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CHEMICAL ACTIVATION OF FEEDING IN THE CARIBBEAN REEF-BUILDING CORAL *MONTASTREA CAVERNOSA*

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Specific feeding activators are being identified for an increasing number of cnidarians from a wide range of habitats. As early as 1942, Pantin demonstrated that individual organic compounds stimulate actions accompanying feeding behavior in *Anemonia sulcata,* and he showed that the presence of food or single organic compounds in the water lowers the threshold of mechanical stimulation necessary to discharge sea anemone nematocysts. After Loomis (1955) demonstrated that glutathione elicits feeding behavior in *Hydra littoralis,* the realization that many other cnidarians also respond to substances present in the tissue fluids of their prey prompted investigators to identify chemical activators for diverse members of the phylum (Lenhoff, 1968 and Lindstedt, 1971a). Whether or not tactile stimuli without chemo-stimuli can induce exploration for nourishment in some species remains unsettled (Lenhoff, 1965), and recent evidence suggests that some organisms may even require two or more activators to produce a complete feeding response (Lindstedt, 1971b and Reimer, 1972).

In this paper we present evidence for activation of feeding in the massive Caribbean reef-building coral *Montastrea cavernosa* (Linnaeus) by single chemical agents, and for differences in receptivity of mouths and tentacles to the amino acids proline, glutamic acid, aspartic acid, and arginine.

Materials and Methods

Montastrea cavernosa is one of the most abundant reef-building corals on the Atlantic coast of Panamá at depths below 1 m. During ecological studies (Porter, 1972 and in preparation), *M. cavernosa* was found to make up as much as 30 per cent of some 10 m^2 plots and to be perhaps the major *in situ* coral contributor by volume and weight of limestone to the permanent reef structure.

M. cavernosa has two distinct morphs in Panamá: a large-polyped variety (average polyp diameter 0.92 cm; expanded tentacle length usually 2× the polyp diameter), and a smaller-polyped form (average polyp diameter 0.48 cm; expanded tentacle length generally $\frac{3}{4}$ the polyp diameter). In addition, the larger variety has protruding polyps and displays wide color variation among colonies, ranging from gray or brown to green, blue, or red. The smaller form invariably has short-necked polyps and is either gray-brown or green-brown in color. Our work was done exclusively on the small-polyped morph. In the laboratory, the larger-polyped form indiscriminately captures and ingests seemingly inert objects

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ranging from filter paper soaked in distilled water to sterilized sand grains and glass beads.

Specimens of *Montastrea cavernosa* were gathered from 6–7 meters depth near the Smithsonian Tropical Research Laboratory at Galeta Island, Panamá Canal Zone. The animals were maintained in flowing seawater tables supplied by water passed first through a bed of sand. For chemical activation studies, specimens were transferred while still immersed to a 12 liter aquarium continually refreshed by running seawater at 1 liter/minute and arranged with their polyps 5–8 cm from the surface. Experiments were conducted in subdued artificial light after sunset, as polyps then displayed fullest extension.

Nineteen amino acids, the sugars glucose, fructose, and sucrose, plus pipecolic acid, and the tripeptide glutathione were surveyed for activity at concentrations of 10^{-1} and 10^{-3} M. Pieces of Whatman #1 filter paper 2 mm^2 were soaked in test solutions or plain seawater and presented either to mouths or to tentacles. The treated papers were positioned with forceps several mm above the polyp, and gently dropped onto the target area. Each polyp was observed for 5 minutes following the presentation to determine time and degree of response. Strong feeding activators elicited envelopment of the paper by tentacular folding, deposition of the test paper within the mouth, and full ingestion.

An extended polyp has a planar surface and its ring of tentacles is oriented radially outward. A full envelopment and closure sequence involves folding all tentacles upward and around the paper, ultimately closing tightly at the mouth, leaving no tentacles exposed. A convenient scoring scheme was adopted, based on degree of polyp closure relative to the fully closed state. Stages were designated 0, 1, 2, 3 or 4, corresponding, respectively, to fully extended, $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, or fully closed. Degree of polyp closure was recorded with the elapsed time. Five minutes proves to be a more than adequate observation interval, as most activators produce visible responses within a matter of seconds. Compounds which induced activity during survey experiments were subsequently investigated at greater length.

Results

Table I demonstrates that glutamic acid is by far the most successful feeding activator, causing full envelopment on every trial. Proline and pipecolic acid, a proline analogue, are also important chemical activators, followed by arginine and aspartic acid. The other amino acids produce responses essentially no different from the seawater-soaked control. The amino acids methionine, glycine, alanine, lysine, threonine, tryptophan, valine, serine, and leucine produce only rare, weak responses which never proceed beyond stage 1 of polyp closure. Isoleucine, histidine, phenylalanine, and tyrosine, as well as glucose, fructose, and sucrose, produce no responses at all. Reduced glutathione, a strong activator in many other cnidarians, does not produce full closure in any instance. Although three quarters of the polyps tested show incipient stages of the process, they usually return to a fully extended state within 5 minutes.

To test for anatomical localization of receptivity, filter papers were applied directly to different parts of the coral polyp. Regions tested were the mouth, the tentacles, and the space of ectoderm between those points. Receptivity proves

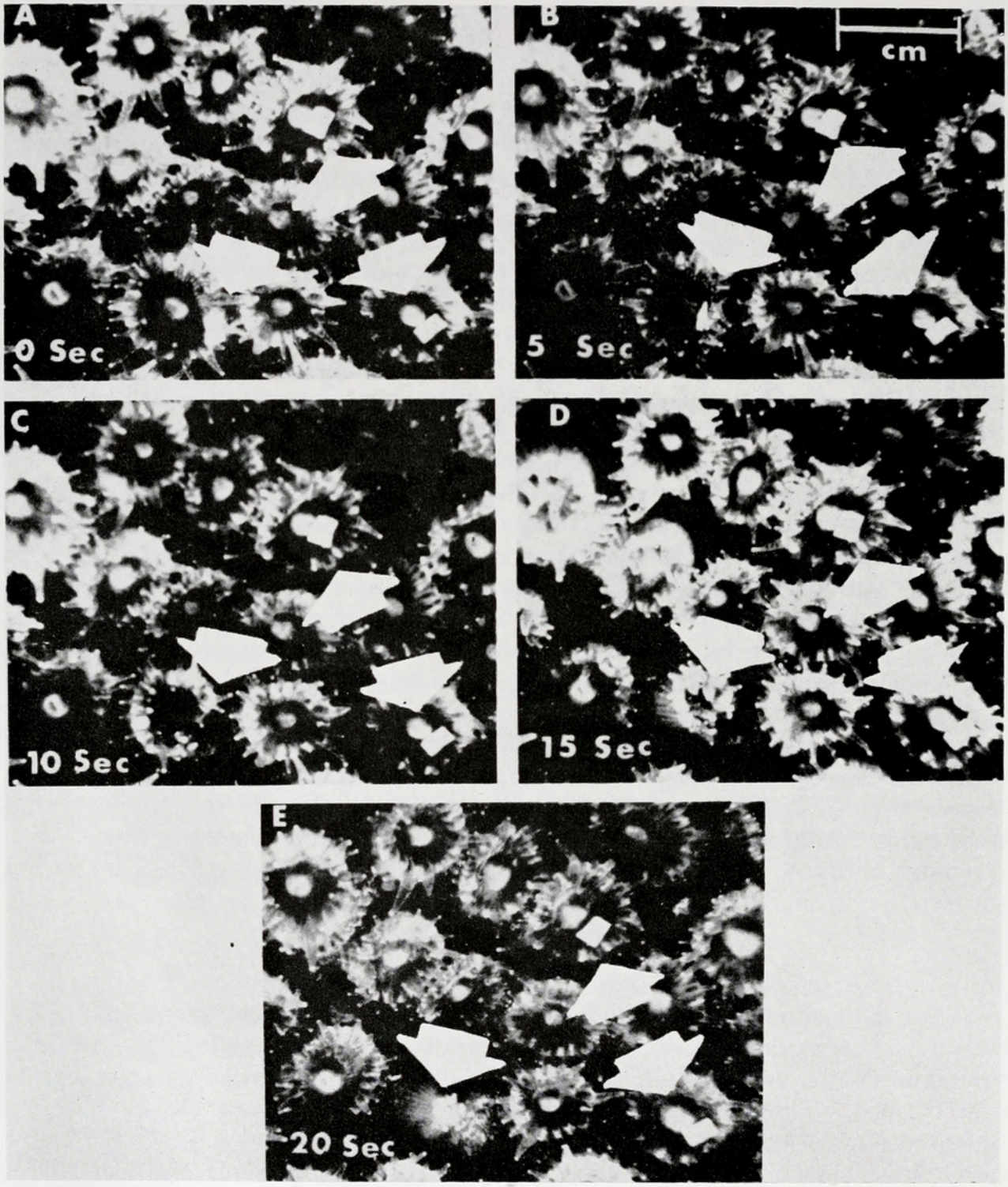

FIGURE 1. Time-lapse photographs of the reactions of *Montastrea cavernosa* polyps to filter paper soaked in 10^{-1} M proline (indicated by left arrow in each photograph) and filter paper controls soaked in seawater (indicated by two right arrows in each photograph). Photograph A shows the coral polyps in State 0, fully open, at the time the three filter papers are dropped. Five seconds later, photograph B shows the polyp with the proline soaked filter paper (left) folding over the paper into State 1, partially closed. Photograph C, ten seconds after dropping, shows the polyp with proline soaked filter paper in State 2; photograph D, 15 seconds after dropping, shows this polyp in State 3; photograph E, 20 seconds after dropping, shows it in State 4, fully closed. Note that the two control polyps (right) do not react to the seawater soaked filter papers. All photographs are 1.5 × life size.

TABLE I

Compounds tested for activation of feeding in the Caribbean reef-building coral Montastrea cavernosa

Compounds	Molar conc.	Number of trials	Degree of polyp closure							
			1		2		3		4	
			Number of polyps reaching this state	Per cent of trials	Number of polyps reaching this state	Per cent of trials	Number of polyps reaching this state	Per cent of trials	Number of polyps reaching this state	Per cent of trials
Seawater control		107	7	6	2	2				
Glutamic acid	10^{-1}	20	20	100	20	100	20	100	20	100
	10^{-2}	15	9	60	5	33	2	13	2	13
	10^{-3}	12	2	17						
Proline	10^{-1}	29	23	79	19	66	17	59	15	52
	10^{-2}	5	4	80	1	20	1	20		
	10^{-3}	5	1	20						
Pipecolic acid	10^{-1}	29	23	79	18	62	15	52	11	38
	0.05	8	4	50	3	38	3	38	1	12
	10^{-3}	13	3	23	2	15	1	8		
Arginine·HCl	10^{-1}	49	27	55	21	43	19	39	17	35
	10^{-3}	19	2	10						
Aspartic acid	10^{-1}	25	19	76	13	52	8	32	8	32
	10^{-3}	5	0	0						
Glutathione	10^{-1}	16	12	75	2	12				
	10^{-3}	5	0	0						
Cysteine	10^{-1}	11	2	18	1	9				
	10^{-3}	5	0	0						
Asparagine	10^{-1}	16	1	6	1	6				
	10^{-3}	5	0	0						

much greater in the region of the mouth with all activators except glutamic acid and glutathione (Table II). The former compound at 10^{-1} M induces full envelopment and closure whether offered to mouths or tentacles. With 10^{-2} M glutamic acid, however, differentiation between the two sites seems possible, as filter papers produce a stronger response when placed on the tentacles. Neither mouths nor tentacles respond strongly to 10^{-3} M concentrations of glutamic acid. Glutathione yields weak responses regardless of position of application.

Proline, pipecolic acid, glutamic acid, and aspartic acid are not significantly different ($P > 0.1$) in terms of response time. Each produces full closure in 30 seconds or less. All four, however, are distinguishable from arginine, which yields significantly delayed responses ($P < 0.05$). Polyps often remain inactive toward arginine-impregnated filter papers for 1 minute or more before showing the first

signs of tentacle movement. Once begun, the envelopment process is usually deliberate and complete.

When a filter paper treated with chemical activator is applied to a polyp already containing an untreated paper, the polyp almost invariably closes only around the treated paper, leaving the control paper exposed. If a distasteful compound is offered, such as 10^{-1} M HCl, the polyp folds immediately, leaving the filter paper outside.

Discussion

Mariscal and Lenhoff (1968) report proline and reduced glutathione to be principal activators in *Cyphastrea ocellina,* an Indo-Pacific coral species, and they find that solutions of these compounds effect mouth opening and tentacle contraction in several other Hawaiian corals. Goreau (1961) indicated that methionine added to seawater causes some Caribbean corals to extrude mesenterial filaments, but that glutathione has little effect on the same animals. Goreau *et al.* (1971) discovered that low concentrations of glycine, alanine, phenylalanine, and leucine trigger a typical feeding response, including extension of tentacles, swelling of the coenosarc, and sometimes extrusion of mesenterial filaments, in the Caribbean corals *Manicina areolata, Eusmilia fastigiata, Isophyllia sinuosa, Mussa angulosa,* and *Scolymia lacera.* Of all these compounds previously implicated in activation studies on corals, only proline elicited predictable feeding behavior in our work on *Montastrea cavernosa.*

Aspartic acid and glutamic acid both elicit feeding responses in *M. cavernosa,* but the structurally analogous asparagine does not. Glutathione a tripeptide consisting of glutamic acid, cysteine, and glycine, likewise fails to produce strong responses. This suggests that the β and γ carboxyl moieties of these compounds are instrumental in the chemical activation sequence and that modification of their terminal acid functions by amide or peptide formation would be expected to diminish activity. Such lower responses are indeed observed with asparagine and glutathione. Strong feeding responses to glutamic acid have been noted in other organisms, including the anemone *Actinia equina* (Steiner, 1957). The greater response to glutamic acid than to aspartic acid in *M. cavernosa* may possibly be ascribed to structural differences between the two, *i.e.* an additional methylene group in the functional side chain of the former molecule. However, aspartic acid (10^{-1} M) shows strongest activity in the mouth region, whereas a single series of tests performed with 10^{-2} M glutamic acid points to the tentacles as sites of greatest glutamic acid receptivity. Such results would not be excepted if the two analogues stimulate the same types of chemorecepors, and imply instead the the existence of separate receptor sites capable of distinguishing between the two molecules. Differential sensitivity between mouth and tentacles may be a general observation in sea anemones (Ross, 1966). Pantin and Pantin (1943) report that the mouth of *Anemonia sulcata* is more sensitive to a wider variety of chemical stimuli than are the tentacles, a pattern repeated in *M. cavernosa* with regard to amino acid sensitivity, as in *Calliactis polypus* (Reimer, 1973).

The response to proline and pipecolic acid suggests that *M. cavernosa* possesses a second type of receptor sensitive to these α-imino acids similar to those demonstrated in *Cordylophora* by Fulton (1963).

An explanation of the response to arginine is largely conjectural. Perhaps a solution of 10^{-1} M arginine may be so concentrated as to inhibit feeding at first, but dilutions to 10^{-3} M provoke no responses worthy of note. Mariscal and Lenhoff (1968) describe a response delay to the proline analogue pipecolic acid in *Cyphastrea ocellina* similar to the lag experienced by us with arginine in *M. cavernosa*. Before responding to pipecolic acid, *Cyphastrea* commonly requires a 1–2 minute lag period, an interval identical to that we found in *M. cavernosa*. Mariscal and Lenhoff suggest the possibility of enteroreception somewhat similar to that discovered in *Hydra* for tyrosine (Blanquet and Lenhoff, 1968). The lag, then, would be the time required for the activator to diffuse into the gastrovacular cavity before the polyp could respond.

Several recent studies performed on sea anemones show that different phases of feeding behavior may be controlled by individual chemical inducers. Lindstedt (1971b) demonstrates that asparagine induces tentacular bending in *Anthopleura elegantissima,* and that glutathione controls the act of swallowing by the anemone once contact with its oral region is made. She finds that aspartic acid also elicits some activity in the tentacle response, but glutamine and glutamic acid are comparatively inactive. On the other hand, it is the γ-glutamyl moiety of glutathione that appears to be most vital to the oral response. Nagai and Nagai (1973), working with the congeneric *A. midorii,* discovered that amino acids mixed with α-starch and water could serve as an artificial feeding inducer for the organism. Alanine, glycine, and histidine each evoke tentaculation; proline produces mouth opening; and cysteine or glutathione effects ingestion.

Williams (1972) similarly separates feeding and pre-feeding responses in *Diadumene luciae.* The pre-feeding, or tentacular, response is stimulated by the presence of certain chemicals in solution, including proline, glutamic acid, and aspartic acid. Filter papers imbibed with glutamic acid, for instance, stimulate only tentacular action, but not ingestion, in *D. luciae.* The oral feeding response in this anemone is most strongly activated by glutathione, several amino acids, and some vitamins of the B-complex.

Separation of oral and tentacular activators may not be as marked in *M. cavernosa* as in the anemones studied, but Tables I and II provide evidence for some such mechanism operating in this coral. Concentrations of 10^{-2} M glutamic acid strongly evoke the early stages of tentacle bending, as does aspartic acid when it is specifically applied to the tentacles. Proline and arginine activity, however, is rather more confined to the mouth region. Such observations are consistent with the reported general behavior of biphasic feeding activators. Glutathione also seems to stimulate the very early stage of tentacular bending, but since full ingestion never follows with this compound, it is difficult to say whether or not the response constitutes an authentic feeding activation. Forrest (1962) shows, for instance, that while glutathione induces prolonged mouth opening and tentacle contraction in *Hydra,* it does not duplicate, and can even inhibit, the natural feeding behavior of the animal. Despite its implication in mouth opening and tentacle contraction as evidence of chemical activation in Hawaiian corals (Mariscal and Lenhoff, 1968), glutathione does not trigger any responses in *M. cavernosa* that could be unhesitantly classed with the envelopment sequences induced by several amino acids.

M. cavernosa is a particularly voracious predator; its feeding response has been observed in the field where naturally occurring concentrations of net zooplankton at times exceed 2.0 mg dry wt m^{-3} (Porter, in press). Capture of live prey by the coral depends largely upon random collisions of zooplankton with extended polyps, inducing nematocyst discharge and subsequent envelopment. Mariscal and Lenhoff (1968) suggest that the puncture of a zooplankter by coral nematocysts causes the release of chemical feeding activators into the water. These authors and others (A. A. Reimer, Biology Department, Pennsylvania State University, University Park, Pennsylvania, personal communication) tested the hypothesis on Pacific species, using polyp mouth opening as a criterion of activator success. The size and voracity of the *M. cavernosa* polyp, however, permit us to duplicate a full capture and ingestion response in the laboratory by using filter papers impregnated with strong feeding activators.

Free amino acids are of equal importance with inorganic ions in the osmoregula-

TABLE II

Compounds tested for localized activation of feeding in the Caribbean reef-building coral Montastrea cavernosa

Compounds	Molar conc.	Number of trials	Degree of polyp closure							
			1		2		3		4	
			Number of polyps reaching this state	Per cent of trials	Number of polyps reaching this state	Per cent of trials	Number of polyps reaching this state	Per cent of trials	Number of polyps reaching this state	Per cent of trials
Proline	10^{-1}									
on mouth		11	11	100	11	100	11	100	10	91
on tentacles		9	4	44	1	11	1	11	1	11
between		9	8	89	7	78	5	56	4	44
Pipecolic acid	10^{-1}									
on mouth		8	8	100	8	100	7	88	7	88
on tentacles		12	8	67	3	25	2	17	2	17
between		9	7	78	7	78	6	67	2	22
Arginine·HCl	10^{-1}									
on mouth		16	11	69	11	69	11	69	10	62
on tentacles		21	7	33	4	19	4	19	4	19
between		12	9	75	6	50	4	33	3	25
Aspartic acid	10^{-1}									
on mouth		12	10	83	8	67	7	58	7	58
on tentacles		11	9	82	4	36				
between		2	2	100						
Glutamic acid	10^{-2}									
on mouth		3	0	0						
on tentacles		9	7	78	5	56	2	22	2	22
between		3	2	67	2	67				
Glutathione	10^{-1}									
on mouth		6	4	67	1	17				
on tentacles		6	4	67	1	17				
between		4	4	100						

tion of crustacean tissue fluids. The six most prominent amino acids reported for members of the class are alanine, arginine, glutamic acid, proline, glycine, and and taurine (Huggins and Munday, 1968). Johannes and Webb (1965) report that living marine zooplankton release amino acids into solution at a rate that increases with water temperature. In warm seas, as much as 30 mg of α-amino nitrogen per gram dry wt of zooplankton per day can apparently diffuse from the animals into the surrounding medium. The composition of the amino acid assemblage varies among individual zooplankton populations.

Cowey and Corner (1963) report that the free amino acid pool of the copepod *Calanus finmarchicus* equals 16 to 20 per cent of the protein amino acid content of the animal. Glycine, taurine, and arginine are major contributors to the pool, but proline and glutamic acid constitute 9.29 and 3.20 μM/g wet wt, respectively. Raymont *et al.* (1968) discovered that free amino acids, chiefly glycine, alanine, and glutamic acid, comprise most of the non-protein nitrogen, amounting to 20 per cent of total cell nitrogen, in *Neomysis integer,* a temperate, shallow-water mysid shrimp. Srinivasagam *et al.* (1971) find that glycine, taurine, and arginine comprise 70 per cent and glutamic acid, proline, and alanine form 15 per cent of the free amino acids of the same organism. These investigators find individual amino acid concentrations in excess of 1 mg/g dry wt in all three zooplankton species they measured. In *Sphaeroma rugicauda,* Harris (1969) measured 2.10 mg proline/100 mg dry wt of the isopod, and quantities of arginine, aspartic acid, and glutamic acid roughly one third this value. Simpson, Allen and Awapara (1959) find 2 μM free glutamic acid and 6 μM arginine per gram of live decapod tissue, and Emerson (1967) reports the free amino acids proline, glutamic acid, and aspartic acid present in *Artemia salina* embryos at more than 1 μg/mg dry weight. All of these figures correspond to 10^{-4} to 10^{-2} M concentrations of the individual amino acids in crustacean tissue fluids, concentrations in the range we observe for excitation of feeding behavior. Zooplankton punctured by nematocysts might be expected to leak their contents into the water near receptor sites, but any direct comparison of these values with concentrations tested by us must take into account dilution from the filter paper, diffusion rates, and ultimate concentration of activator in the microenvironment near chemoreceptors.

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SUMMARY

1. Nineteen amino acids, pipecolic acid, glutathione, glucose, fructose, and sucrose were surveyed as potential chemical activators of feeding in the massive Caribbean reef-building coral *Montastrea cavernosa.*

2. Glutamic acid, proline, pipecolic acid, arginine, and aspartic acid active feeding in this species. Its polyps fully ingest pieces of filter paper impregnated with these compounds.

3. Glutamic acid, proline, pipecolic acid, and aspartic acid produce full envelopment in 30 seconds or less. Arginine, however, requires one minute or more before eliciting closure.

4. Sensitivity is greater at the mouth for proline, aspartic acid, and arginine, but greater on the tentacles for glutamic acid.

5. *Montastrea cavernosa* responds to compounds of several chemical structural groups and therefore possibly has different chemoreceptors sensitive to each of these groups.

6. Since a variety of crustacean zooplankton have been shown to contain comparable concentrations of some of these activators, the release of such compounds following puncture of zooplankton by coral nematocysts may elicit the observed capture and ingestion behavior in *Montastrea cavernosa.*

LITERATURE CITED

BLANQUET, R. S., AND H. M. LENHOFF, 1968. Tyrosine enteroreceptor of *Hydra*: its function in eliciting a behavior modification. *Science,* **159**: 633–634.

COWEY, C. B., AND E. D. S. CORNER, 1963. Amino acids and some other nitrogenous compounds in *Calanus finmarchicus. J. Mar. Biol. Ass. U.K.,* **43**: 485–493.

EMERSON, D. N., 1967. Some aspects of the free amino acid metabolism in developing encysted embryoes of *Artemia salina* the brine shrimp. *Comp. Biochem. Physiol.,* **20**: 245–261.

FORREST, H., 1962. Lack of dependence of the feeding reaction in *Hydra* on reduced glutathione. *Biol. Bull.,* **122**: 343–361.

FULTON, C., 1963. Proline control of the feeding reaction of *Cordylophora. J. Gen. Physiol.,* **46**: 823–838.

GOREAU, T. F. 1961. Comment in H. M. Lenhoff, Activation of the feeding reflex in *Hydra littoralis.* Pages 230–231 in H. M. Lenhoff and W. F. Loomis, Eds., *The Biology of Hydra.* University of Miami Press, Miami.

GOREAU, T. F., N. I. GOREAU AND C. M. YONGE, 1971. Reef corals: Autotrophs or heterotrophs? *Biol. Bull.,* **141**: 247–260.

HARRIS, R. R., 1969. Free amino acid and haemolymph concentration in *Sphaeroma rugicauda* (Isopoda) during adaptation to a dilute salinity. *J. Mar. Biol. Ass. U.K.,* **50**: 319–326.

HUGGINS, A. K., AND K. A. MUNDAY, 1968. Crustacean Metabolism. Pages 271–378 in O. Lowenstein, Ed., *Advances in Comparative Physiology and Biochemistry,* Vol. 3. Academic Press, Inc., New York.

JOHANNES, R. E., AND K. L. WEBB, 1965. Release of dissolved amino acids by marine zooplankton. *Science,* 150: 76–77.

LENHOFF, H. M., 1965. Mechanical stimulation of feeding in *Epiactis prolifera. Nature,* **207**: 1003.

LENHOFF, H. M., 1968. Chemical perspectives on the feeding response, digestion, and nutrition of selected coelenterates. Pages 157–221 in M. Florkin and B. T. Scheer, Eds., *Chemical Zoology,* Vol. 2. Academic Press Inc., New York.

LINDSTEDT, K. J., 1971a. Chemical control of feeding behavior. *Comp. Biochem. Physiol.,* **39A**: 553–581.

LINDSTEDT, K. J., 1971b. Biphasic feeding response in a sea anemone: control by asparagine and glutathione. *Science,* **173**: 333–334.

LOOMIS, W. F., 1955. Glutathione control of the specific feeding reactions of *Hydra. Ann. New York Acad. Sci.,* **62**: 209–228.

MARISCAL, R. N., AND H. M. LENHOFF, 1968. The chemical control of feeding behavior in *Cyphastrea ocellina* and in some other Hawaiian corals. *J. Exp. Biol.,* **49**: 689–699.

NAGAI, Y. AND S. NAGAI, 1973. Feeding factors for the sea anemone *Anthopleura midorii. Mar. Biol.,* **18**: 55–60.

PANTIN, C. F. A., 1942. The excitation of nematocysts. *J. Exp. Biol.,* **19**: 294–310.

PANTIN, C. F. A., AND A. M. P. PANTIN, 1943. The stimulus to feeding in *Anemonia sulcata. J. Exp. Biol.,* **20**: 6–13.

PORTER, J. W., 1972. Patterns of species diversity in Caribbean reef corals. *Ecology,* **53**: 745–748.

PORTER, J. W., in press. Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa. Second International Symposium on Coral Reefs, Australia,* in press.

RAYMONT, J. E. G., J. AUSTIN AND E. LINFORD, 1968. Biochemical studies on marine zooplankton. V. The composition of the major biochemical fractions in *Neomysis integer. J. Mar. Biol. Ass. U.K.,* **48**: 735–760.

REIMER, A. A., 1972. Glutathione-proline activation of feeding behavior in the zoanthid *Palythoa psammophilia* Walsh & Bowers. *J. Exp. Mar. Biol. Ecol.,* **10**: 177–181.

REIMER, A. A., 1973. Feeding behavior in the sea anemone *Calliactis polypus* (Forskål, 1775). *Comp. Biochem. Physiol.,* **44A**: 1289–1301.

ROSS, D. M., 1966. The receptors of the Cnidaria and their excitation. *Symp. Zool. Soc. London,* **16**: 413–418.

SIMPSON, J. W., K. ALLEN AND J. AWAPARA, 1959. Free amino acids in some aquatic invertebrates. *Biol. Bull.,* **117**: 371–381.

SRINIVASAGAM, R. T., J. E. G. RAYMONT, C. F. MOODIE AND J. K. B. RAYMONT, 1971. Biochemical studies on marine zooplankton. X. The amino acid composition of *Euphausia superba, Meganyctiphanes norvegica,* and *Neomysis integer. J. Mar. Biol. Ass. U.K.,* **51**: 917–925.

STEINER, G., 1957. Über die chemische Nahrungswahl von *Actinia equina* (L.). *Naturwissenschaften,* **44**: 70–71.

WILLIAMS, R. B., 1972. Chemical control of feeding behavior in the sea anemone *Diadumene luciae* (Verrill). *Comp. Biochem. Physiol.,* **41A**: 361–371.