Variation Is the Spice of Life. Focus on “Cycle-to-Cycle Variability of Neuromuscular Activity in Aplysia Feeding Behavior”

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Most of us prefer small standard deviations in our experiments. This preference presumably has two sources. First, we were trained as undergraduates using examples with one answer (the $K_m$ of an enzyme), and large standard deviations reflected experimental errors. Second, more subtle and more pernicious, is a tendency to think that the message is the mean. However, in many cases, the message is clearly the range. For instance, although average human faces can be constructed, and these average faces are highly appealing, very few people have one (Langlois and Roggman 1990; Perritt et al. 1994). Despite this preference, humans have an extraordinarily wide facial range. When studying human facial evolution, the primary question is thus probably not why the average but why the variety.

A similar issue arises in motor-pattern generation, in which a stereotyped motor pattern is often implicitly assumed to exist for each motor task. The task’s motor pattern is then defined by averaging repeated performances of it, and variation around this mean often is ascribed to preparation damage or uncontrolled variables. Because animals perform multiple tasks, this organization would require multiple neural networks (1 per task) or multi-tasking networks that are modified to produce multiple outputs. Both solutions entail additional nervous system complexity with presumed additional metabolic cost (Laughlin 2001). An alternative (not necessarily exclusive) is to not produce task-optimized outputs but to produce the same wide range of outputs regardless of the task being performed. For each task, a subset of these outputs will likely perform it at least reasonably well with this “just-good-enough” inefficiency being “cheaper” than having multiple networks, or complex, multi-tasking networks, that do task each perfectly.

The article in this issue (Horn et al., p. 157–180) from the labs of Vlad Brezina and Klaude Weiss on Aplysia feeding highlights this issue. Aplysia feed on algae with a wide variety of sizes and shapes, and one might imagine Aplysia optimize their feeding movements for each alga type. However, Horn et al. show that Aplysia feeding motor-pattern parameters (cycle period, neuron burst durations) are highly variable both in vivo and in vitro. Remarkably, this variability remains even when Aplysia eat a uniform strip of sea weed (an invariant task). Both the feeding muscles (Weiss et al. 1993; Brezina et al. 2000) and the feeding neural network (Sweedler et al. 2002; Koh et al. 2003) are highly modulated, and thus the variability could arise from history-dependent effects. However, when these effects are minimized by comparing only successive cycles, much of the variability remains. The authors use motor-nerve stimulation to show that the variability is also not due to randomness in muscle response, and most of the variability therefore originates in the motor-pattern-generating network itself. Many Aplysia bites will consequently be suboptimal, and some may result in no food intake whatsoever. Aplysia thus apparently uses a just-good-enough strategy in which, provided most bites result in some food intake, it doesn’t matter whether they are perfect bites.

One could argue that Aplysia uses this strategy because its nervous system has insufficient neurons to calculate alga-specific optimum-feeding movements. However, all nervous systems are metabolically expensive, and there is thus presumably always evolutionary pressure to generate behavior with the smallest possible number of neurons. The need to compromise between always generating optimal behaviors and the cost of maintaining the neurons this would require thus likely applies to all animals. Just-good-enough strategies are most useful in situations in which a range of related tasks are present in the environment (and thus producing a range of motor outputs means that a fairly good result will fairly often occur regardless of the task at hand) and in which the cost of failures is low. Large “random” variability is therefore unlikely in locomotory motor patterns. For instance, although in terrestrial locomotion substrates are often highly variable and large cycle-by-cycle variations are therefore required to well match step and substrate, this matching cannot be done with random cycle-by-cycle variation because the cost of failure (falling) is probably prohibitive. Alternatively, in swimming and flying the media are relatively uniform, there is hence really only one task and thus no obvious advantage to producing cycle-by-cycle variations.

Mastication is another story, however, as we eat foodstuffs with a wide variety of physical properties, and even suboptimal chewing would provide some food processing without serious deleterious effects. Only recently have techniques been developed that allow complete description of human chewing movements (Buschang et al. 2000), and whether chewing is optimized as a function of foodstuff is unclear. However, even when great care is taken to regularize chewing (a single food type—gum—chewed on only 1 side) and only the 10 most similar chews (of 50-60 total) are analyzed, humans show considerable movement parameter variability (SDs approximately ±30%) (Buschang et al. 2000). This work focused on the means of the parameters rather than their variation, and the variability could thus arise from irregularly spaced bouts of regular chewing, slow variation in long chewing bouts, or Aplysia-like chew-by-chew random variation. Nonetheless, these data suggest that, for some motor patterns, humans may also use a just-good-enough strategy. However, as Horn et al. well demonstrate, proving this will require recognizing that, in some cases, the most functionally important component of a system’s output is not its mean but its variability and range.
REFERENCES


