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Learning in Cnidaria: a summary

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ABSTRACT

Based on a systematic literature search, I recently reviewed learning in the phylum Cnidaria, animals possessing a nerve net as a nervous system but no centralized brain. I found abundant evidence of non-associative learning, both habituation and sensitization, but only sparse evidence of associative learning. Only one well-controlled study on classical conditioning in sea anemones provided firm evidence, and no studies firmly supported operant conditioning in Cnidaria, although several provided suggestive evidence. More research on associative learning in this phylum is needed.

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Cnidaria comprise corals and sea anemones, hydras, box jellyfish, and true jellyfish, the latter two being two distinct classes in the phylum [1]. They are one of two phyla of animals without centralized brains but possessing a nervous system. The other such phylum is Ctenophora, comb jellies, not to be confused with jellyfish. Cnidaria and Ctenophora both possess nerve nets, a network of diffuse nerves throughout the body without a centralized clump that could be called a brain [1–3], although ring structures in Cnidaria have been likened to central nervous systems [3,4]. Two other phyla have no nervous system at all, Porifera (sponges) and Placozoa (which does not have a common name [1,5,6], although elements of neuron-like functioning can be found in both phyla [5,7,8]. Cnidaria is the sister group to Bilateria, the huge conglomerate of animal phyla possessing bilateral symmetry that includes the most studied animals such as flies, mice, and humans.

I wondered if and how much the animals with nerve nets can learn. Finding no reviews at all, I decided to launch into a systematic review myself [3]. For Ctenophores, I could not find any study that addressed learning, even though the nervous system of this phylum has been well characterized [9]. The systematic review thus focused solely on Cnidaria. This piece provides a highlights package.

Learning theorists distinguish between non-associative learning, habituation and sensitization, and associative learning, classical conditioning and operant conditioning, with an uncategorized variety that can be called more complex learning [10]. The studies reviewed, and hence the review itself [3] concerned the well known traditional varieties of non-associative and associative learning. A two-phrase summary goes: lots of evidence for non-associative learning, sparse evidence for associative learning.

In non-associative learning, the phenomenon of habituation means that repeated presentation of the same type of stimulus leads to reduced responding to that kind of stimulus. Habituation has been found in hydras, jellyfish, and sea anemones [3]. Sensitization is, in a sense, the opposite of habituation because sensitization leads to increased responding to a stimulus, induced by either repeated presentation of the same kind of stimulus or by some unrelated stimulus experienced before the triggering stimulus. The latter phenomenon can be capsulized as: **B** by itself leads to little responding, but **A** followed by **B** leads to much responding. **A** here sensitizes the response to **B**. Sensitization has been much studied in Cnidaria, but systematic studies were confined to sea anemones, so that investigation in other classes of Cnidaria are warranted.

An example is that vibrational stimuli at key frequencies characteristic of prey sensitizes the response to touch [11]. In the sea anemone *Haliplanella luciae*, a few bursts of vibrational stimuli lead to an increase in the number of nematocysts being discharged to touch. To put it too dramatically and anthropomorphically, sensitization in sea anemones works like a careful detective, who wants to amass enough evidence that the prey is there before firing the expensive guns that

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nematocysts are. The stingers for which this phylum is known are one-use guns: once fired, the entire cell is spent and a new stinging cell must be built. Thus, being touched by something might indicate an edible morsel is at hand, but it could also stem from some debris. But with vibrations characteristic of prey preceding the touch, the odds tilt in favor of game to kill and eat.

When it comes to associative learning, I found only one well-controlled study on classical conditioning, in the sea anemone *Cribrina xanthogrammica* [12], with other evidence suggestive but not convincing. In classical conditioning, an initially neutral stimulus, the conditioned stimulus (CS), predicts the arrival of some biologically significant stimulus, the unconditioned stimulus (UCS). With enough pairings of the CS and UCS, presentation of the CS alone elicits a response in anticipation of the UCS. In Haralson et al.'s study [12], electric shock was used as the UCS. It by itself causes the folding of the oral disk. The CS was 15 s of light presented before the onset of shock. After conditioning, the light alone led to oral-disk folding. In the study, a suite of controls served to rule out non-associative explanations such as sensitization.

Since the publication of my review, one other study on classical conditioning in sea anemones *Nematostella vectensis* has appeared [13]. This study also used shock as the UCS and a period of light as the CS. A suite of control tests again ruled out nonassociative interpretations.

In my review [3], no solid evidence of operant conditioning in Cnidaria could be found, but some findings were nevertheless suggestive. In operant conditioning, an animal does something to obtain some outcome, including avoiding certain noxious stimuli. As early as 1905, one study subjected sea anemones (*Metridium marginatum*) to repeated presentations of food held with tweezers, only to have the morsel snatched out from their esophagus before the animal could swallow it [14]. The sea anemones later rejected this kind of food. Were tweezers being shoved into their esophagus aversive to the sea anemones, so that they associated the food with aversiveness, or was this a case of habituation to repeated presentations? In a more modern study [15], sea anemones (*Condylactis gigantea*) were shocked for eating food. Some sea anemones learned to avoid that kind of food. A full suite of controls for non-associative interpretations, however, was missing.

This state of knowledge suggests that more studies of operant conditioning in Cnidaria should be carried out, studies with proper controls for non-associative interpretations. Since all available evidence on associative learning has been carried out on sea anemones, studies on other classes are also needed. As argued before, establishing not only what various taxa of animals can learn, but also what they cannot learn, is crucial for piecing together the evolution of learning [16].

Another reason for studying associative learning in Cnidaria is to probe what underpinning hardware is necessary for this kind of learning. If Cnidaria can show associative learning, and so far, the evidence is in the affirmative, then a central brain is not necessary for associative learning. It is possible that the nervous system is not necessary at all for associative learning, but the evidence is still uncertain. In plants, one demonstration of associative learning [17] has failed to be replicated [18]. Demonstrations of associative learning in single-celled eukaryotes are usually considered intriguing but not definitive [19], although one recent report contains plenty of controls for ruling out non-associative interpretations [20]. The positive results to date on associative learning in Cnidaria and single-celled eukaryotes suggest that more research on learning in various taxa without brains is called for.

In conclusion, Cnidaria do learn. They show plenty of cases of non-associative learning, both habituation and sensitization, and two solid cases of classical conditioning. More research on associative learning in Cnidaria is needed, as is more research on sensitization in other taxa than sea anemones.

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Disclosure statement

No potential conflict of interest was reported by the author.

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