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SHORT COMMUNICATION

Oscillators and servomechanisms in navigation and orientation

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ABSTRACT

I summarize my recent theorizing on orientation and navigation across life. Organisms use navigational servomechanisms working with oscillators to get to goals. Navigational servomechanisms track errors from the best direction of travel and initiate action to correct the error. They work with endogenously generated action patterns, oscillations produced by oscillators, to adjust the course of travel. The theme applies to all scales of life from micrometers to thousands of kilometers. Servomechanisms and oscillators also characterize some other domains of cognition.

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Reflexes, oscillators, and servomechanisms have been called basic units of action, in animals [1]. I have recently proposed that variations on the theme of servomechanisms working with oscillators describe the orientation and navigation of lifeforms across all scales [2,3]. I distinguished orientation from navigation proper, although both notions are commonly considered forms of navigation. Organisms *orient* to get to a better place, a place with more preferred characteristics irrespective of its particular location, such as a bacterium climbing up a chemical gradient. Organisms *navigate* to get to one particular place, such as an ant finding its way back to its own nest, and not any other ant nest.

A navigational servomechanism functions to keep an organism traveling toward its goal [4]. The central component of a servomechanism, a comparator or integration center, compares a specification of the target heading with current sensory and perceptual information on the course of travel. Any discrepancy constitutes error, and in a well-functioning servomechanism, the course of travel is adjusted to reduce the error, completing a negative feedback loop. More recently, I hit on the theme that the adjustments are made on oscillators [2,3].

Oscillators are systems that endogenously generate periodic actions, oscillations. Thus, oscillations are the regular, cyclic outputs, while oscillators are the systems that generate such oscillations. In animals, the notion was promoted in the 1930s by von Holst (chapter 4 in Gallistel's [1] book). Some oscillators may stem from the working of servomechanisms. For instance, mutually inhibiting servomechanisms with the correct parameters could produce regular oscillations [5] (see their Figure 4). Navigational servomechanisms working with oscillators vary in how sophisticated they are and how much they connect with the oscillations. Some highlights follow.

Brief review across all scales

The most widespread form of orientation interrupts occasionally the oscillators driving forward movement, thus barely working with the oscillators [2,3]. It is found in bacteria (*Escherichia coli* [6]; *Salmonella enterica* [7]), archaea [8], single-celled eukaryotes (*Paramecium* [9]), and nematode worms (*Caenorhabditis elegans* [10]). The bacterium *E. coli* possesses a few flagella that propel locomotion. When the motor driving the flagella turn steadily in either direction [6]—and I was imprecise about this aspect in the articles [2,3] that I am now summarizing—the flagella bundle together and oscillate as a tail, driving forward movement. When the motor reverses—at random times in a random-rate process [11]—the flagella come apart, and the prokaryote takes a spin to face a random new direction. To orient with random changes of direction, for example, ascending a 'desired' chemical gradient, the rate of interruptions is adjusted [2,3]. When the going gets better, the re-orientation rate is reduced. When the going does not get better, the rate is increased. The mechanism keeps working at a peak of the chemical gradient, where things do not get better, so that the organism turns a lot around the peak.

A mechanism in which the rate of some locomotory action is adjusted in response to stimulus conditions is called a *kinesis*, in the cases just reviewed, *chemokinesis*,

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which is one form of chemotactic behavior. Such chemokinesis requires a short memory of the chemical concentration a moment ago, to compare with the present concentration [6].

The nematode *C. elegans*, which possesses 302 neurons in a network of ganglia, oscillates left-and-right, or transversely, as it moves forward [12]. Being much bigger than prokaryotes or typical single-celled eukaryotes such as *Paramecium*, it uses transverse oscillations in a second servomechanism called weathervaning [13]. If the concentration is better on the left side, the animal turns more to the left than to the right. This form of chemotaxis is true chemotaxis: the comparison of chemical concentration (whether it is going up or down with a turn), now results in picking on average a better direction of travel instead of a random new direction. This mechanism might have been a big evolutionary leap in orientational sophistication. It is also found in the larvae of *Drosophila* flies [14].

Recent observations show that various species of ants execute transverse oscillations as they travel [5,15]. Transverse oscillations must be formed using the oscillations that form the common tripod gait in insects [1]. Transverse oscillations are adjusted in the service of navigation. For example, ‘meandering’, a proxy measure of oscillations, increases when the traveler has encountered experimentally engineered difficulties [16,17]. Both the kinematics and the why-and-wherefore of transverse oscillations are current topics of research.

Finally, on the globetrotting scale, seven species of turtles roam the oceans of Earth [18,19]. To swim, turtles use coupled oscillations of the front flippers, paddling in phase as in the butterfly stroke [20]. Waves can knock them off the intended course, and various servomechanisms correct such deviations. Against waves that roll them (rotate them around the front-to-back axis), for example, the two front flippers paddle at different depths.

Brief discussion

One key reason why navigational servomechanisms work with oscillators is that oscillators are needed to orchestrate the locomotory effectors. Flagella, cilia, wings, or limbs must move in regular, coordinated cycles and not flail at random. But transverse oscillations seem add an extra twist. They allow spatial comparisons to pick a better direction of travel, of which weathervaning is an example. They also balance the motivation of reaching a goal with information seeking by exploration and active sensing [5]. Transverse oscillations help to gather sensory input from different directions. Whenever things have not gone well in travel and the agent becomes more ‘uncertain’, however uncertainty be coded, oscillations should increase to gather more information [3,16,17]. Both theoretically and empirically, however, we have much more to unravel.

Finally, oscillators and servomechanisms are common in life, well beyond orientation and navigation. My reviews document some of these, including primate cognition [2,3]. My going thesis is that oscillators and servomechanisms are not only basic units of action in animals, but basic units of life in all lifeforms.

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