

Navigation in non-human organisms: Servomechanisms working with oscillators

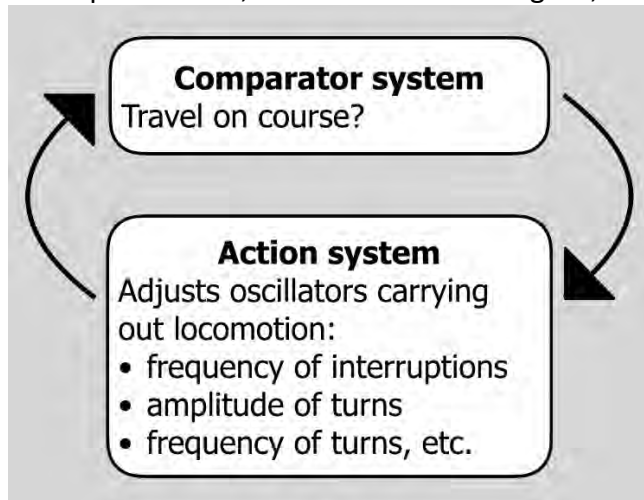
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In a book called *The Organization of Action*, Gallistel (1980) described three basic units of action: the reflex, oscillator, and servomechanism. The reflex is a stereotypical action triggered reliably by a particular class of stimuli called adequate stimuli. An oscillator is an endogenous mechanism for generating regular periodic action, oscillations. Oscillations are the periodic actions and the oscillator is the system that generates them. A servomechanism is an error-correcting device that operates continuously. An internal device known as a comparator or integration centre compares a 'desired' setting on a variable to the current reading of that variable as supplied by the senses. The difference between the observed current value and the setting or reference value on the variable constitutes error. Error drives action in a servomechanism in a negative-feedback loop that reduces the error. In a servomechanism, unlike a reflex, the action must change the very input that drives the mechanism in the first place. I have recently proposed that servomechanisms working with oscillators constitute a universal paradigm across life for navigation by mobile organisms, from micrometres to thousands of kilometres of travel (Cheng, 2022, 2023).

Navigation and orientation move a traveller towards a goal. I distinguish the two terms. In orientation, the traveller is aiming to get to a better place, by some criteria of better and worse, but not to any particular goal. A bacterium or worm ascending a chemical gradient signaling food is an example. In navigation, on the other hand, the traveller is aiming to get to one particular place. A honeybee or ant trying to get back to its own nest, and not just any nest, is an example. In both orientation and navigation, servomechanisms working with oscillators propel the traveller.

A navigational servomechanism works to aim the traveller towards a goal. Any deviation from the goal direction constitutes an error, and the error drives action to reduce the error in a negative feedback loop (Cheng 1995, 2012; Figure 1). Different mechanisms code the goal direction in different ways. In path integration, the goal direction is specified by a vector encoding the direction and distance to the starting point, typically the home (Wehner 2020). In view-based navigation, the goal direction is specified by a particular view to aim at in travelling. I have maintained this conception for more than a quarter of a century now (Cheng, 1995), but recently, I have found that navigational servomechanisms work with oscillators, in more or less sophisticated ways, in guiding travel (Cheng 2022, 2023; Figure 1). At this point, examples best illustrate. I will highlight a few cases from the very small to the very large, before discussing the import of this scheme.

Figure 1. Navigational servomechanism. A comparator system compares current sensory and perceptual information with goal information and adjusts oscillators carrying out locomotion to keep on course, oscillators such as flagella, cilia, wings, and limbs.



Illustrative cases

Perhaps the simplest and most widespread mode of orientation is to occasionally interrupt the oscillators carrying out locomotion, and change direction of travel. The bacterium *Escherichia coli* is considered a simple bacterium, but it still possesses some 30 kinds of chemoreceptors and can go up or down a chemical gradient, a process known as *chemotaxis* (Koshland 1980; Sterling and Laughlin 2015; Cheng 2022). The microbe moves by beating its ~5 flagella in an oscillatory system. When the motors driving the flagella turn in one direction, all the flagella bundle up into one long tail that oscillates like the tail of a sperm, and the bacterium moves forward. Occasionally, the motors turn the other way, and all the flagella come apart, interrupting the oscillations and the forward movement. The organism takes a spin that orients it in a random direction. When the motors resume steady turning, the microbe travels in this new, randomly chosen direction.

How can occasional random changes of direction achieve goal-directed movement? By adjusting the rate of such interruptions, a process called *chemokinesis*. A kinesis is a mechanism that adjusts the rate of some behaviour based on input; it does not on average pick a better direction of travel. In the literature, this process of chemokinesis is often called *chemotaxis*. We can say that chemokinesis is one variety of chemotaxis. The rule is simple: When the going is getting better, the rate of direction change is reduced; when the going is not getting better, the rate of direction change increases (Koshland, 1980; Cheng, 2022). The bacterium adapts to the current level of chemical concentration so that it can detect small changes in concentration as it moves. It is far too small to detect the difference in chemical concentration across its tiny body. It thus has use a memory of the concentration a short time (up to 1 second) ago. With this mechanism, the bacterium ascends to a peak of chemical concentration, where things do not get any better, and the organism ends up milling around there. This scheme works well enough that two scientists could force undergraduate students to adopt this strategy in a computer game (Marken & Powers, 1989), and the students, like *E. coli*, succeeded in ascending to the peak of a goal gradient.

The mechanism of adjusting the rate of random direction changes is common in small organisms. While the effectors that drive locomotion are different, essentially the same

servomechanism is used in chemotaxis by the domain of Archaea, another branch of prokaryotes besides bacteria (Quax, Albers, & Pfeiffer, 2018). The effectors that drive Archaea, called archaella, have a different evolutionary origin from the flagella that propel bacteria like *E. coli*, but Archaea are thought to have borrowed some of the machinery for their chemokinesis from bacteria. Chemokinesis is also practiced by much bigger but still single-celled eukaryotes such as *Paramecium* (van Houten 1978), and by the nematode *Caenorhabditis elegans* (Srivastava et al. 1999). If *E. coli* were a small sailboat, *Paramecium* would be a big cruise ship. *Paramecium* occasionally backs up and spins in a random direction, a process called an avoidance response because that is what the eukaryote does on bumping into something (van Houten, 1978; Sterling & Laughlin, 2015). The worm *C. elegans* sports a small nervous system of 302 neurons, and with nerves and muscles for locomotion, we find an additional, more powerful mechanism based on lateral (left-to-right) oscillations, perhaps a major evolutionary transition in orientational mechanisms.

Oscillators coordinating with one another drive the muscles of *C. elegans* to make the worm ‘wiggle’ right and left (Sterling & Laughlin, 2015). The muscles are located dorsally and ventrally, but the worm turns on its side, so that dorsal and ventral contractions turn into left-right wiggles. With enough spatial separation now arising from the lateral oscillations, the nematode can compare the chemical concentration on the right and left sides (Iino & Yoshida, 2009)—unlike *Paramecium* and *E. coli*, for which the spatial chemical gradient is far too small to detect (Sterling & Laughlin 2015). On the basis of the left-right comparison, the worm can turn more to the left or right. Lateral oscillations allow an organism to execute true chemotaxis, in which the directional change is not random but, on average, leads to a better direction for travel. As noted, chemokinesis, in contrast, only changes the rate of some behaviour. *Drosophila* larvae also use this form of true chemotaxis (Wystrach, Lagogiannis, & Webb, 2016). Lateral oscillations allow them to compare spatially the chemical concentrations on the left and right sides, and adjust their turn sizes accordingly.

Recent observations of navigating ants show that these much-studied navigators also oscillate left and right, on top of their regular oscillations of their 6 legs (Murray et al. 2020; Cheng 2022; Clement et al. 2023). These oscillations are adjusted in the service of navigation. For example, any manipulation that increases what we would colloquially call uncertainty leads to more and bigger oscillations: ants ‘meander’ more in such circumstances. If an ant is picked up after it has travelled a familiar route home and placed back somewhere on its route again, that increases the meandering on the next run home (Wystrach, Schwarz, Graham, & Cheng, 2019). Recent, as yet unpublished observations from my group suggest that a change in the usual view home also leads to more meandering. “Uncertainty” is an informal and perhaps anthropomorphic term. It is still unclear what ants encode by way of such uncertainty. Perhaps, it reflects familiarity (certainty) vs. unfamiliarity (uncertainty) in their views and other sensory cues (Baddeley et al. 2012; Clement et al. 2023).

Ants use panoramic views in navigation (Wystrach et al. 2011; Freas & Cheng, 2022). One plausible mechanism generating lateral oscillations is that views inform the navigator whether they are too far to the left or right of the goal heading, so that the lateral oscillations keep adjusting the direction of travel to keep to the best direction (Clement et al., 2023; Wystrach, 2023 preprint). More empirical and modelling work are needed on this topic.

On a global scale, sea turtles roam the oceans of the world, staying within a large safe zone using geomagnetic cues (Lohmann & Lohmann, 2019; Cheng, 2022; Freas & Cheng,

2022). They code the inclination (the slope of the geomagnetic field with respect to the horizontal surface of the Earth) and the intensity of the magnetic field to obtain a sense of 'where they are' in the world. The phrase in quotes points to the fact that the turtles may not be locating themselves at a particular longitude and latitude in the world. In fact, the group that produced most of the research (Putman et al. 2011; Lohmann & Lohmann, 2019; summary: Cheng & Freas, 2022) posit that the turtles simply know which directions to head in when given particular geomagnetic conditions, far more like knowing a bunch of routes around their safe zone. Waves, however, give them problems in keeping to their desired heading.

Waves constantly knock them off their desired course of travel in all three rotational planes, yaw (left-right), pitch (head up and down), and roll (around the front-to-back axis). Sea turtles swim by power strokes of the front flippers, oscillating in synchrony like the butterfly stroke (Avens et al. 2003). Servomechanisms working with oscillating flippers adjust the turtle's course of travel against rotations in roll, pitch, or yaw. Against rolls, for example, the two front flippers stroke at different depths to rebalance the body. These studies of what I am calling servomechanisms are conducted in the lab, it being difficult to track sea turtles in their natural ocean habitat. But it is well worth the effort to investigate their adjustments in the face of waves in natural conditions.

Discussion

Thus, across all scales of travel, servomechanisms work with oscillators in navigating organisms (Cheng, 2022, 2023; Freas & Cheng, 2022). These mechanisms differ in sophistication. Interruptions of forward movement in chemokinesis do nothing more than occasionally stopping the oscillators that are driving locomotion. A big evolutionary 'invention' came in the form of lateral oscillations, which allow an organism to adjust turns to the left and right and pick a better rather than a random direction of travel. Such lateral oscillations require a scale up in size and perhaps neurons and muscles, a topic well worth investigating further. At the sophisticated end, desert ants adjust oscillations in various ways in response to circumstances, such as oscillating more in what can be considered more uncertain conditions.

My view is that oscillators serve much more than orientation and navigation. They are so common in life that they, along with servomechanisms, are likely basic units of life. Other realms of cognition too adjust oscillators to accomplish tasks. Mammalian brains are characterised by intrinsic rhythms that serve cognition, known by various Greek letters such as theta and gamma (Buzsaki, 2019). Many kinds of cognitive performance, in attention, perception, and memory, waxes and wanes in cycles (Cheng, 2023). A complex brain may not be able to organise its activities, informally, get its act together, without oscillating cycles (VanRullen, 2016). The multi-nucleated but single-celled 'intelligent' slime mould *Physarum polycephalum* lives on oscillations. Its entire cytoplasm sloshes back and forth, and adjustments to such oscillations allow it to search for food, avoid nasty chemicals, make decisions, and do other seemingly smart tasks (Reid, 2023).

Servomechanisms are also common in life, and I venture to say that life is not possible without servomechanisms. Various scholars in psychology have put forth the view that human cognition and action operate in servomechanistic fashion (Miller et al., 1960; Powers, 1973; Carver & Scheier, 1998). Physiology features servomechanisms in maintaining homeostasis, perhaps the central theme in physiology (Stanfield, 2016). My brief summary on the why and wherefore is that oscillators are needed to organise one's own activities,

including internal physiology, while servomechanisms are needed to adjust to circumstances in the world (Cheng, 2022, 2023). Servomechanisms and oscillators are not just basic units of action and basic components of navigation. They are basic units of life.

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