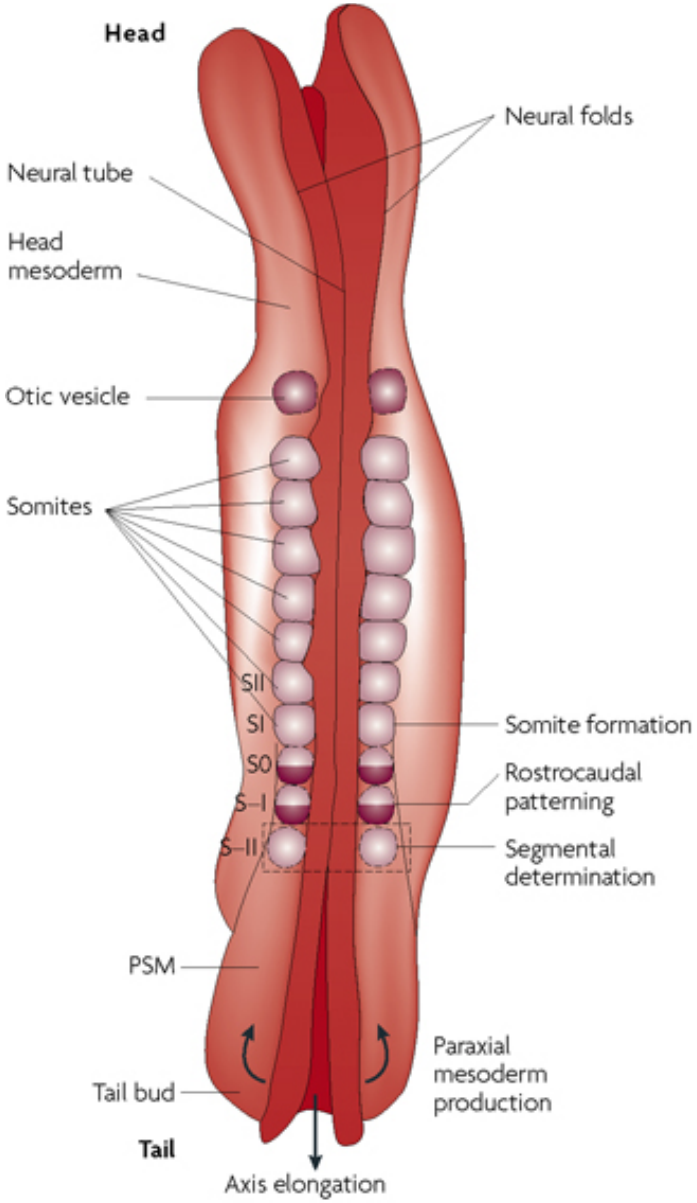
E.
Segmentation

(in embryological development)

Vertebrae

- Humans: 33, chickens: 55, mice: 65, corn snake: 315
- Characteristic of species
- How does an embryo “count” them?
- “Clock and wavefront model” of Cooke & Zeeman (1976)



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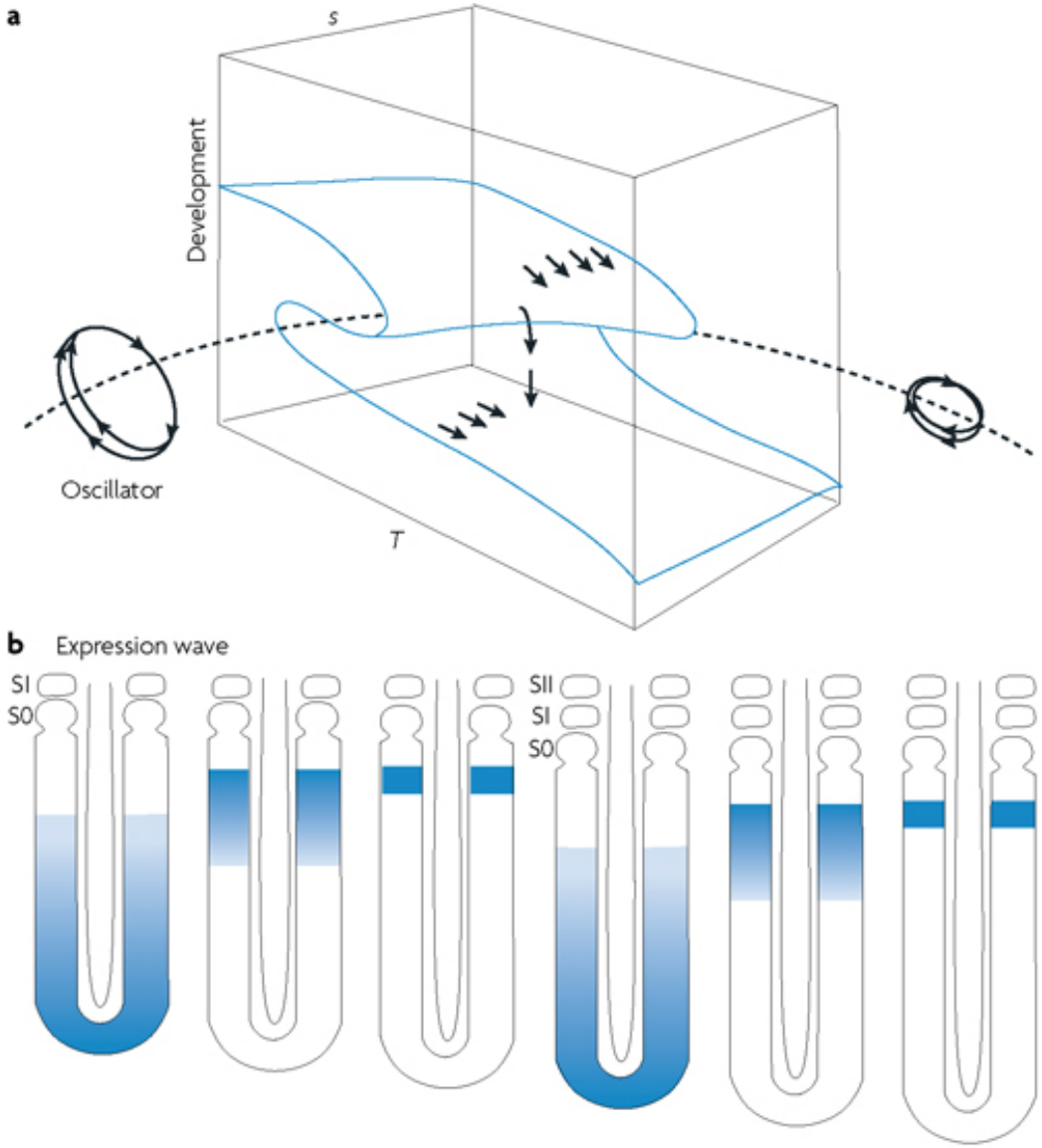
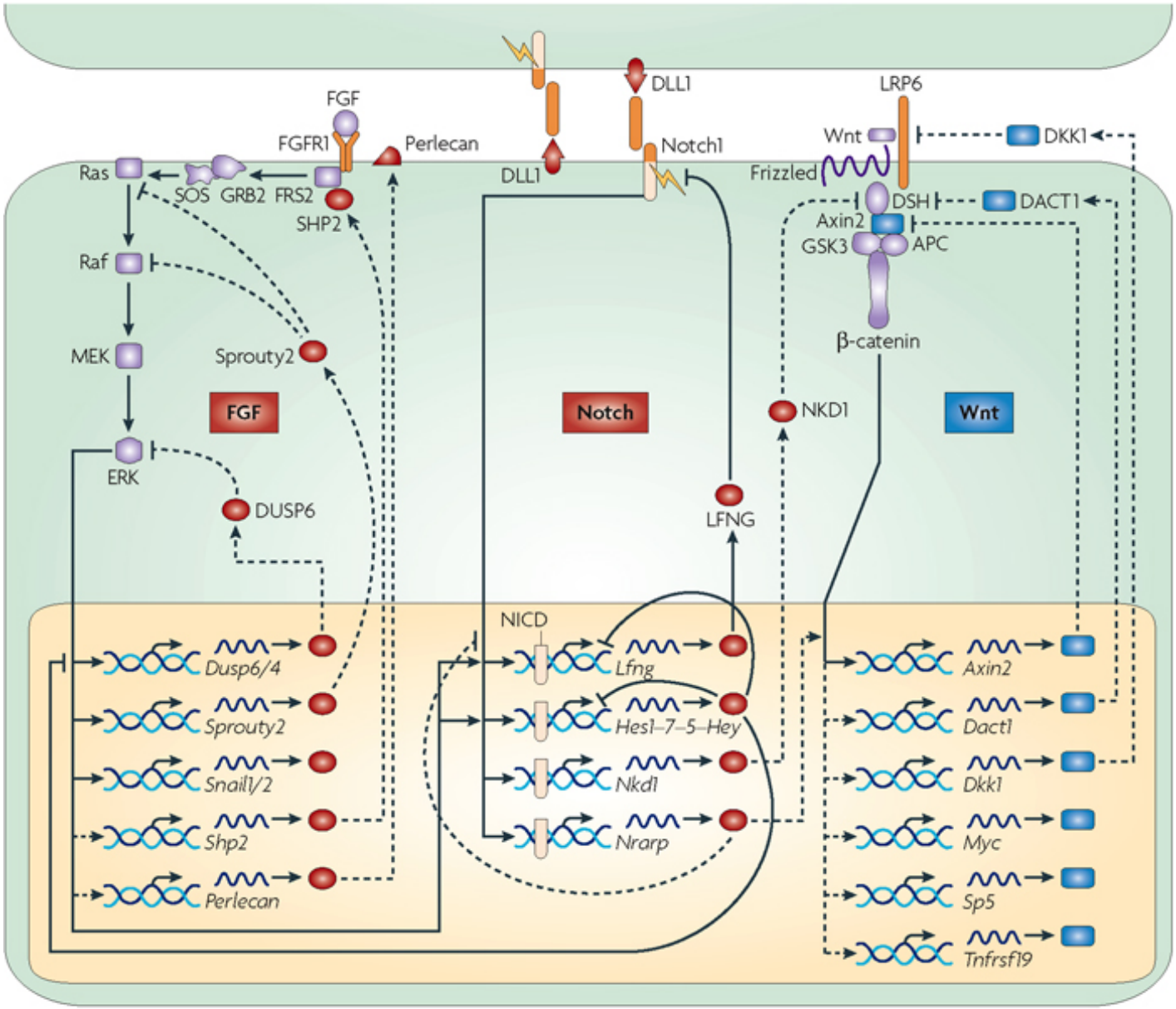

a
S
Development
Oscillator
T
b
Expression wave
SI
S0
SII
SI
S0



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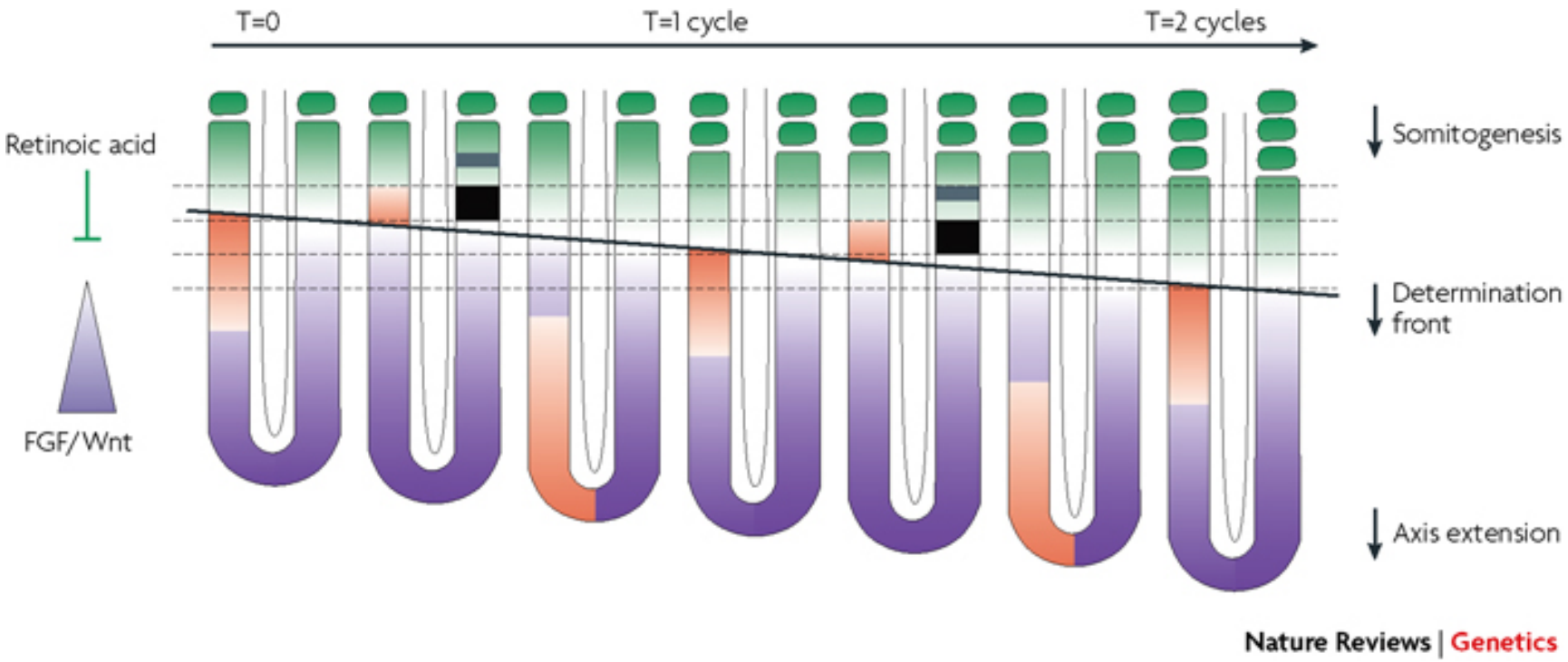
T=0
T=1 cycle
T=2 cycles
Retinoic acid
FGF/Wnt
Somitogenesis
Determination front
Axis extension
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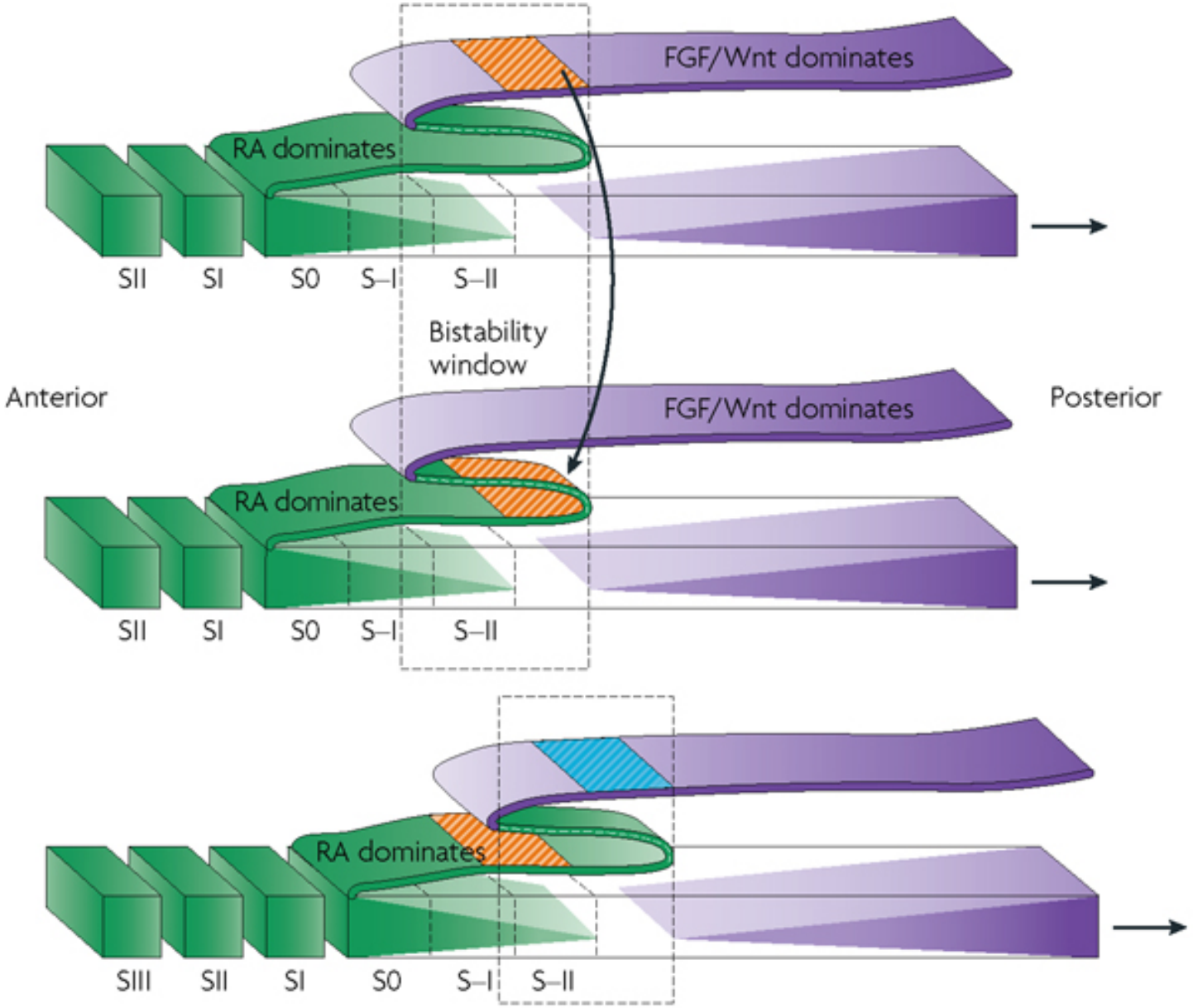
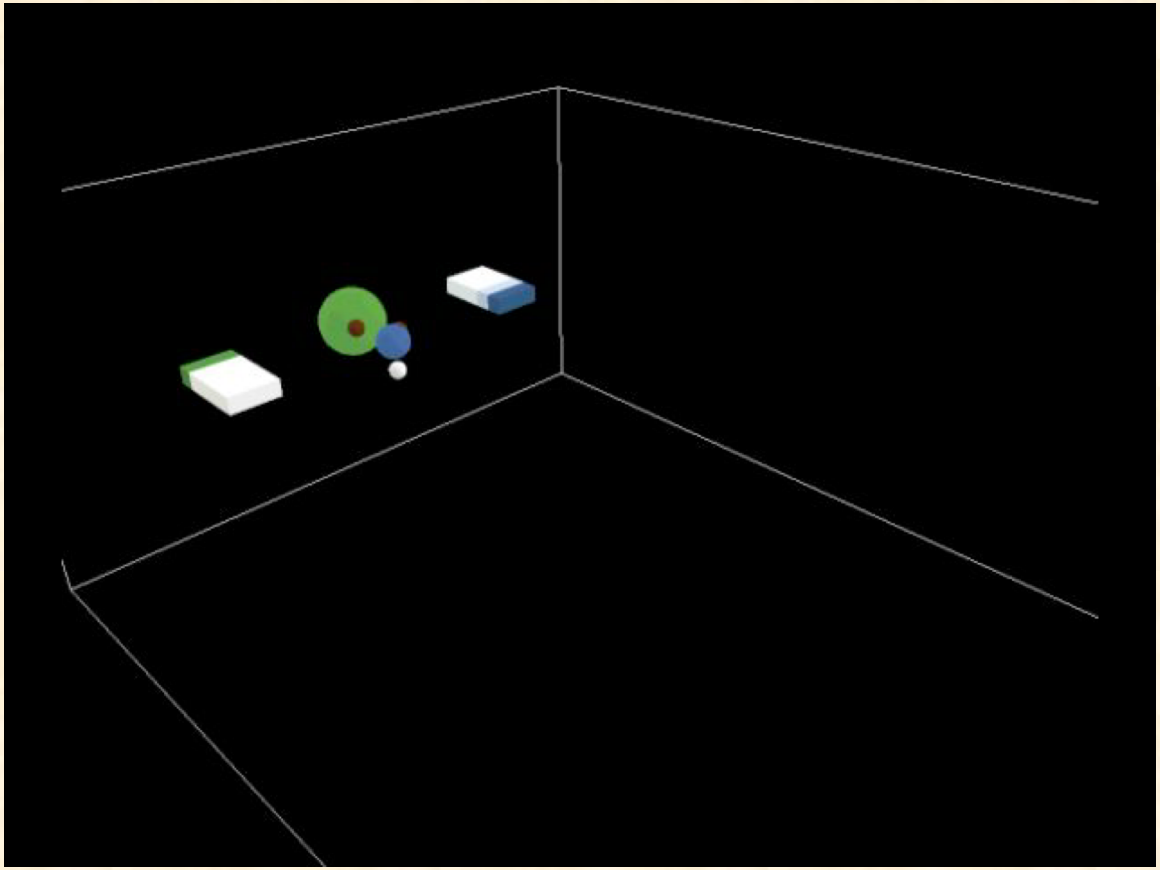

FGF/Wnt dominates
RA dominates
SII
SI
S0
S–I
S–II
Bistability window
Anterior
Posterior
FGF/Wnt dominates
RA dominates
SII
SI
S0
S–I
S–II
RA dominates
SIII
SII
SI
S0
S–I
S–II

Simulated Segmentation by Clock-and-Wavefront Process

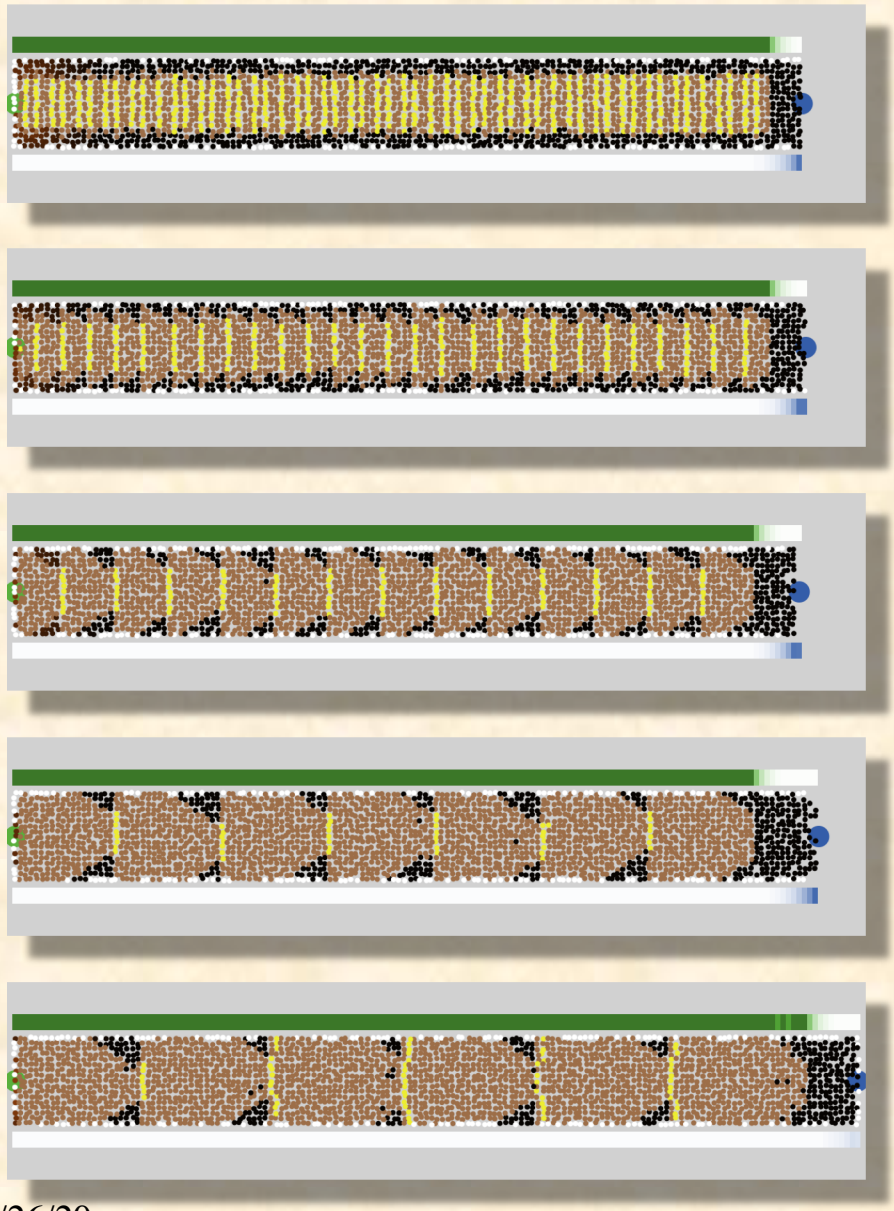


Run Segmentation-cells-3D.nlogo

2D Simulation of Clock-and-Wavefront Process

Run Segmentation-cells.nlogo

Effect of Growth Rate



- Segment length = growth rate × pacemaker frequency
- Number of segments = pacemaker frequency × growth duration

NetLogo Simulation of Segmentation

Run Segmentation.nlogo

Segmentation References

1. Cooke, J., & Zeeman, E.C. (1976). A clock and wavefront model for control of the number of repeated structures during animal morphogenesis. *J. Theor. Biol.* **58**: 455–76.
2. Dequéant, M.-L., & Pourquié, O. (2008). Segmental patterning of the vertebrate embryonic axis. *Nature Reviews Genetics* **9**: 370–82.
3. Gomez, C., Özbudak, E.M., Wunderlich, J., Baumann, D., Lewis, J., & Pourquié, O. (2008). Control of segment number in vertebrate embryos. *Nature* **454**: 335–9.