

Feeding behavior of the medicinal leech, *Hirudo medicinalis* L.

Michael H. Dickinson and Charles M. Lent

Center for Neuroscience and Division of Biology and Medicine, Brown University, Providence, Rhode Island 02912, USA

Accepted January 19, 1984

Summary. 1. We have investigated the organization of feeding behavior by the medicinal leech, *Hirudo medicinalis* L. Hungry leeches position themselves at the water surface when they are in a resting state, and they are alerted by either mechanical or photic stimuli.

2. Alerted leeches orient into water waves and swim toward their apparent source with accuracy. They also exhibit an optokinetic orientation by swimming into moving bars of light.

3. Swimming ceases when *Hirudo* contact any surface which they explore by crawling, and upon finding a warm region, they bite. Biting has a thigmotactic component and a temperature preference of 37–40 °C.

4. *Hirudo* ingest blood meals averaging 8.9 times their initial weight. After feeding, leeches seek deeper water by crawling and they avoid warm surfaces.

5. Feeding by the medicinal leech has several behavioral alternatives which can be employed once the leech is alerted. Further, the act of feeding, itself, substantially alters the behavior of this sanguivorous annelid.

Introduction

Mechanical sensitivity is an especially important modality for leeches. The gnathobdellid leech, *Hirudo medicinalis* L. detects low amplitude movements of the water surface by means of mechanosensory hair cells which are borne in clusters within segmental sensilla (Derosa and Friesen 1981; Phillips and Friesen 1982). Seven pairs of these compound sensory structures are located upon the central annulus of each segment in the mid-body regions of the leech, and they contain photoreceptors

as well (Kretz et al. 1976). Sensilla are also very abundant upon the anterior sucker and prostomium of the leech. Medicinal leeches will orient accurately by swimming, or occasionally crawling, toward a point source generating surface waves (Young et al. 1981). Similar mechano-sensitive orienting behavior by crawling is well-documented in the Glossophoniid leech, *Protoclepsis* (Herter 1929).

The research upon the behavioral responses of *Hirudo* to a variety of stimuli, both natural and unnatural, has been reviewed by Mann (1962). When *Hirudo* are placed into water with a temperature gradient, most come to rest at 20–21 °C (Kaiser 1954); however, they will attach to surfaces which have been warmed to 30 °C (Mann 1962). Even though medicinal leeches respond to light and shadows, they orient toward vibrating sources in diffuse light or even total darkness (Young et al. 1981).

The chemical sensitivity of *Hirudo* is clearly demonstrated by their rapid attachment onto glass rods which have been held under the armpit of a person (Mann 1962). When leeches were exposed to a wide variety of chemicals, most of them attempted to escape from agents that were by and large toxic (Kaiser 1954). The maintenance of feeding requires certain chemical constituents within the fluid being ingested, while the presence of others, such as strong potassium chloride solutions will interrupt ingestion (Galun and Kindler 1966).

Despite the eclectic nature of these reported data, there is no comprehensive overview of the organization of the feeding behavior by the medicinal leech. This gap in our knowledge is especially surprising because *Hirudo* has emerged over the last decade as an organism with increasing importance for fundamental investigations into cellular and developmental neurobiology (Muller et al.

1981). The ecological aspects of foraging by various leech species are discussed by Sawyer (1981). We report here upon our studies of the organization of the feeding behavior of the medicinal leech. Hungry individuals have behaviors which differ distinctively from those of satiated animals. Feeding behavior is associated with the high levels of activity which are seen only several months after the ingestion of a single large blood meal. The feeding behavior has several components which enable leeches to find and attach to their mammalian prey with adaptability.

Materials and methods

Hirudo were obtained from European suppliers and maintained in aerated aquaria filled with artificial pond water (Muller et al. 1981), and kept on a 12:12 L:D cycle at 15 °C. Leeches generally arrived well fed, but after 3–4 months began to exhibit distinctive signs of hunger. Whenever we compare the behavior of hungry leeches to that of well-fed ones, the latter group always consisted of leeches whose feeding we had carried out within the previous month.

Distribution. We placed a group of hungry and a group well-fed leeches separately into a plastic hemisphere (60 cm dia.) which was filled with pond water to a depth of 17 cm. We thoroughly agitated each group, and after allowing 3 h for them to come to rest, measured the height of their anterior and posterior suckers with respect to the water surface. The animals in both groups were easily capable of crawling to any position within the chamber. A hemisphere avoids any bias resulting from leech thigmotaxis (Mann 1962).

Orientation. Leeches were placed individually into a 35 cm square styrofoam behavioral arena filled with 2 cm of pond water. Each animal was positioned in the center of the chamber and once it came to rest for 5 s, vibration of the water was begun. The water surface was agitated by a wave source consisting of a variable speed motor moving a wooden dowel at rates of 1–4 Hz via a cam. The rod was positioned 1 cm below the water surface immediately outside a 30 cm circle of aluminum screening. The 5 cm high fence was concentrically encircled by a layer of polyfoam, and together they substantially reduced any reflected waves. The position of the wave source was periodically altered by 90° in order to avoid biasing the results by possible extrinsic factors (e.g., windows, heat, overhead lights). Behavioral sequences were recorded through an RCA CCTV camera mounted directly above the chamber, and its output was stored on cassettes in a Panasonic VHS tape recorder with freeze-frame capability. Most leeches swam, rather than crawled, from the center of the chamber. Their angular orientation, with respect to the source, was measured upon the tape frame displaying that moment when swimming or crawling was initiated by releasing the posterior sucker.

To test for any orienting responses to moving bars of light, leeches were placed into the center of a plastic rectangular arena (10 × 40 cm). Bars of light from a 40 W incandescent bulb were moved longitudinally at velocities of 0.2–0.4 m/s. The light was chopped by a rotating metal cylinder with 2 open slits (ca., 20° ea.) rotating at 2–5 Hz. The cylinder was about 25 cm above the arena and was driven with a variable speed motor. Individuals were tested and rated as to whether they oriented into or with the direction of light movement or whether they

failed to respond after 30 s of stimulation. Controls were run with the motor turning and the light off.

Biting. *Hirudo* will bite warm surfaces, and we obtained quantitative measures of their biting frequency by placing sheets of Parafilm M (American CanCo, Greenwich, CT) upon warmed test surfaces. After leeches bite the parafilm, their tri-radiate incisions are easily discerned and counted under the dissecting microscope (see Fig. 3 A). For one set of experiments, parafilm was wrapped around a 500 ml bottle which was continuously irrigated with water at a desired temperature (25–55 °C). The bottle was positioned within a 21 cm square screen fence inside a 35 cm square styrofoam arena. The arena contained 4 cm of 25 °C pond water and groups of 10 leeches were placed within the screen and a motor driven cam vibrated the bottle, when necessary. A screen cover was placed upon the top of the 6 cm high square fence to contain the leeches. For other experiments, the biting frequency of individual leeches was assessed by placing them upon a sheet of parafilm lying upon a thermostatically controlled slide-warming tray. Individuals were restrained under a weighted 5 cm Petri dish for a trial period, an impression of the Petri was imparted to the film and the bites were counted within each circular trial area.

Feeding. Leeches were fed upon 37 °C 'blood', which was a 50:50 (V/V) mixture of discarded human erythrocytes (95–98% haematocrit) and Leibovitz L-15 culture medium (Microbiological Assoc., Bethesda, Md.). Blood was prepared, warmed, and placed into 15 ml polystyrene test tubes covered with a single layer of parafilm. The conical ends of these tubes were removed which facilitated the removal of any clots and the addition of more blood during feeding bouts, as needed. Leeches were weighed and offered the film-covered end of test tubes. Hungry leeches attached in 5 s or less and we restricted their exploration of the tube of the film surface with a sleeve of Tygon tubing. Once they bit the film and began to pump blood, they were positioned in pond water by securing the tube to a rigid bar. When feeding ceased and the leeches dropped from the test tube, they were immediately reweighed.

Results

Distribution

It is commonly observed that most medicinal leeches, when stored in glass containers such as gallon jars or aquaria, hang on the sides slightly above the water surface suspended by their anterior suckers. The distribution experiments reported here provide quantitative data which substantiate these observations. The position of the average anterior sucker of 35 hungry leeches was 0.7 ± 1.0 cm ($\bar{X} \pm 1$ SEM) above the water surface and that of the average posterior sucker was 0.6 ± 0.9 cm below. Thirty well-fed leeches were in significantly deeper water with their anterior and posterior suckers at 10.2 ± 1.5 and 9.2 ± 1.2 below the water surface ($p < 0.001$, t test). Such behavioral selection of shallow sites in the water places hungry leeches in a position to detect water waves which are most effectively transmitted at the surface and substantially attenuated by small increases in depth

(Young et al. 1981). Furthermore, well-fed leeches are unaffected by these surface waves because of the greater depths they select.

Orientation

A hungry leech spends long periods lying quietly at the water surface with both suckers attached to the substratum. However, its behavior is substantially altered by several stimuli including a sudden mechanical shock, handling, a drastic change in light level, or repetitive surface waves. Any of these alerting stimuli cause a leech to detach its anterior sucker, and often flare the prostomial 'lips' around its buccal cavity. This flaring behavior dilates the velum and even occasionally everts the three jaws. We have only seen this behavior in hungry, alert leeches. Flaring may serve to expose any receptors of the prostomium and buccal cavity more fully to the environment. If no additional stimuli reach an alert leech, it will resume a resting posture in some tens of minutes. If, however, repetitive water waves impinge upon the alerted leech, it will orient its anterior toward the source of the disturbance while keeping the posterior sucker attached. After a few seconds of this longitudinal orientation, it begins dorso-ventral undulations, detaches the posterior sucker and swims in the general direction of the source. The swimming is most often in a straight line, and *Hirudo* most often swim with the body directed upwardly. This upward direction of the body usually causes the head to emerge about 2–4 mm above the water surface during oriented swimming. Leeches will often swim in circles if the water is less than 2 cm deep because they are unable to establish a full body wave for swimming in that depth and roll onto their sides.

The angular orientation toward a point source of vibration is surprisingly accurate: with almost half of the observed trials within $\pm 30^\circ$ (Fig. 1). These data are similar to those of Young et al. (1981) who found that 65% of their orientation trials were within $\pm 22.5^\circ$ of the source.

We had observed that a strobe light, flashing at rates of 3–8 Hz, will alert most resting leeches into crawling or swimming. However, the stroboscopic flashing does not provide an adequate stimulus source for any significant orientation. Since propagating surface waves are moving lenses, they could provide a stimulus source for optokinetic orientation (Fraenkel and Gunn 1940). When submerged leeches are exposed to moving bars of light (waves), most will orient and swim into the oncoming waves. Quantitative data for optokinetic orientation

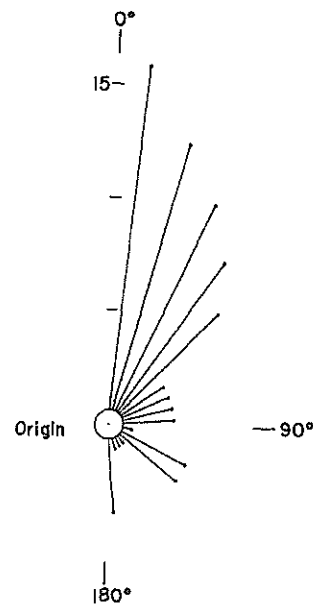


Fig. 1. The angular orientation with which *Hirudo medicinalis* swim toward a vibrating point source. Each vector is drawn from the origin where the trials were initiated. Their length is the number of trials in which leeches swam within each $+10^\circ$ angular bin. There were a total of 83 trials: 16 were oriented to within $\pm 10^\circ$ of the source, for example, while 3 were between 80 and 90° .

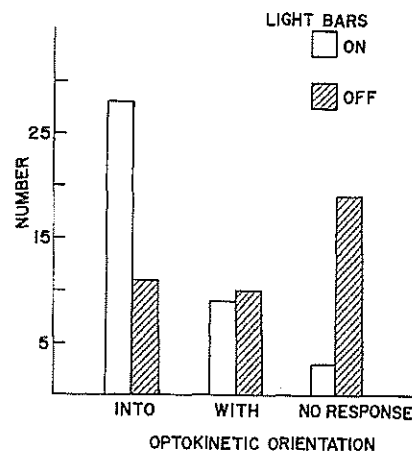


Fig. 2. Optokinetic orientation of *Hirudo medicinalis* to moving bars of light. Data were collected from one group of 10 leeches; 4 trials each (2 with the light on and 2 off). With the light source on, 28 swam into the direction of the moving light bars, 9 with the bars, and 3 failed to respond within 30 s. With the light off, but the motor turning, 19 failed to respond, 11 swam into and 9 with the fictive direction of the light bars

are presented in Fig. 2. It can be seen there that leeches swam into the direction of light wave movement in 28 out of 40 trials. Only 9 moved with the light waves, a number which is indistinguishable for those which moved in either direction in the absence of moving bars of light. Only three

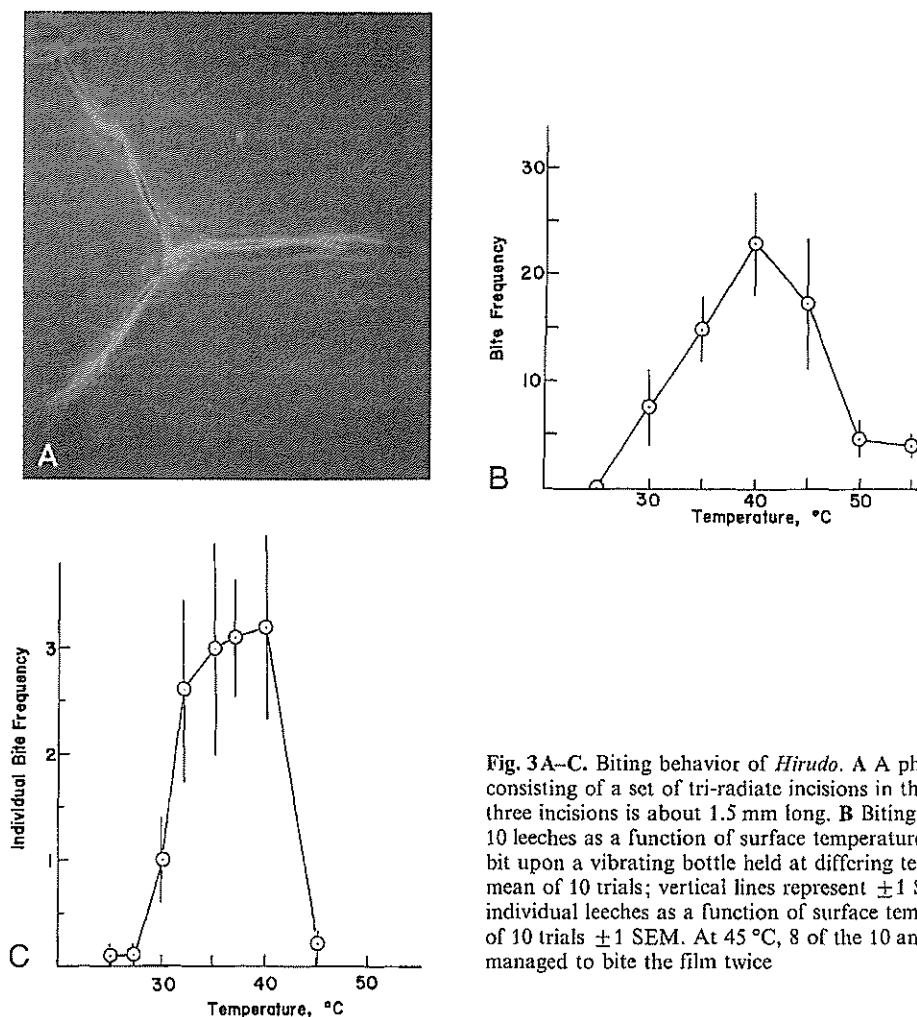


Fig. 3A-C. Biting behavior of *Hirudo*. A A photomicrograph of a single bite consisting of a set of tri-radiate incisions in the parafilm sheet. Each of the three incisions is about 1.5 mm long. B Biting frequency of groups of 10 leeches as a function of surface temperature. Groups in 25 °C pond water bit upon a vibrating bottle held at differing temperatures. Each point is the mean of 10 trials; vertical lines represent ± 1 SEM. C Biting frequency of individual leeches as a function of surface temperature. Each point is the mean of 10 trials ± 1 SEM. At 45 °C, 8 of the 10 animals died, even though one managed to bite the film twice

failed to respond when exposed to moving bars of light; however, in the dark (no light waves and the motor turning), nearly half of the leeches did not respond. These data demonstrate that *Hirudo* respond to light waves by orienting into them and swimming toward their apparent source. This is the same direction they swim into mechanical surface waves in constant light or dark (Young et al. 1981). The leech has photoreceptors within its segmental sensilla which bear the mechano-sensitive hair cells (Kretz et al. 1976). These segmental photoreceptors could readily detect the longitudinal differences in the intensity of the light from the surface waves and mediate the observed optokinetic orientation. Thus, it appears that the leech utilizes parallel sensory processing of mechanical and photic stimuli to orient itself toward the source of surface ripples.

Alert, hungry leeches often initiate swimming bouts which are interposed between longer periods

of quiescence resting at the water surface. The patterned behaviors of these leeches maintains them in shallow water, adaptively repositioning them to different regions would they fail to detect prey. On the other hand, well-fed leeches tend to crawl, nearly continuously, and usually stop in the corners of behavioral arenas. Such a positive thigmotaxis (Fraenkel and Gunn 1940) would tend to place well fed leeches under rocks, and as was noted above, at some depth.

Biting

When an orienting leech contacts a surface with its anterior end, swimming ceases, and it usually explores by crawling. If it finds a region which is warmer than its ambient water, the leech will bite it. A single bite is shown within parafilm by the micrograph in Fig. 3A. This tri-radiate pattern is identical to the shape of the wounds leeches

make in human skin. On occasion, an elevation of as little as 1 °C is sufficient to evoke biting. The frequency with which groups of leeches bite a vibrating bottle is shown as a function of temperature by Fig. 3B. Biting is obviously affected by the temperature, and at 25 °C, the ambient temperature, there are no bites. However, as the bottle temperature rises to 40 °C, the biting frequency increases, reaching a maximum of 23 per 10 min. At higher temperatures, the biting frequency falls off sharply. Thus, these groups of leeches have a temperature preference for biting, with 40 °C evoking the maximal response. These data show also that leeches usually bite repeatedly upon warm parafilm surfaces. If the vibrating bottle is not warm, the leeches do not bite it, even though many of them obviously orient to the bottle and thoroughly explore its surface.

The patterns of thermal preference in biting frequency are shown for individual leeches by Fig. 3C. For these experiments, the leeches were kept in air, under a Petri dish, and temperatures in excess of 45 °C for 10 min were usually lethal. The advantage of these experiments is that they assess only biting behavior, and the data contain no orientational or social components which could appear in the group experiments. Nevertheless, the data for individual leeches are surprisingly similar to those seen for groups of leeches. Individuals rarely bite a 25 °C surface and a maximum rate of about 3 bites per 10 min trial occurs between 37 and 40 °C. This is, coincidentally, the range of core body temperatures in most mammals (Prosser 1973). The bites are usually spaced, confirming our visual observations that leeches re-explore between individual bites. Most bites are found within 5 mm of the edge of the Petri-dish and less than 1% are in the central regions of the circular test areas. Leeches tend to bite in crevices, and this thigmotactic component of feeding probably causes them to select folded surfaces of their prey for biting. Such protected positions would assist leeches in remaining attached to their mammalian hosts during their prolonged feeding bouts. Well-fed leeches will not bite a 35 °C surface, a temperature which often evokes biting even by leeches which are only moderately hungry. Rather, these well-fed animals raise their anteriors as though attempting to avoid the warm surface. Thus, 37–40 °C appears to be a strongly evocative stimulus to hungry leeches, and a repellent one to well-fed leeches.

Feeding

When a bite draws blood, the leech pumps it from the buccal cavity into its crop by rhythmic, per-

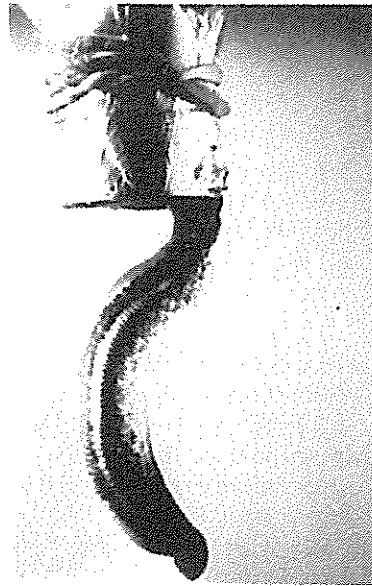


Fig. 4. A photograph showing a medicinal leech feeding upon 'blood' through a sheet of parafilm secured to the base of an inverted test tube. The body is thrown into a strong dorso-ventral flexion. The small convexity on the head overlies the pharynx whose peristaltic pumping produces visible movements of this region. The 15 ml test tube has a 1.8 cm diameter

istaltic contractions of its muscular pharynx. In over 50 trials, we have never seen a leech re-bite the film after initially drawing blood, even in those instances when a clot interrupted blood flow. About one quarter of our experimental animals fed while suspended in a U-shaped position with both suckers attached to the film, and the majority fed hanging only by their anterior suckers. As the leech becomes distended during feeding, it displays characteristic motor patterns. There are usually peristaltic contractions of the body wall which often alternate with sinusoidal, dorso-ventral flexions resembling swimming behavior (Fig. 4). The patterning of peristalsis and flexions is most often variable, but can be surprisingly regular in some individuals. One leech, for example, interposed 3 or 4 rhythmic peristalses between 12 to 15 flexions in a highly regular pattern for the entire feeding bout. The feeding bouts usually last between 20 and 40 min. Peristalsis usually dominates during the earlier phases of feeding, while flexions become dominant and stronger during the later phases of a feeding bout. The pumping of the pharynx produces visible movements of the anterior portions of the body and usually occurs at rates of 1.3 to 1.7 Hz. Body movements continue throughout feeding until the leech drops from the parafilm.

Leeches are extremely distended by the ingested blood, and a typical group of 20 leeches which weighed 1.0 to 1.5 g ingested blood which weighed 8.9 ± 0.2 ($\bar{X} \pm \text{SEM}$) times their initial weight. This volume of ingested blood is impressive, even for as extreme an intermittent feeder as the leech. About half of this weight increase is lost within one week which restores most of the locomotor motility to the leech.

Alerting Hierarchy

We have observed repeatedly that the leech must be alerted before orientation, exploration, biting, or feeding can occur. In order to provide quantitative data for such anecdotal observations, we placed a group of 10 leeches into a behavioral arena, and allowed them about 30 min to become quiet and assume resting postures. We then introduced 40 °C water into the biting bottle, and after 10 min, 7.8 ± 1.2 bites had been administered (4 trials). When the bottle was agitated at 40 °C, for an identical period, the now alert leeches nearly tripled their biting frequency with some 22.8 ± 5.7 bites (Fig. 3B). Young et al. (1981) noted as well that leeches would change the state of their feeding behavior when they were either handled or exposed to water wave vibration.

Discussion

The feeding behavior of the medicinal leech comprises several distinct components which are summarized by Fig. 5. These include alerting, orientation, exploration and biting-feeding. Broad arrows represent the more probable behavioral sequence, and the thin arrows represent alternative pathways or choices available to the leech. A hungry leech seeks shallow water, optimally positioning its sensory apparatus to detect surface waves. If a leech is not alerted, it initiates swimming bouts to new locations. This behavioral strategy is effective for hunting mammals which enter water only for infrequent, brief periods.

Any mammal entering the water will generate mechanical shocks by its footfalls, a rapid decrease and increase in the light level by its moving shadow, and surface waves by its entry and any subsequent drinking. Any one of these constitutes an alerting stimulus; together, they probably interact and alert all nearby resident leeches. The alert status appears as a prerequisite to all the other behavioral components of feeding. A warm stimulus, for example, will not usually evoke biting by a hungry, resting leech. Once alerted, however, the leech will bite a warm surface, or it will orient toward the

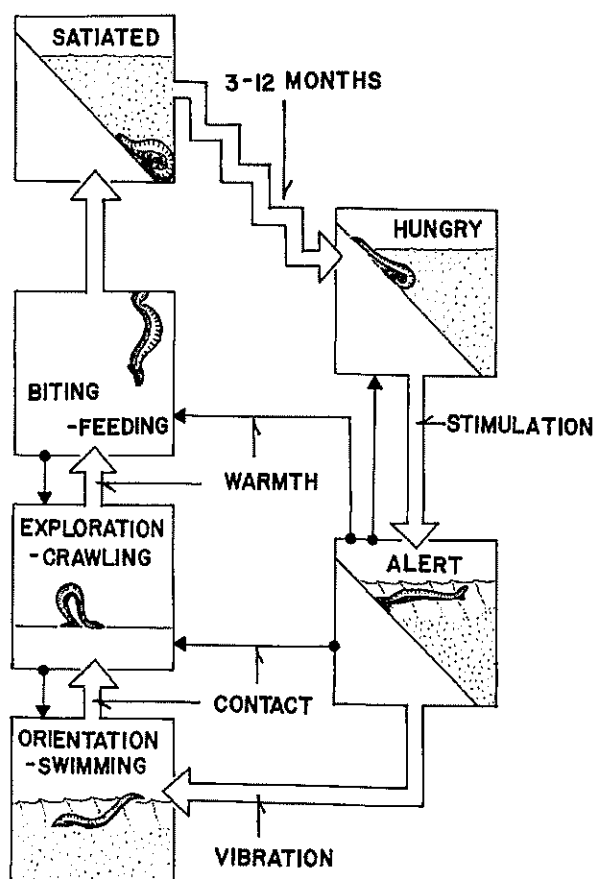


Fig. 5. Behavioral components utilized by *Hirudo medicinalis* in feeding. The major, more probable, pathways are depicted by large arrows, and behavioral alternatives are shown by smaller arrows

source of vibratory or light waves, or it will explore any surface that it contacts. Thus, except for alerting, no mandatory, sequential hierarchy exists for these components of feeding behavior, and the leech has a flexible behavioral repertoire which enables it to detect and locate prey in a variety of situations.

The leech orients and usually swims toward a ripple source, and while the mechanical movements of these ripples are an effective orienting stimulus, the waves of light generated by these ripples are themselves sufficient to produce swimming which is oriented toward the source. Should a leech find itself at depths which are devoid of mechanical movements from the surface waves, the ripple patterns of the light alone would probably evoke a swimming oriented toward the potential prey. And since a leech usually swims in a upward direction, it would move toward the surface as well.

A mammal produces surface waves upon entering the water, but these cease when it stops to

drink. We have noted that several seconds of continuous wave stimulation is necessary for an alert leech to initiate swimming. Therefore, we strongly suspect that the maximally effective stimulus source for leech orientation is the lapping movements of the tongue of a drinking mammal. The orienting leech will explore any surface it contacts and will bite preferentially upon 37–40 °C surfaces which are folded into acute angles. Thus, the nasal cavity, pharynx and underside of the tongue are probably the preferred sites for leeches to feed upon. Should an orienting leech contact an inanimate object, such as a rock, it will re-initiate swimming after a few seconds of surface exploration, if the leech continues to detect surface ripples. Should an exploring leech bite upon a surface which fails to produce blood, such as calloused, thick skin, it will re-explore and bite again. Thus, the behavioral repertoire of the medicinal leech has sufficient alternatives to enable it to feed upon mammals which enter the water at some distance or even in those rare instances where they touch the leech. Furthermore, leeches can locate prey even when there are interposed, inanimate objects.

There can be little doubt that chemosensitivity plays an important role in leech feeding behavior. *Hirudo* will attach to pieces of wax which have been handled, ignoring those pieces which have not, even though both are at the same temperature. Further, if a moderately hungry leech does not bite a warm surface, it can be stimulated into biting by wiping whole blood onto the parafilm. However, leeches bite such surfaces only once. Remembering that leeches which could not draw clotted blood through parafilm did not re-bite, we suspect that blood chemicals serve to maintain rather than initiate feeding.

The behavior of well-fed leeches differs from that of hungry ones. Satiated leeches tend to crawl, seek deeper waters, and position themselves under rocks. Should a well-fed leech encounter the warm skin of a mammal by chance, it will crawl away rather than bite. Thus, the entire behavior of this sanguivorous annelid is altered by the completed act of feeding. During the several months which are required to digest a full blood meal, the behavior of the hungry animal slowly returns. Such differences in behavior are presumably reflected by alterations within the nervous system of the leech. We have seen inexplicable long term differences in the amplitudes of the action potentials within Retzius cells; serotonergic effector neurons (Lent 1982). Furthermore, we have also seen facilitating monosynaptic connections from mechanosensitive pressure cells onto the Retzius cells which are pres-

ent during certain time periods, lasting several months, and which are absent during other similarly long periods (K.T. Keyser and C.M. Lent 1976, unpublished). It appears then, that physiological studies upon the leech nervous system should always stipulate the feeding status of the experimental animals used as precisely as possible.

It has been demonstrated recently that bathing *Hirudo* in serotonin produces three effects upon their feeding behavior: (1) a reduction in the latency of swim initiation toward a vibrating point, (2) an increase in biting frequency, and (3) an increase in the size of blood meals (Lent and Dickinson 1984). Further, mechanical and thermal stimuli which evoke feeding behavior, synaptically excite identified serotonergic neurons, while stimulation of these cells produces salivation and pharyngeal peristalsis: physiological responses which are associated only with feeding. Thus, there appears to be a highly specific neurochemical control of the rich behavioral repertoire which is utilized by the medicinal leech in feeding.

References

- Derosa YS, Friesen WO (1981) Morphology of leech sensilla: observations with the scanning electron microscope. *Biol Bull (Wood's Hole)* 160:383–393
- Fraenkel GS, Gunn DL (1940) The orientation of animals. Oxford University Press, London
- Galun R, Kindler SH (1966) Chemical specificity of the feeding response in *Hirudo medicinalis* (L.). *Comp Biochem Physiol* 17:69–73
- Herter K (1929) Reizphysiologisches Verhalten und Parasitismus des Entengels *Protoclepsis tessellata* O.F. Müller. *Z Vergl Physiol* 10:273–308
- Kaiser F (1954) Beiträge zur Bewegungsphysiologie der Hirudinea. *Zool Jb Allg Zool* 65:59–90
- Kretz JR, Stent GS, Kristan WB (1976) Photosensory input pathways in the medicinal leech. *J Comp Physiol* 106:1–37
- Lent CM (1982) Serotonin-containing neurones within the segmental nervous system of the leech. In: Osborne NN (ed) *Biology of serotonergic transmission*. John Wiley, London, pp 431–456
- Lent CM, Dickinson MH (1984) Serotonin integrates the feeding behavior of the medicinal leech. *J Comp Physiol* 154:457–471
- Mann KM (1962) *Leeches (Hirudinea)*. Their structure, physiology, ecology and embryology. Pergamon Press, London
- Muller KJ, Nicholls JG, Stent GS (eds) (1981) *Neurobiology of the leech*. Cold Spring Harbor, New York
- Phillips CE, Friesen WO (1982) Ultrastructure of the water-movement-sensitive sensilla in the medicinal leech. *J Neurobiol* 13:473–486
- Prosser CL (1973) *Comparative animal physiology*. Saunders, Philadelphia
- Sawyer RT (1981) Leech biology and behavior. In: Muller KJ, Nicholls JG, Stent GS (eds) *Neurobiology of the leech*. Cold Spring Harbor, New York, pp 7–26
- Young SR, Dedwyler RD, Friesen WO (1981) Responses of the medicinal leech to water waves. *J Comp Physiol* 144:111–116

