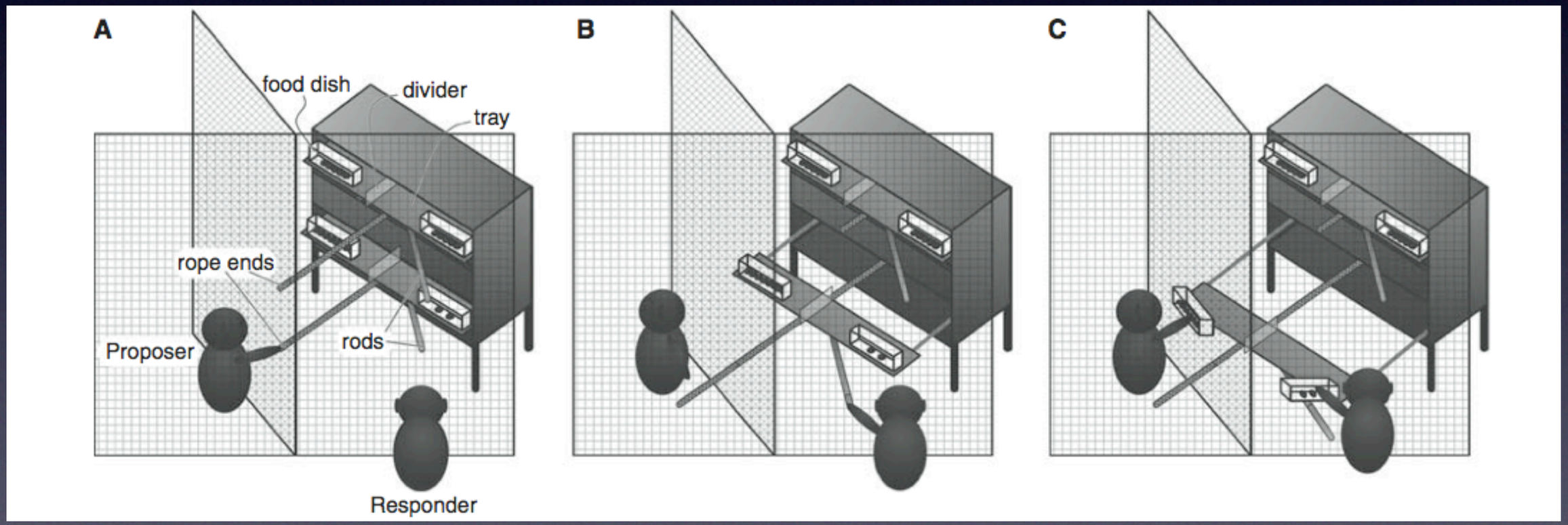
Brosnan et de Waal 2003 (capucins)

Chimpanzees are indifferent to the welfare of unrelated group members

Joan B. Silk[1], Sarah F. Brosnan[2,3], Jennifer Vonk[4], Joseph Henrich[2], Daniel J. Povinelli[4], Amanda S. Richardson[3], Susan P. Lambeth[3], Jenny Mascaro[3] & Steven J. Schapiro[3]

Chimpanzees Are Rational Maximizers in an Ultimatum Game

Keith Jensen,* Josep Call, Michael Tomasello



Chimpanzees Are Rational Maximizers in an Ultimatum Game

Keith Jensen,* Josep Call, Michael Tomasello

Game	Proposer Offers	Payoffs Proposer	Payoffs Responder	Responder Rejections
5/5	39 (75%)	8	2	2 (5%)
	13 (25%)	5	5	0 (0%)
2/8	45 (87%)	8	2	3 (7%)
	7 (13%)	2	8	0 (0%)
8/2	53 (100%)	8	2	6 (11%)
		8	2	
10/0	29 (54%)	8	2	4 (14%)
	25 (46%)	10	0	11 (44%)

évolution culturelle de l'altruisme ?

Kin selection and altruism

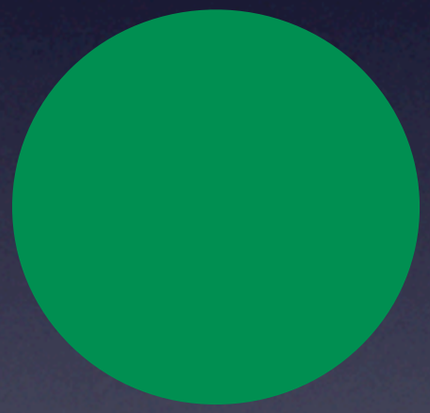
- Altruistic traits are *deleterious* traits, they should never evolve by natural selection
- But altruism can evolve if altruistic individuals interact preferentially with other altruistic individuals

évolution culturelle de l'altruisme ?

- équation de Price et règle de Hamilton
- transmission culturelle affecte R
- transmission culturelle affecte B et C

Sélection culturelle de groupe

Trait social génétique



Sélection culturelle de groupe

Trait social génétique

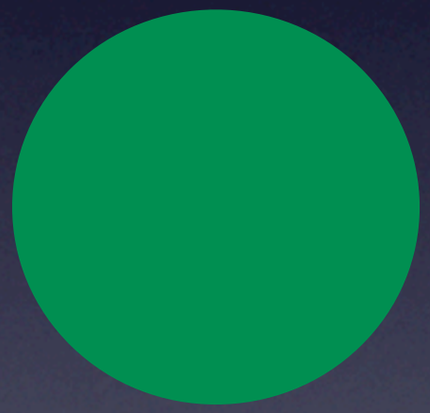
Sélection culturelle de groupe

Trait social génétique

Apparition et fixation de mutants tricheurs

Sélection culturelle de groupe

Trait social culturel



Sélection culturelle de groupe

Trait social culturel

Naissance
ou immigration

Sélection culturelle de groupe

Trait social culturel

Cooperation on graphs

- Individuals interact within a continuous network (based on geography, or other factors)
- Individuals imitate their neighbour according to “payoff-biased” imitation (see later)

Cultural transmission

- Expressing altruism toward a genetically unrelated partner is a *deleterious* trait from the point of view of a gene
- Genes cannot code for such behaviors
- Culture can... but what is controlling cultural transmission?

ex. 1: conformism

- in average the most frequent behaviors are the most efficient
- frequency is a good proxy for efficiency (a simple heuristic)
- but this is a very indirect and unreliable proxy
- Many reasons can bring about a majority of individuals to express maladaptive behaviours

ex. 1: conformism

- e.g., a group can be founded (by chance) by altruistic individuals (helping with no reward)
- individuals mistakenly apply the “conformist heuristic” and become altruistic even though it is a deleterious behavior
- conformism lead to altruism to the precise extent that it is mistaken

ex. 2: payoff-biased imitation

- individuals imitate their neighbors and therefore altruistic individuals tend to be surrounded by other altruists
- altruistic individuals hence reach a larger payoff than selfish individuals, but this is not due to their own action but to their neighbors' actions
- payoff is thus a poor indicator of the efficiency of one's action
- individuals are better off being selfish but they become altruists because they mistakenly imitate high payoff peers

altruism as a by-product

- imitation (conformist, prestige, or payoff-biased) cannot be adaptive for its very effect on altruism
- but it might be adaptive for other reasons
- altruism would thus be an unfortunate by-product of imitation rules evolved for other reasons