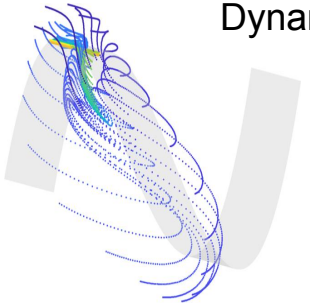
Game Theory of Developmental Processes

	2, 0	1, 0
	0, 1	-1, -1

2-player egg purse shape game
(a hypothetical example)



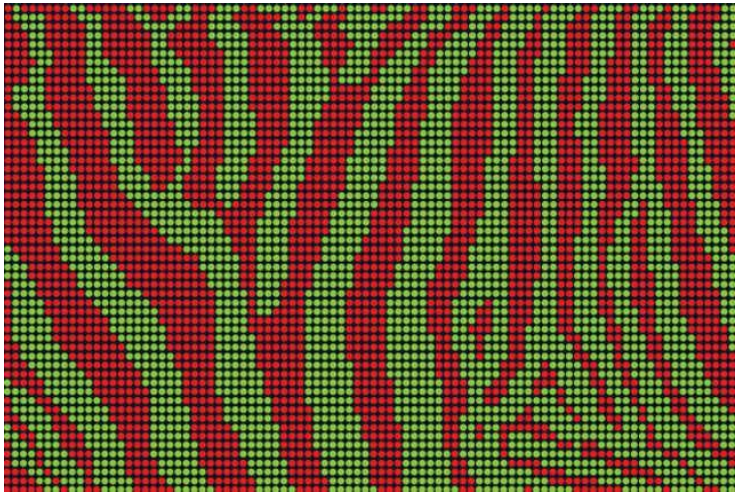
Dynamics Days XL
(2021)

Bradly Alicea

@balicea1

CS06: Games, Development,
and Pattern Formation

Variation, Morphogenesis, and Learning/Adaptation



Developmental Agents

General Case

Agents (taking the form of cells, morphogenesis, gene products) emit states. A developmental game is the strategic interactions of these states.

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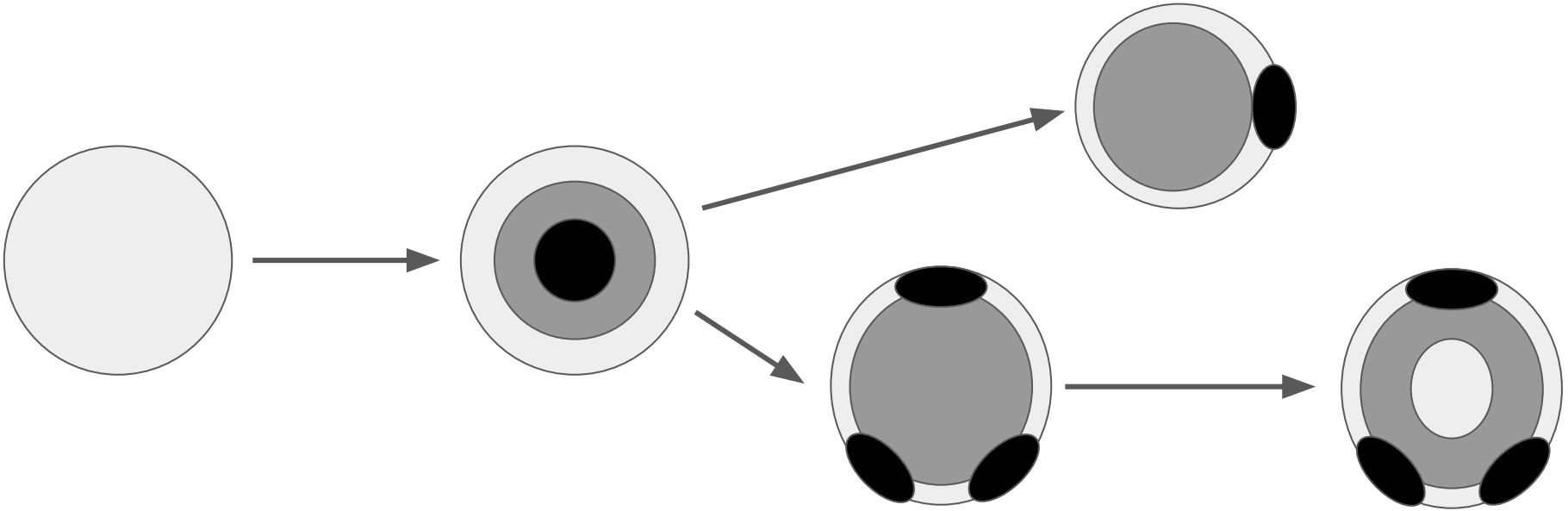


Developmental Agents

General Case

Agents (taking the form of cells, morphogenesis, gene products) emit states. A developmental game is the interactions of these states.

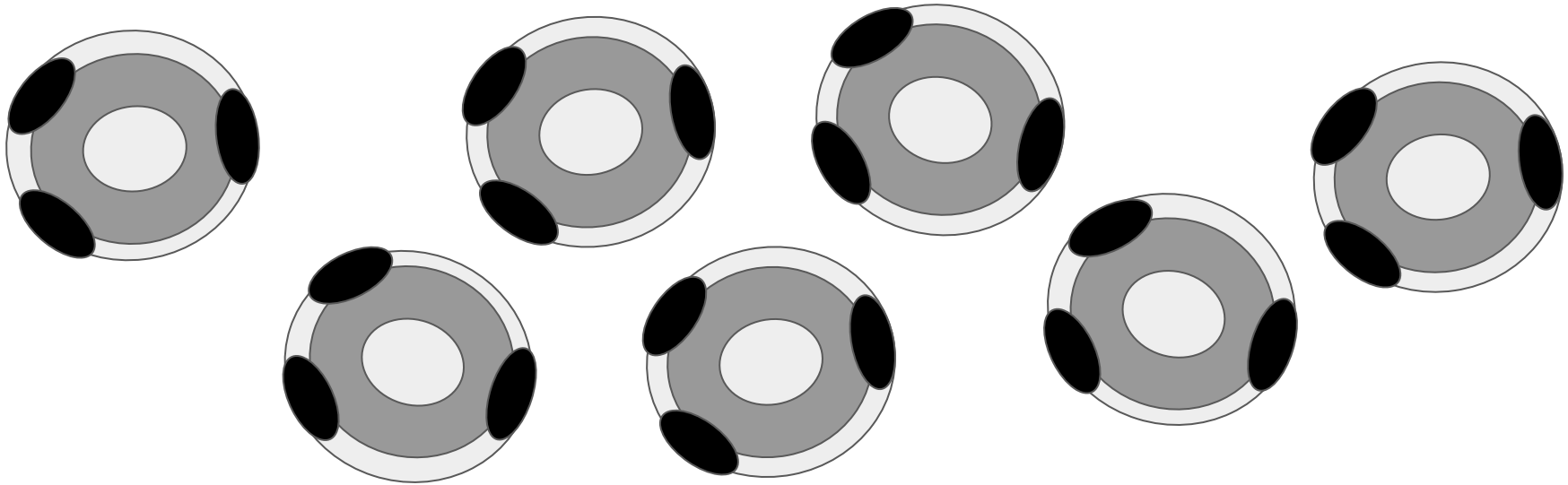
Ontogenetic Agents

Specific Case

Does not use cognition to execute behaviors -- instead intentional strategies are related to transformational processes (movement, differentiation, growth, and regulation).

Coordination Between Ontogenetic Agents

Coordination can result from collective behavior over time, or perfect coordination can be assumed *a priori*.



Developmental Tradeoffs

Model the internal state of an ontogenetic agent.

- agent needs to maximally conserve energy, invest in one set of strategies over another.

Energetic scarcity can lead to pure strategy suite (only a single strategy employed).

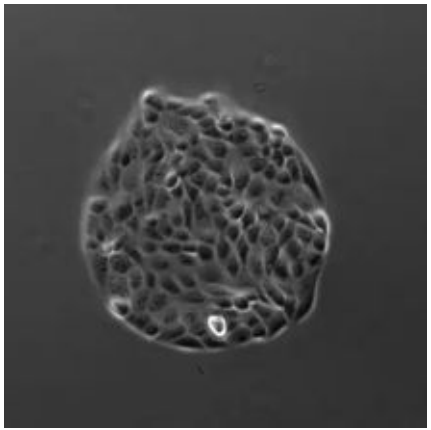
Can also change the composition of different agents (heterogeneity).

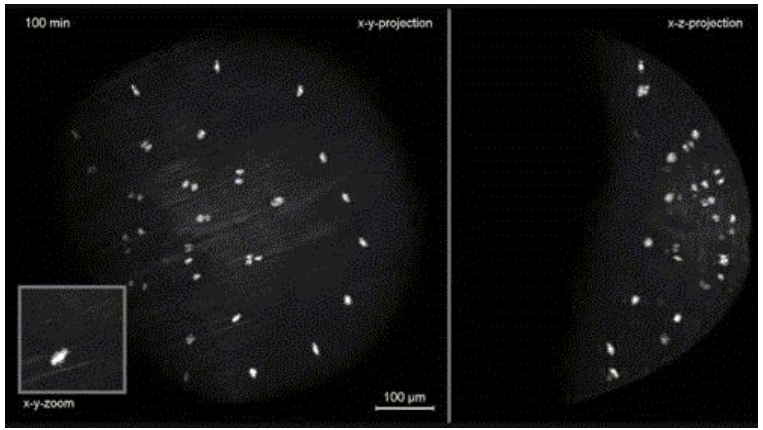
- ontogenetic agents with more available energy have greater degree of complexity, with capacity for a greater number of strategies.

Biological Intentionality

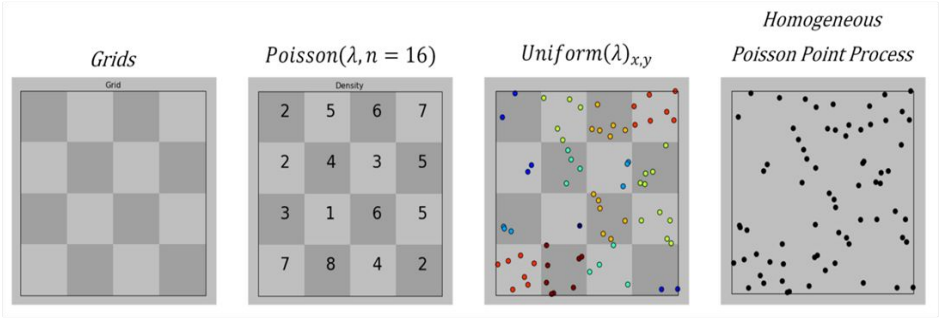
Rather than assume goal-directed behavior among the ontogenetic agents, bio-intentionality is a means to achieve some functional imperative or to improve individual fitness.

- examples include phenotypic plasticity, cell migration, and excitation/inhibition circuits.





0-player Games



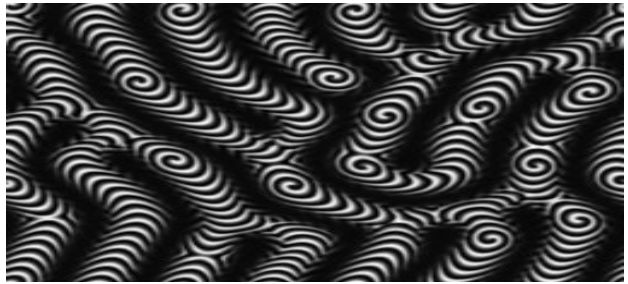
Stack Exchange: How to generate nD point processes
https://stats.stackexchange.com/questions/16282/how-to-generate-nd-point-process

Example: Conway's Game of Life (GoL).

Cells operate as a point process that emit a state of "dead" or "alive".

- have only an indirect influence on spatial dimensionality, lifelike attributes captured in these dimensions.

0-player Games



Example: Conway’s Game of Life (GoL).

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Application to Development

- Turing morphogenesis (reaction-diffusion), where particles compose a population of 0-dimensional agents, and morphogens act indirectly to transform population into a spatial pattern.

- equilibrium is reached when a stable morphogenetic pattern is achieved.

0-player game Payoff Matrix

With this payoff structure, cell will tend to stay “alive”.

Payoff to stay alive increases when particle is part of a pattern.

Alive	**Dead**
0.8	0.2

Asymmetric payoff is determined by information (local biochemistry, global fitness).

0-player game Payoff Matrix

With this payoff structure, cell will tend to stay “alive”.

Payoff to stay alive increases when particle is part of a pattern.

Alive	Dead
0.8	0.2

With this payoff structure, cell will vacillate between “dead” and “alive” (equiprobable).

Alive	**Dead**
0.5	0.5

1-player Games

Example: Game Against Nature.

An ontogenetic agent will play an intentional strategy against a quasi-random natural process (e.g. weather, entropy).

- payoff structure will be solely dependent upon a process-driven objective (e.g. increase in fitness, maximization of error correction).

Application to Development

- generic developmental processes as a game of developmental Minesweeper.

Game Against Nature

Single rational player plays a *pure* or *mixed* against nature (*random*, *mixed* strategy). Strategy: carry an umbrella (U) or not (N).

Random generator of discrete states.

Forecast is imperfect information, informs deployed strategy by other opponent.

Observer Strategy	U	N	N	U	U	U	N
Payoff	0	1	-1	1	1	0	1

Developmental Minesweeper

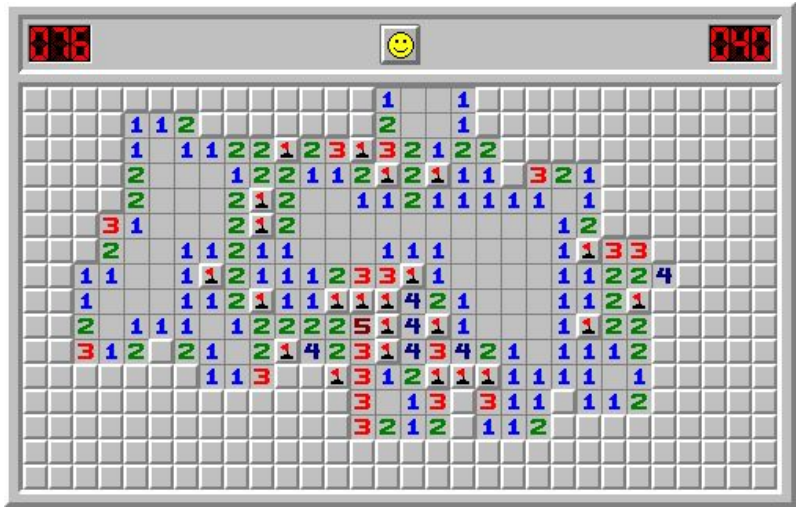
Minesweeper as a game between nature and a single ontogenetic agent:

Mines: lethal mutations.

- nature places lethal mutations in a 2-D genome, ontogenetic agent is blind to these locations.

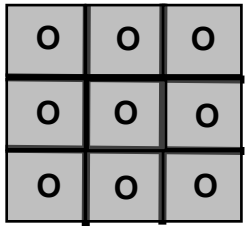
Null Squares: degrees of freedom.

- We can also add in other information to be uncovered, ontogenetic agent is also blind to these features.



2-player Games

Example: Naughts and Crosses (Tic-Tac-Toe)

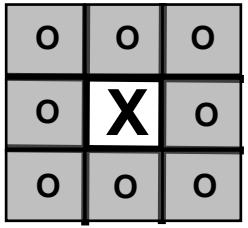


First-mover advantage:

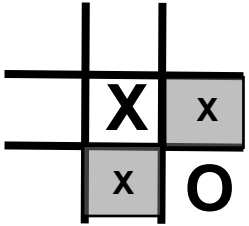
- Timing of cell division and differentiation: first cells/cell lineages to differentiate determines subsequent activities in the embryo.

- (biological) Stackleberg equilibrium: optimal play + first-mover advantage = no clear winner. No one cell lineage or type dominates.

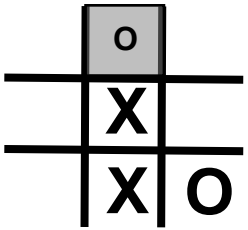
First Move



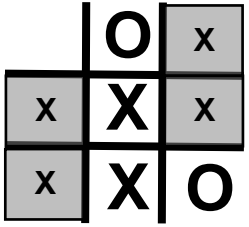
Second Move



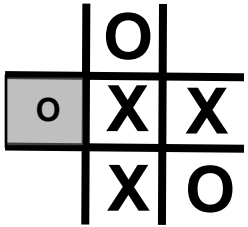
Third Move



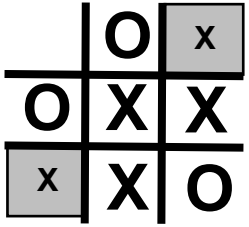
Fourth Move



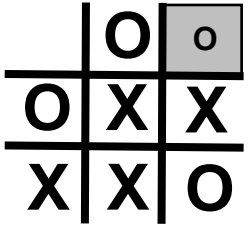
Fifth Move



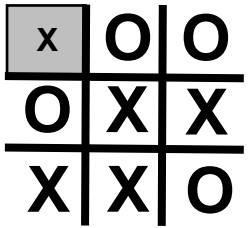
Sixth Move



Seventh Move

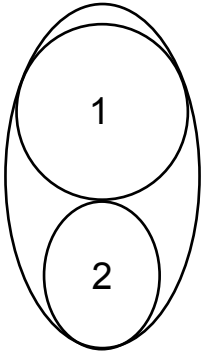


Eighth Move

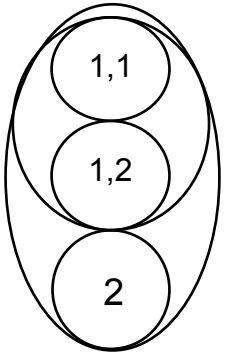


Stone et.al, *Biosystems*, 173, 73-82 (2018).

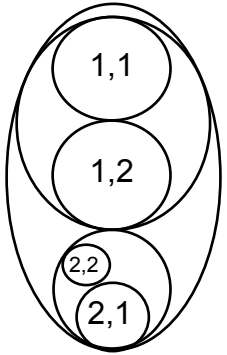
First Move



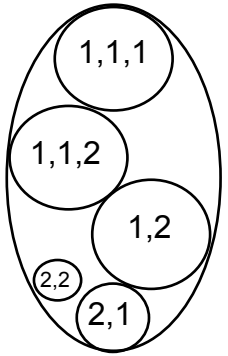
Second Move



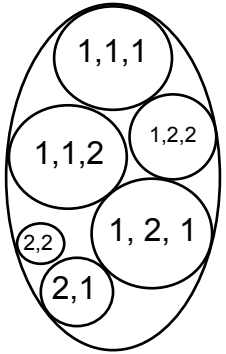
Third Move



Fourth Move



Fifth Move



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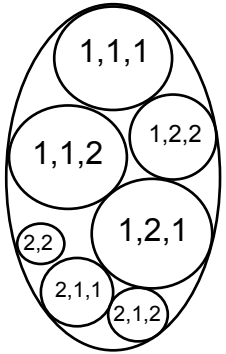
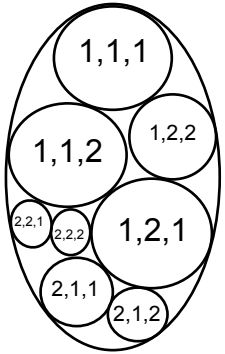


Seventh Move



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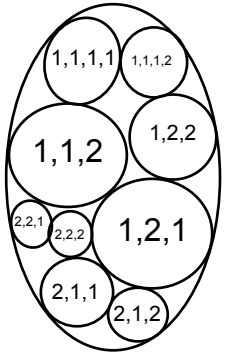
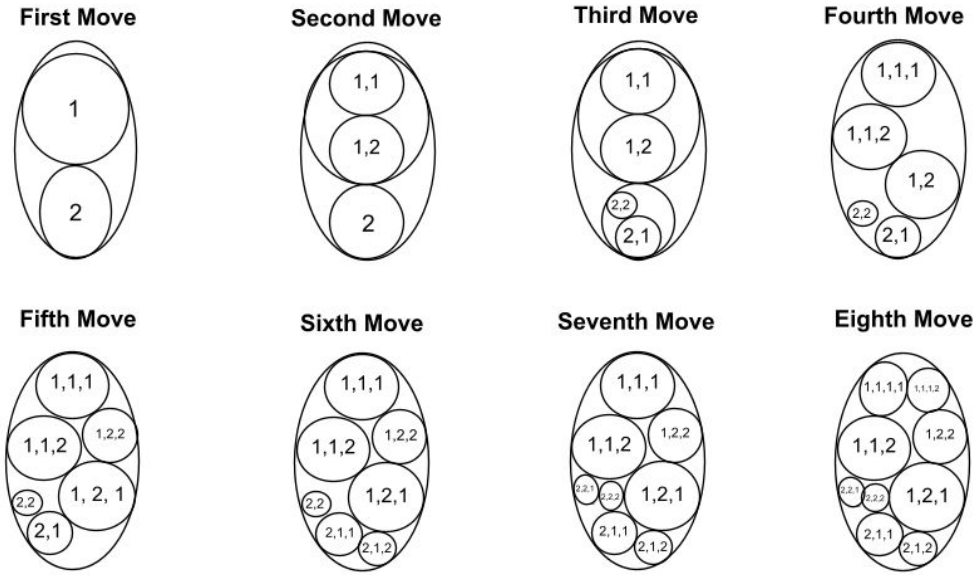




Stone et.al *BioSystems*, 173, 73-82 (2018)

Embryo can also be analyzed as a first-mover (Stackleberg) game:

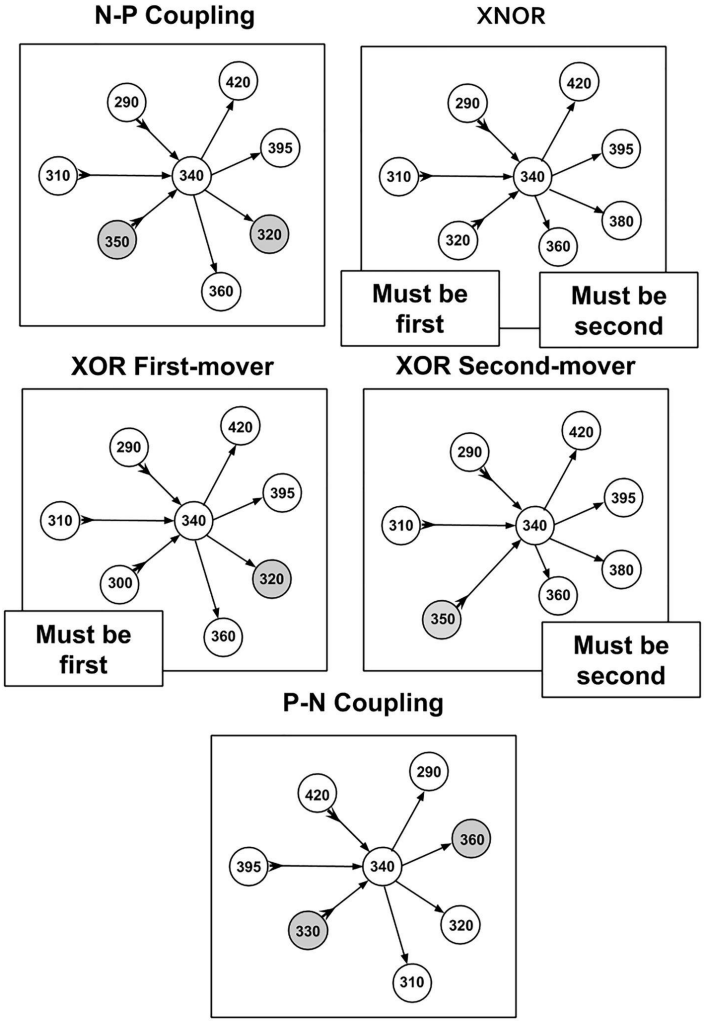
- advantages are in terms of size, for differentiated tissues it could be in terms of function, structure.

Sublineage 1 and 2 are established, 1 has a size/position advantage.

Second move: sublineage 1 mother divides before 2, advantage (leader).

Third move: sublineage 2 mother divides (folllower).

Fourth move: another division event in sublineage 1, further advantage for 1.



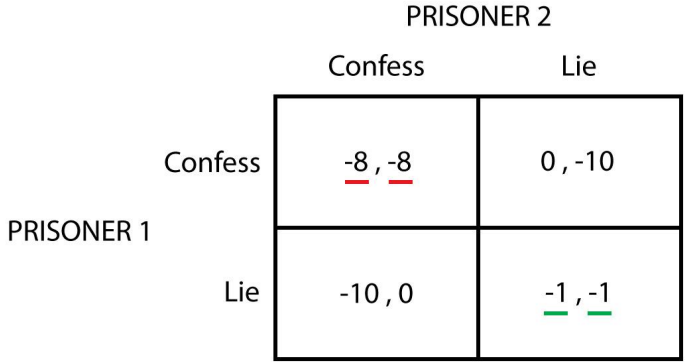
First-player Dynamics in Connectome Formation

Analyze synaptic connectivity data in *C. elegans* using first-mover model (Stackleberg competition)

- potential pre- and post-synaptic relationships.
- yield various strategies for establishing connections.

Alicea, *Frontiers in Cellular Neuroscience*, 14, 524791. (2020).

2-player Games



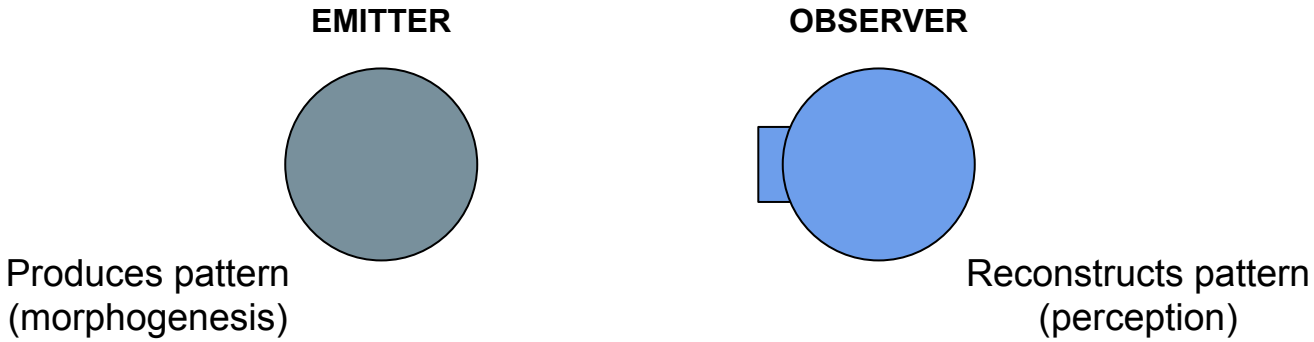
Example: Prisoner's Dilemma (PD) and Iterated PD

Individual vs. group incentives:

- defect to seek maximization of individual payoff (but often suboptimal), cooperate to maximize pairwise (or group) payoff.
- in Iterated PD case, game is played repeatedly (dynamically).

Application to development:

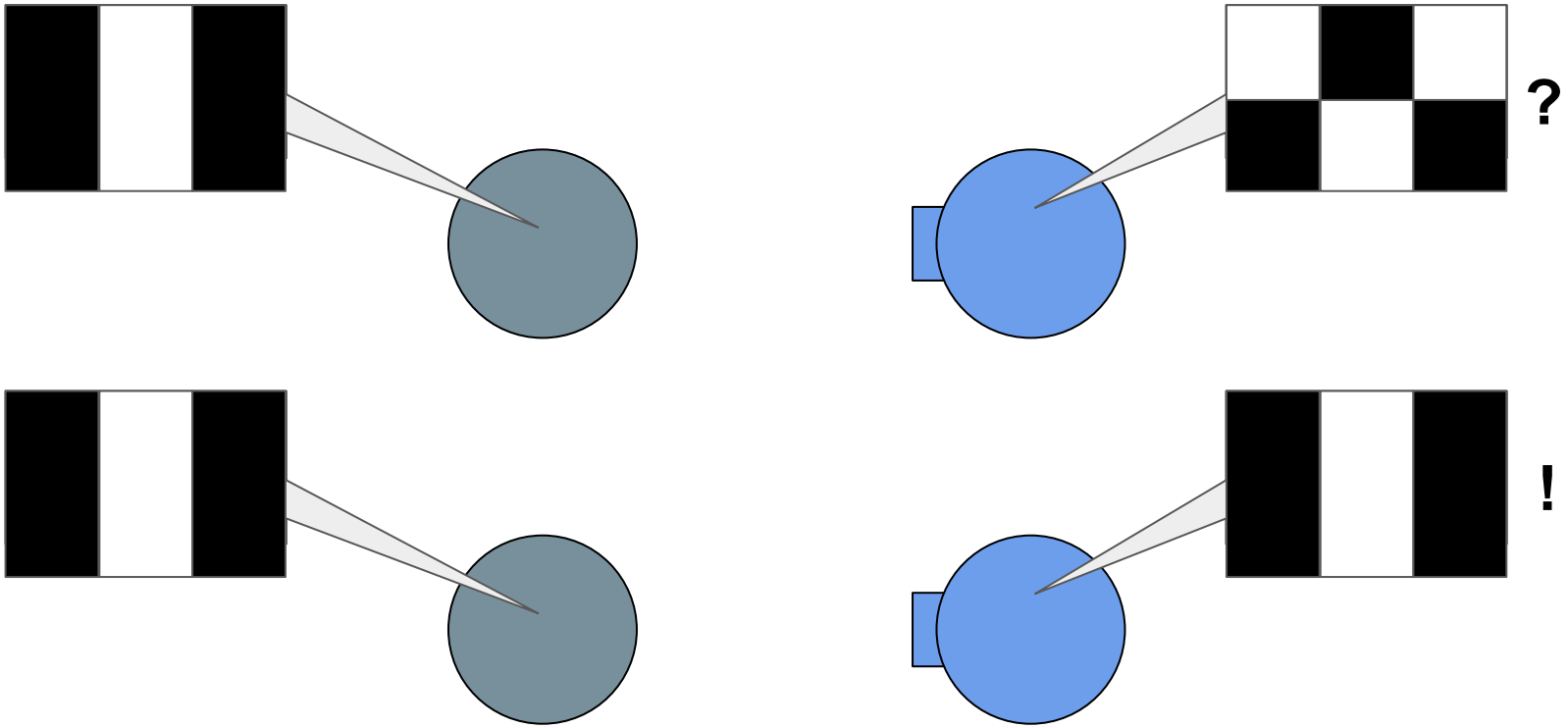
- A pair of ontogenetic agents with complementary mechanisms (pattern recognition, pattern formation).



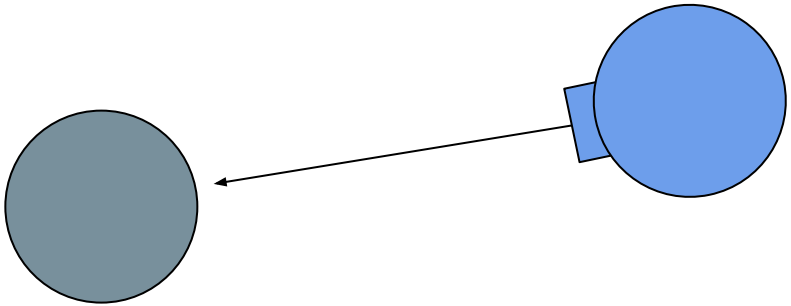
What is the relationship between morphogenesis and perception?

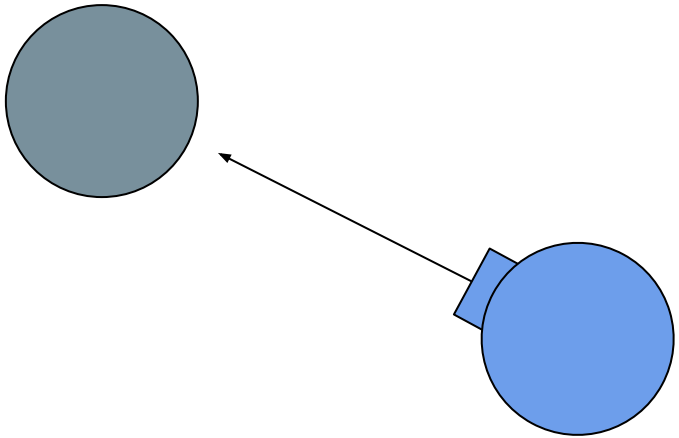
Using this model, we can treat this as either a predator-prey relationship, or a competitive/cooperative game.

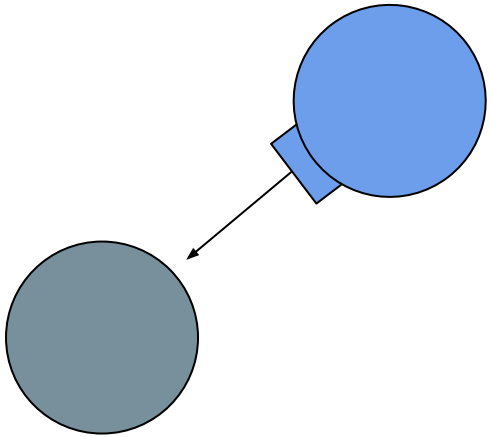
- pareidolia (perception/morphogenetic coevolution), camouflage (matching pursuit game).
- predator hunts prey (prey must conceal itself), or prey is dangerous to predator (kills with venom).



Pursuit-evation game (distinct from a PD game) when observer tries to identify partial phenotypes, while the emitter tries to conceal its phenotype as a coherent pattern.





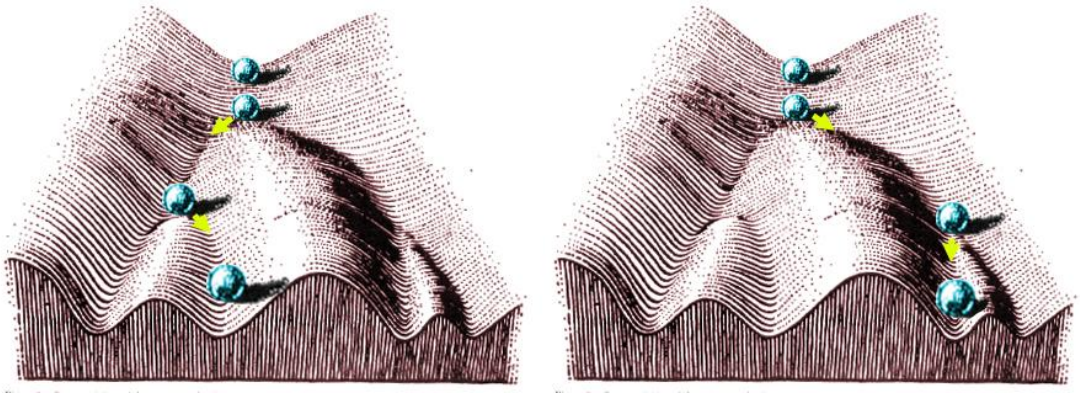


Interesting connections between the pursuit-evasion utility function (iterative payoffs) and Reinforcement Learning.

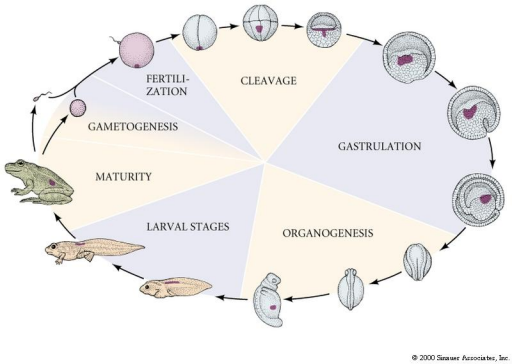
Developmental Stable States (DSS)

Evolutionary Stable States: given perturbations, a set of strategies can be found that return system to initial state and resist invasion by mutant strategies.

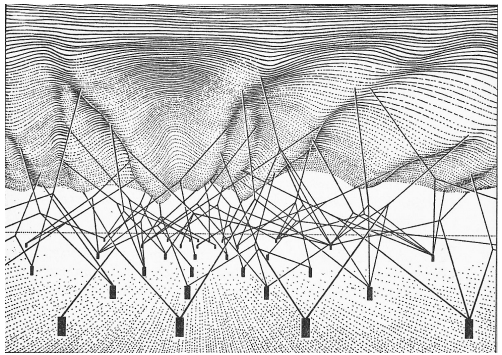
Developmental Stable States might work in a similar manner, and mimic the canalization of development proposed by Waddington.

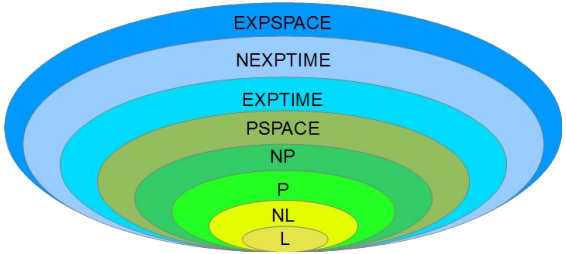


A route to understanding combinatorial complexity

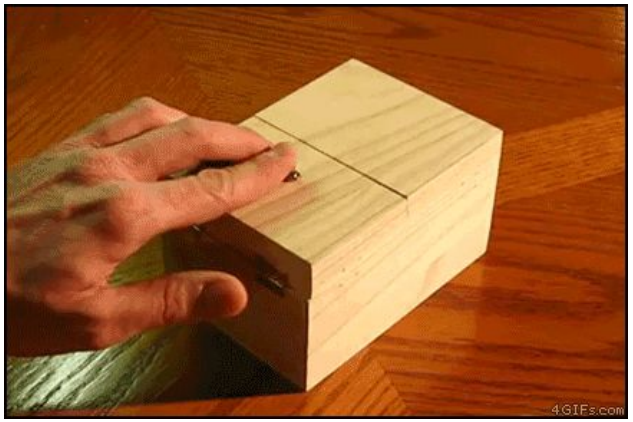


Epigenetic Landscape





Thanks for your Attention!



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