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OLD AND NEW PERSPECTIVES ON THE BEHAVIOR OF HYDRA

BY

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INTRODUCTION

For many people, the first introduction to Abraham Trembley is Baker's (1952) scholarly biography. One feature of Baker's account which puzzled me when I read this book was the great interest with which Trembley's work on hydra was received by the learned societies of Europe. For the year following the first report of Trembley's results, nearly every issue of the *Philosophical Transactions of the Royal Society of London* contained second hand accounts about hydra, or first hand reports of observations made on these animals, including a letter by Trembley himself. According to Baker, the reception of hydra was equally enthusiastic in France. And interest in hydra was not confined to scientists and natural historians of the day. Literary figures, including Fielding, Smollet, Goldsmith, and Voltaire among others, wrote more popular accounts in praise of or denigration of the recently introduced curiosity. From our prospect, looking back over 240 years, it is a bit difficult to understand what the fuss was about. Today the discovery of a new, nearly microscopic organism of limited capabilities would go unnoticed beyond a small group of specialists.

The importance of hydra which was revealed through Trembley's observations is that the organism is an animal, but an animal with a number of plant-like properties. It should be emphasized that it is the behavior of hydra that convinced Trembley, his contemporary audience, and essentially everyone who has looked at the organism since, that hydra is an animal. As Trembley * put it:

> "... we could not deny... that these Polyps are animals when we observe their locomotion, and especially when we see them seize small creatures, and carry them to their mouth with their arms, swallow them, and digest them."

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* Quotes from Trembley, except where otherwise indicated, are from a recent translation by S. G. Lenhoff and H. M. Lenhoff of *Mémoires, pour servir à l'histoire d'un genre de polypes d'eau douce, à bras en forme de cornes* (Jean & Herman Verbeek, Leiden, 1744).

But hydra was a strange animal for Trembley and his eighteenth century contemporaries since it was an animal with a number of features that normally were associated only with plants, including inconstancy in the number of body parts (tentacles), reproduction by budding, and especially a marked ability to regenerate from small pieces.

Hydra captured the public's interest in part because it was a novelty, a small animal, easily kept in captivity, which would readily regenerate when transected. Interestingly, the finding that hydra could regenerate whole organisms from small pieces was quickly followed by attempts to find similar regeneration in other animals. Soon starfish and annelid worms were found to have pronounced regenerative capacity and hydra was no longer unique as an animal known to be able to regenerate from parts.

But in addition to its interest as a curiosity, hydra was important for it appeared to provide a bridge between the two great groups of living organisms then recognized, the animals and the plants. In Trembley's time a major theory about the organization of the world held that the organisms of the living world formed a continuous, unbroken series from the most base to the most sublime, a series referred to as the Great Chain of Being. Hydra, demonstrated to be an animal by its behavior but yet plant-like in several ways, appeared to fill an important gap in the Great Chain. Part of this paper will consider the importance given to hydra as a member of the Great Chain of Being.

Trembley's observations on the behavior of hydra were significant not only because they established hydra's position in the animal world, but also because they were painstaking, careful, and largely correct. Trembley's contributions formed a firm foundation for subsequent studies of hydra's behavior. Studies on the behavior of hydra have not been part of the mainstream of biological endeavor since Trembley's time, but they have formed one of the active and important tributaries. The second part of this paper will briefly explore some of the recent extensions of Trembley's observations on hydra's behavior.

HYDRA AND THE GREAT CHAIN OF BEING

The concept of a Great Chain of Being, a linear continuum, without gaps, which includes all living things on earth (and sometimes inanimate and spiritual things as well) was an important component of western thought for a rather long period. The classic work on the subject is that of Lovejoy (1936) which reviews thoughts about the great chain from Plato through the eighteenth century. One of the foremost proponents of a great chain was Leibniz who wrote:

> All the different classes of beings which taken together make up the universe are, in the ideas of God who knows distinctly their essential gradations, only so many ordinates of a single curve so closely united that it would be impossible to place others between any two of them, since that would imply disorder and imperfection. Thus men are linked with

> the animals, these with the plants and these with the fossils, which in turn merge with those bodies which our senses and our imagination represent to us as absolutely inanimate. And, since the law of continuity requires that when the essential attributes of one being approximate those of another all the properties of the one must likewise gradually approximate those of the other, it is necessary that all the orders of natural beings form but a single chain, in which the various classes, like so many rings, are so closely linked one to another that it is impossible for the senses or the imagination to determine precisely the point at which one ends and the next begins—all the species which, so to say, lie near to or upon the borderlands being equivocal, and endowed with characters which might equally well be assigned to either of the neighboring species. Thus there is nothing monstruous in the existence of zoophytes, or plant-animals, as Budaeus calls them; on the contrary, it is wholly in keeping with the order of nature that they should exist. And so great is the principle of continuity, to my thinking, that not only should I not be surprised to hear that such beings had been discovered—creatures which in some of their properties, such as nutrition or reproduction, might pass equally for animals or for plants, and which thus overturn the current laws based upon the supposition of a perfect and absolute separation of different orders of coexistent beings which fill the universe;—not only, I say, should I not be surprised to hear that they had been discovered, but, in fact, I am convinced that there must be such creatures, and that natural history will perhaps someday become acquainted with them, when it has further studied that infinity of living things whose small size conceals them from ordinary observation and which are hidden in the bowels of the earth and the depths of the sea. (Quoted and translated in Lovejoy, 1936.)

To give another example, in 1699 Edward Tyson, a British physician, wrote:

> Tis a true remark, which we cannot make without admiration, that from minerals, to plants; from plants, to animals; and from animals, to men; the transition is so gradual, that there appears to be a very great similitude, as well as between the meanest plant, and some minerals; as between the lowest rank of men, and the highest kind of animals. (Quoted from Gould, 1983.)

This theory about continuity of life forms was part of the background into which hydra was introduced, and it was certainly part of the reason for the enthusiastic reception given hydra by the learned world. Many observers took hydra as a link between the two major groups of organisms then known, the plants and the animals (but seemingly not Trembley himself, at least not in his public writings).

Trembley's work was officially introduced to England in a letter by J. F. Gronovius which was published in the *Philosophical Transactions of the Royal Society of London* (1744). The same issue of the *Philosophical Transactions* which contains Gronovius' letter also includes a letter from an anonymous correspondent remarking on Trembley's results as these were presented by Réaumur to the Académie Royale des Sciences in Paris. This letter clearly treats hydra in the context of the great chain of being. In discussing Trembley's findings on budding and regeneration by hydra, the anonymous correspondent notes:

> The best philosophers have long observed very strong analogies between these two classes of beings (i.e. animals and plants): and the moderns, as they have penetrated further into nature, have every day found reason to extend that analogy: some have even with great probability talked of a scale of nature in which she, by an insensible transition, passed from the most perfect of animals, not only to the most imperfect, and thence to the most imperfect of vegetables, but even through corraline bodies, and minerals, to the very earths and stones, which seem the most inanimate parts of our globe.

A somewhat later and more expanded version of the "scale of nature", in which hydra fills a gap between unsegmented worms and sensitive plants, is seen in Table 1. Charles Bonnet, who was one of Trembley's closest correspondents, accepted hydra's position in the continuum between plants and animals and raised the question as to the nature of hydra's soul which was presumably as divisible as was the animal possessing the soul (for a discussion of Bonnet's concern see Dawson, 1984).

Leibniz's assertion, quoted above, that there must be organisms between animals and plants, was seemingly prophetic. One admirer, writing in 1793 about the earlier interest in hydra, stated:

> The greatest glory is that of the German Leibniz, who did not live to know of the actual observation of this organism, yet who before his death predicted its existence through his confidence in the basic principles which he had learned from nature. (Sander, as quoted in Thienemann, 1908.)

Although Leibniz may have fully expected there to be organisms with both plant-like and animal-like features, one gets the strong impression from his *Mémoires* that Trembley did not. At several points in his *Mémoires* Trembley describes his incredulity at his own observations on hydra's behavior, reproduction and regeneration, largely because the set of observations did not fully correspond with what was to be expected of an animal, nor to what was to be expected of a plant. Further, Trembley does not discuss the Great Chain of Being in his *Mémoires,* nor does he seem to be much influenced by this concept. In fact, throughout the *Mémoires* Trembley emphasizes his attempts to determine if his new organism was an animal or a plant, and he treats these two categories as representing a valid dichotomy. Were he a believer in the Great Chain of Being, a more appropriate approach would have been to stress, as did several later authors (see Ritterbush, 1964, pp. 122-141), that hydra is an amalgam of both plant and animal qualities. As mentioned above, Trembley finally decided that hydra was an animal, and it was the behavior of the organism which led to this conclusion.

TABLE 1.

The Great Chain of Being, by an anonymous Thuringen author, about 1780 (from Thienemann, 1908).

33	God (The Trinity)	16	Flowering Plants
32	Christ	15	Palms
31	Angels	14	Grasses
30	The Blessed	13	Ferns
29	Guardian Spirits	12	Moss
28	Quadrupeds (including man)	11	Fungi
27	Birds	10	Truffles
26	Fish	9	Algae
25	Amphibia and Reptiles	8	Soft Corals
24	Arthropods	7	Stony Corals
23	Shelled Molluscs	6	Gems
22	Echinoderms	5	Minerals
21	Shell-less Molluscs	4	Rocks
20	Segmented Worms	3	Sulphur
19	Unsegmented Worms	2	Salts
18	Polyps	1	Earth
17	Sensitive Plants		

RECENT STUDIES OF HYDRA'S BEHAVIOR

Contractility: "... I saw the Polyps contract so suddenly and so forcefully that their bodies looked like mere particles of green matter and their arms disappeared from sight altogether." (*Mémoires*)

With the instruments and techniques available to Trembley, hydra appeared to be composed of a single, tubular "skin"; a skin which Trembley rightly concluded "must contain not only all the organs necessary for the nutrition and growth of the polyps, but also those needed to carry out their movements." We now know that the "skin" of hydra is actually two epithelial layers, an outer ectoderm and an inner endoderm, each of which is essentially one cell layer thick. The sudden contractions described by Trembley are a result of contraction of ectodermal musculature. The ectodermal epithelial cells have elongate, longitudinally-arranged, basal extensions which contain contractile filaments (reviewed by Lentz, 1966; Westfall, 1973). Contraction of the muscular tails of the epithelial cells is initiated by a propagated electrical potential generated by these cells, probably by a depolarization of the basal cell surfaces (Passano and McCullough, 1964; Josephson, 1967; Josephson and Macklin, 1969). These electrical potentials have been called contraction pulses or contraction burst pulses.

As was recognized by Trembley, contractions (and associated electrical potential changes) occur spontaneously as well as in response to stimulation such as jarring or electrical shocks. Spontaneous potentials occur singly and in bursts, and it is during bursts of potentials that the animal is reduced to a small blob with stubby arms.

Hydra does have a nervous system (see Heimfield, David, this symposium), but the role of the nervous system in controlling hydra's behavior is still uncertain. Animals treated so as to make them nerve-free still respond to electrical or mechanical stimulation by giving coordinated column contraction. In nerve-free animals, as in normal ones, there is propagation along the column of electrical potentials evoked by stimulation, although in nerve-free animals the conduction velocity of these potentials is distinctly slower than normal (Campbell et al., 1976). Spontaneous activity, however, does not seem to occur in the absence of nerve cells, making it seem likely that nerve cells are the pacemakers generating the patterns of periodic, spontaneous contractions characteristic of the behavior of normal hydra.

Polyp elongation following contraction is a result of both relaxation of the ectodermal musculature and contraction of circularly-arranged muscular tails in the basal portions of the endodermal cells. There are electrical potentials, called rhythmic potentials because they often occur in a regular pattern, which are associated with endodermal cell contractile activity, but the generation of these is yet not understood (Passano and McCullough, 1965; Kass-Simon, 1973, 1976).

Techniques have been developed which allow recording in essentially unrestrained, normally-behaving hydra of contraction pulses, rhythmic potentials and the electrical events associated with tentacle movements and contraction (reviewed in Josephson and Rushforth, 1983). The patterns of spontaneous electrical activity and associated behaviors have been quantified in detail, as has the effect of light and mechanical disturbance on the behavioral patterns (see summaries in Rushforth, 1967, 1973). However, very little is yet known about the mechanisms coordinating activity between the ectodermal and endodermal muscle layers, on the genesis of the spontaneous activity patterns, or on the receptor mechanisms through which external stimuli modulate spontaneous activity.

Rushforth (1967) has characterized habituation of hydra to mechanical stimuli, seen as a decline in the number of animals contracting in response to repeated presentations of mechanical agitation. Lenhoff and Lenhoff, in the introduction to their recent translation of Trembley's *Mémoires,* note that Trembley too remarked on habituation of hydra to repeated mechanical disturbance. Plate X of the *Mémoires* shows a group of polyps attached to the case of a caddis fly larva. In the legend to this figure, Trembley noted that the polyps were not induced to contract by the motion of the caddis worm; we may now interpret this phenomenon as occurring almost certainly because they had become habituated to the continued movement to which they were subjected.

Locomotion: "The Polyps move forward by means of their ability to extend, contract, and bend in all directions" (*Mémoires*).

Trembley described two important modes of locomotion in hydra, somersaulting and inch-worm like movements, in both of which the tentacles and base alternately attach and detach. Trembley noted that these movements could occur over solid objects or along the underside of a water surface. Later observers have described additional means of locomotion; including floating by means of gas bubbles formed at the base of the animal, and slow gliding movements involving the basal disk (Table 2, discussed more fully in Rushforth, 1973). The mechanisms used to produce the coordinated muscular contractions necessary for the sequenced activity of locomotion are nearly as unknown today as they were in Trembley's time.

TABLE 2.

Modes of locomotion in hydra (from a table of information collected by Rushforth (1973) which should be consulted for the original references).

Mode	Source
Inchworm or caterpillar movements	Trembley, 1744
Walking on substratum using tentacles	Jennings, 1906
Somersaulting	Trembley, 1744
Passive gliding downward from water surface	Schaffer, 1754
Floating by means of gas bubble	Wagner, 1904
Active gliding along substratum on base	
With aid of tentacle and body movements	Marshall, 1882
Without aid of tentacle and body movements	Wagner, 1904
Walking along water's surface film	Trembley, 1744

Trembley noted, as have many workers since, that hydra are positively phototactic: they move toward light and gather in the most brightly illuminated portions of a container. One intriguing observation reported by Trembley, which to the best of my knowledge has not been reinvestigated, is that movement toward a daytime light source continues into the darkness of a subsequent night. This, if verified, would be a particularly important observation for it would demonstrate that hydra has a long-term memory, an information store which can guide its movements long after the directing stimulus has been removed. How this might be achieved with a neuromuscular system which, by present views, is quite simple in structural and functional organization would pose a real and important puzzle.

Feeding: "They are voracious Animals: their Arms extended into the Water, are so many small Snares which they set for Numbers of small Insects that are swimming there. As soon as any of them touches one of the Arms, it is caught." (A. Trembley in *Phil. Trans. Roy. Soc., London,* 1744.)

The behavior of hydra which has been most often studied is that set of acts associated with prey capture and ingestion. Feeding on a small crustacean such as an *Artemia* nauplius typically begins with the prey striking one of the outstretched tentacles of the polyp, and becoming attached there by nematocyst discharge. The portion of the tentacle proximal to the prey then contracts, often spiralling inward, which brings the prey near the mouth. As the prey nears the mouth, the surrounding tentacles concertedly flex in the oral direction. This sometimes results in adjacent tentacles contacting the prey and pushing it toward the mouth. Concerted tentacle flexions may be repeated several times during and after ingestion of the prey. Finally, the mouth opens, creeps around the prey, and closes about it (Josephson, 1965). The frequency of concerted tentacle movements is increased during and immediately after feeding, but the frequency of column contractions and of the usual spontaneous tentacle contractions is depressed (Rushforth and Hofman, 1972). Thus feeding involves a series of coordinated events culminating in prey ingestion and digestion. The behavioral components of feeding include: 1. nematocyst discharge; 2. tentacular movements; 3. mouth opening, creeping about the prey, and subsequent closure; and 4. inhibition of endogenous body and tentacle contractions.

a) *Nematocyst discharge.* Trembley was clearly puzzled at why prey stick to a hydra's tentacles. He reasoned that the tentacles were not covered with glue, for if the tentacles were simply sticky they should adhere to one another when they touched, which they did not. Trembley did suggest that the tentacles might be able to form suction cups analogous, in miniature, to those on the tentacles of a cuttlefish, but this is clearly presented as a speculation. Trembley's contemporary, H. Baker, found that in alcohol-fixed, air-dried hydra the "... arms are thick beset with hairs, or rather sharp hooks" (Baker, 1743). Baker suggested that these "hairs" were somehow drawn into the tentacle or laid flat along the tentacle in living animals, and that they were the devices used by the animal to grasp prey. These "hairs" discovered by Baker are discharged nematocysts.

The classic account of the use of nematocysts by hydra during feeding, locomotion and defense is that of R. F. Ewer (1947). Contact with prey organisms causes discharge of two of the hydra's four types of nematocysts: the desmonemes, which upon discharge can wrap around projecting bristles or spines of a prey and entrap it; and the stenoteles which can penetrate the prey's exoskeleton and impale it (see Tardent, this symposium). One of the other two types of nematocysts, the atrichous isorhizas, discharge upon prolonged contact with non-food substances. It is these nematocysts which are used to attach the tentacles to the substrate during locomotion. The functions of the last nematocyst type, the holotrichous isorhizas, is less clear; they are probably used defensively.

Nematocysts were classically considered independent effectors, devices whose discharge depended only on stimuli directly impinging on them with no organismal control (e.g. Parker and van Alstyne, 1932; Pantin, 1942). More recently, evidence has accumulated indicating that nematocyst responses in hydra and other cnidarians are modulated by the nutritional state of the animal and even by the nature of the substrate to which the organism is attached (Burnett, Lentz and Warren, 1960; Davenport, Ross and Sutton, 1961; see review by Mariscal, 1974). Interestingly, Trembley is quite definite that the stickiness of the tentacles of hydra is under polyp control, and varies with the nutritional state of the animal. He states "Frequently the Polyps allow the Prey to slide over their arms without restraining them; had the Polyps been hungry, they would have seized them the moment they touched the arms." And later "... it would appear that it is within the Polyp's power either to set in motion, or not to set in motion, whatever operations are needed to clasp the animals that touch its arms."

The mechanisms by which nematocyst discharge is modified in a fed hydra are still controversial. In investigating organismal control of nematocyst discharge, it was first necessary to determine if the reduced effectiveness of prey capture upon feeding to repletion is simply a consequence of nematocyst depletion. It is not, as was shown, among other ways, by a reduction in the effectiveness of prey capture by one head of a two-headed animal following feeding of the other head; and by reduced prey capture in animals in which food substances had been directly injected into the enteron (Smith, Oshida and Bode, 1974). It has been proposed that the factor depressing nematocyst effectiveness in well-fed animals is gut distension (Burnett et al., 1960); accumulation in the enteron of some metabolite resulting from prey digestion (Smith et al., 1974); or accumulation of inhibitory factors, probably originating from the discharged nematocysts themselves, in the animal's environment (Ruch and Cook, 1984).

b) *Tentacle movements, mouth opening.* Mouth opening and tentacle movements quite like those seen during normal feeding are evoked by exposing hydra to dilute concentrations of the tripeptide reduced glutathione (GSH), a common chemical constituent of the body fluids of animals (Loomis, 1955; later work reviewed by Lenhoff, 1974, 1981). This observation led Loomis to suggest that normal feeding responses are activated by GSH which is released from a wounded prey. Results from many subsequent studies have strengthened this assertion, including the finding that GSH inhibits endogenous column and tentacle contraction, which is another aspect of the normal feeding response (Rushforth and Hofman, 1972). The behavioral responses evoked by GSH in order of decreasing sensitivity are concerted tentacle flexions, tentacle writhing, and mouth opening (Rushforth and Hofman, 1972; Koizumi, Haraguchi, and Ohuchida, 1983). This order is the same as the temporal order in which these events occur during feeding, which raises the possibility that the sequential appearance of different behavioral components is due in part to a gradually increasing GSH concentration in the hydra's environment. Campbell, in this symposium, presents evidence leading to the remarkable conclusion that the mouth is formed anew each time that the animal opens it. Recent studies on the chemical control of feeding have used mouth opening and tentacle responses as bioassays, testing the effects of glutathione analogs and inhibitors in order to characterize the chemoreceptors of the feeding response (eg. Lenhoff, 1974; Lenhoff *et al.,* 1983; Hirakawa and Kijima, 1980; Hanai, 1981; Cobb *et al.,* 1982; Koizumi *et al.,* 1983).

In contrast to the many investigations of the chemoreceptors of feeding, little attention has been given to the mechanisms coordinating contraction of individual tentacles and groups of tentacles. It has been noted that only the portion of a tentacle proximal to the point of prey attachment contracts in bringing the prey to the mouth (Josephson, 1965; Rushforth and Hofman, 1972). This suggests that conduction in the tentacle is polarized in the oral direction. It also confirms a similar observation made over 200 years earlier by Trembley who wrote:

> To bring the Millepede (i.e. the prey) near the anterior end of the Polyp, the arms need but to contract and bend only those parts between their base and the place where the Millepede is entangled. Often the part of the arm which extends from the spot where the Millepede is entangled to the tip contracts only slightly and continues to hang down in the water while the other part is wound around the prey which it has seized and drawn to the mouth.

c) *Prey ingestion.* How the mouth of a hydra is able to creep over a prey and thus ingest it is quite mysterious. Seemingly only contact with the inside of the mouth is necessary for it to creep over an object since an inert object will be swallowed if it is placed in the mouth, and an isolated hypostome will creep slowly up the shaft of a pin inserted through the mouth (Rushforth, 1973). The consequence of the creeping movement of the quite extensible mouth is well described in my last quote from Trembley:

> "... as soon as the arms have brought a victim to the mouth, it immediately opens further and always in proportion to the size of the animal which the Polyp is to take into its body. Little by little its lips spread out until they adjust precisely to the shape of the prey."

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