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# Visual and Chemical Release of Feeding Behavior in Adult Rainbow Trout

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## Abstract

Feeding behavior of adult rainbow trout (*Oncorhynchus mykiss*) is released by visual and/or chemical stimuli. Detection of either a conditioned visual or a conditioned chemical stimulus creates an excitatory feeding state within the central nervous system which turns on feeding behavior composed of swimming, turning and biting/snapping actions. Particular amino acids that are highly effective physiological taste stimuli that are also detected through olfaction (e.g. L-proline, L-alanine, L-leucine) release the initial sequence of food searching and biting/snapping behaviors; however, an effective olfactory, but poor gustatory, stimulus (e.g. L-arginine) is rarely effective behaviorally. After bilateral removal of the paired olfactory organs, visual stimuli alone release the entire set of feeding behavior patterns. Since amino acids that are highly potent physiological taste stimuli do not release either feeding behavior or reflex biting/snapping actions in adult anosmic rainbow trout, it is postulated that the olfactory system detects potent taste stimuli and provides the afferent input for arousal and the release of all feeding activity patterns. *Chem. Senses* 22: 375–382, 1997.

## Introduction

Chemical stimuli, which release escape and feeding behaviors in aquatic vertebrates, are detected simultaneously by olfactory and taste systems. The present report concerns both appetitive and consummatory stimuli that promote feeding behavior in fishes. We previously demonstrated in catfish, animals in which the extra-oral taste system is probably the best developed of all teleosts, that taste mediates innate feeding behavior while olfaction facilitates conditioned discrimination of amino acids (Valentinčič and Caprio, 1994a; Valentinčič *et al.*, 1994). The present report determines whether the olfactory or gustatory system of the rainbow trout, a teleost with a taste

system similar to the majority of fishes in not possessing an extensive distribution of extra-oral taste buds, is the main chemosensory system controlling feeding behavior. For both intact and anosmic channel catfish, the amino acids that evoked the greatest neural activity from facial, glossopharyngeal and vagal taste nerves (Caprio, 1978; Davenport and Caprio, 1982; Kanwal and Caprio, 1983; Kohbara *et al.*, 1992) were most effective in releasing biting/snapping behavior (small and large amplitude jaw movements respectively, comprising the same behavior) (Valentinčič and Caprio, 1994b). Our previous studies also showed that olfactory detection of a conditioned amino

acid caused increased central nervous system excitation, as evidenced by a longer search time in intact channel catfish for the test stimuli than occurring by taste alone in anosmic catfish. These results indicate that olfactory input was responsible for the ability of catfish to associate a specific amino acid with a food reward. For rainbow trout (*Oncorhynchus mykiss*, Walbaum, formerly *Salmo gairdneri*, Richardson), electrophysiological recordings indicated that while the olfactory system responded well to the majority of amino acids (Hara, 1973), the peripheral taste system was highly responsive to only a few amino acids, such as L-proline (Marui *et al.*, 1983; J. Kohbara and J. Caprio, unpublished data), which is a poor olfactory stimulus. To determine the relative importance of each chemosensory system in releasing specific feeding behaviors, amino acids were tested that are highly stimulatory to either gustatory receptors and/or to olfactory receptors.

## Materials and methods

### Experimental animals and maintenance

Rainbow trout (22–37 cm) obtained from the Povodje fisheries farm located near Ljubljana, Slovenia, were maintained individually in 210 l (for the smaller fish) and 420 l aquaria. The fish were fed daily at regular intervals with cod muscle and industrial feed pellets. The same 11 rainbow trout were tested repeatedly in each experiment. A continuous flow of dechlorinated tap water, equal to the aquarium volume, was delivered every 2 h to the aquaria housing the experimental rainbow trout. An air-lift system also circulated the aquarium water at a rate of more than one aquarium volume per hour through internal calcium carbonate gravel filters containing 10% of the aquarium volume. Air stones were positioned at opposite front ends of each aquarium. Water temperature in the test aquaria was maintained at 14–17°C in spring and 18–21°C in summer.

The buccal cavity of the farm-raised rainbow trout obtained was moderately infected with trophonts of *Ichthyophthirius multifiliis*. Malachite green treatment, modified for the length of the parasite life cycle at low temperature, was applied at 17°C to kill the theronts during their free swimming phase. Treatments included: day 1, 180 µg/l; day 2, 90 µg/l; days 3–14, 45 µg/l. Experiments were initiated 14 days after the medication was completed and the same healthy animals were used during the subsequent 8 months.

### Stimulus presentation

Amino acid stimuli (Fluka; Chemika-Bio-Chemika, Fluka Chemie AG, Buchs, Switzerland) were delivered from Pasteur pipettes operated via an air pressure system from a distance of 3 m. The air pressure system consisted of 3 ml syringes connected through Tygon tubing (0.3 mm inner diameter) to other 3 ml syringes suspended above each aquarium to which Pasteur pipettes were attached. Prior to testing, the removable Pasteur pipettes were washed in hot water five times for 1 min each and equilibrated five times for 2 min each with dechlorinated tap water from the same water source which supplied the aquaria. To ensure that stimulus eddies ('odor plumes') reached the fish in <30 s, two stimulus delivery pipettes were positioned near the front glass at opposite ends of each aquarium. The two 2 ml Pasteur pipettes were discharged simultaneously into the water surface, which was intensely distorted by the aeration system. Injection of control and test solutions onto the turbulent area of each aquarium eliminated the possibility that the rainbow trout used the distortion of the water surface during the addition of a test chemical as either a visual or mechanical stimulus. Within 3 s after stimulus delivery, the test chemicals were diluted >300-fold; within 5–25 s, the time within which the stimulus contacted the fish, a 300- to 3000-fold dilution of chemicals occurred within the most concentrated nuclei of the stimulus eddies (odor plumes) (Valentič *et al.* 1994a). This estimated diluted concentration of the stimulus which reaches the fish is termed the 'contact concentration'. After 2 min, 0.01 and 1 M amino acid stimulus solutions in the 210 l aquaria were diluted to  $2 \times 10^{-7}$  and  $2 \times 10^{-5}$  M respectively. The same stimulus was diluted to  $10^{-7}$  and  $10^{-5}$  M respectively, in 420 l aquaria. Two parameters of feeding activity, swimming and biting/snapping, were evaluated from video recordings of experimental sessions. Swimming activity was measured by counting the number of turns of the fish which were >90° for 90 s subsequent to stimulus presentation, whereas consummatory biting/snapping activity was quantified by counting the number of bites/snaps that occurred during this 90 s period. The fish were not rewarded after stimulation with amino acids.

The present experiments were conducted in a manner that reduced the possibility that fear and escape behavior would be released in rainbow trout that would conflict with feeding excitation and behavior. During the application of a chemical stimulus to an aquarium, two individuals, one video-recording (JVC, sVHS) the fish, the other operating

the stimulus injection system, were positioned >2.5 m away from the aquaria and out of visual range of the fish. Prior to the presentation of a visual stimulus (i.e. either the head or arm of the person that regularly fed the fish), the animals were first conditioned to the presence of the experimenter in front of the aquarium. During video-recordings, each aquarium was illuminated by two 60 W tungsten bulbs, while the room was kept at low light conditions. Precautions, such as masking the signal light of the camera, were taken to eliminate the possibility of the trout visually detecting the camera. Each test experiment was preceded or followed by a control water presentation. Control experiments were also video-recorded and subsequently evaluated.

### Anosmic animals

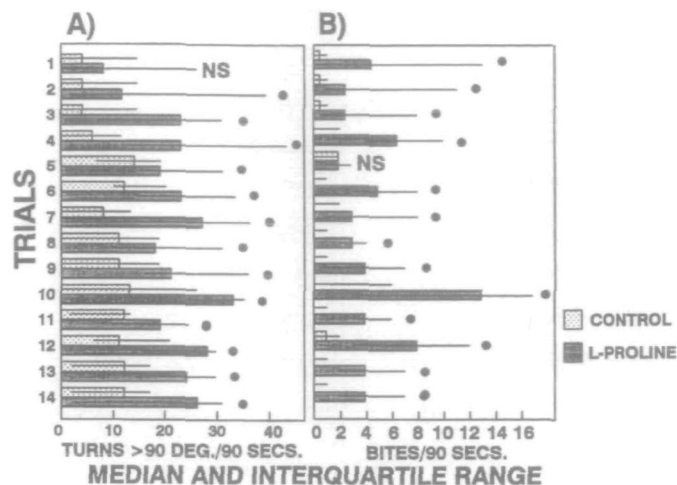
To produce anosmic rainbow trout, the olfactory organs were extirpated under Tricaine (ethyl-3-aminobenzoate methanesulfonate) (1:8000) anesthesia presented in the gill irrigation water. Immediately after the surgery, the fish were released into a heavily aerated aquarium where they recovered within 10–30 min and accepted food on the same day. The first experiments with anosmic rainbow trout were conducted 5 months after the surgery, subsequent to the surgical wound being re-covered by connective tissue. At this time, the animal's responsiveness to visual stimuli was not influenced by past surgical procedures. No regeneration of the olfactory organ was observed in rainbow trout 8 months after bilateral removal of their olfactory organs.

### Statistics

Since in the present experiments the criteria (i.e. homogeneity of variance and normal distribution of the data) needed for the application of parametric statistics were not met, a non-parametric statistic (Wilcoxon rank test) was applied to compare the number of turns and bites/snaps during control and test periods; the data were therefore presented as medians and interquartile ranges.

### Results

Food searching behavior in adult rainbow trout is composed of swimming, turning, biting/snapping and the picking-up of potential food items. In the present experimental conditions, these behaviors were released by visual and chemical stimuli. Visual stimuli included the experimenter who provided the food reward in the experi- mental

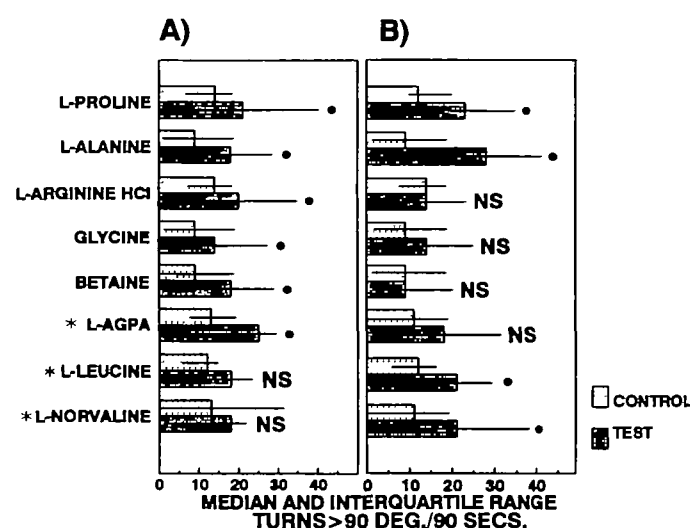


**Figure 1** Searching (A) and biting/snapping (B) behaviors.  $n = 11$  fish/trial (turning and biting behaviors were evaluated in the same experiments). Contact concentration = 0.3–3.0 mM. For Figures 1–6, compounds marked with dot indicate a significantly greater ( $P < 0.05$ ;

paradigm and food items, such as pieces of cod flesh. Chemical stimuli were amino acids which potentially activated both taste and olfactory systems of the rainbow trout. The biting/snapping behavior of rainbow trout occurred in a variety of contexts: (i) repeated non-directed bites/snaps without additional stimulation during search swimming; (ii) repeated non-directed bites/snaps in the area of air bubbles emanating from the aeration system; (iii) directed bites/snaps aimed at stones at the bottom of the aquarium which were taken into the mouth, chewed and ejected; the fish also picked up and subsequently spit out small inedible objects suspended in the aquarium water; (iv) directed bites/snaps at the aquarium walls and air tubing.

Rainbow trout usually began searching and/or biting activity within 6–30 s after stimulus injection into the aquarium. Swimming (Figure 1A) and biting (Figure 1B) behaviors were released within a few seconds of L-proline contact (0.3–3 mM). Rainbow trout generally responded with rapid turns and sometimes swimming in a circle within the cloud of the diluted L-proline stimulus. The repeatability of the results for the swimming and snapping behaviors which did not exhibit habituation is indicated in Figure 1, where 14 L-proline tests were presented to the same 11 rainbow trout. In 12 tests, the number of turns >90° made by the rainbow trout after L-proline stimulation was significantly ( $P < 0.05$ ) greater (>2-fold) than after presentations of water controls (Figure 1A). The fish also bit significantly more during presentations of L-proline than

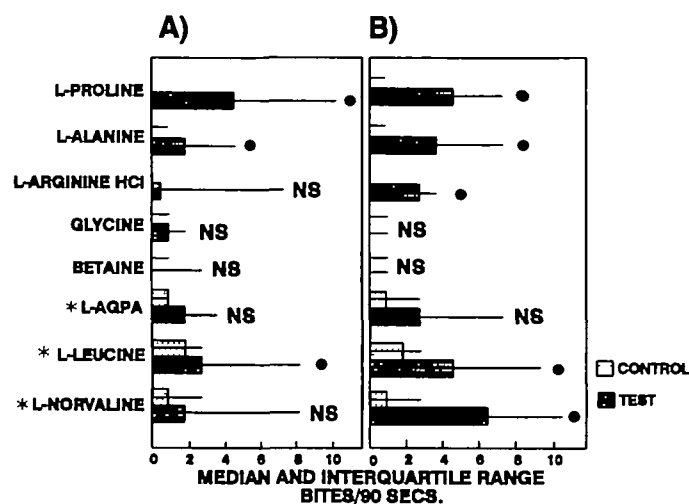




**Figure 2** The effectiveness of different compounds in releasing swimming behavior measured as turns  $>90^\circ$  at low (A) (0.003–0.03 mM) and high (B) (0.3–3.0 mM, 0.03–0.3 mM only for those indicated by an asterisk) stimulus concentrations. In Figures 2 and 3, \* indicates that a different test concentration was applied as described in the Results section. The same 11 fish were tested in panels (A) and (B). AGPA, L- $\alpha$ -amino- $\beta$ -guanidino propionic acid.

did water controls (Figure 1B). The median number of bites in nine of 14 tests was greater than four; the highest median value in the 14 tests with 11 animals each was 13 bites, whereas the lowest median value was two bites. With one exception, the lower quartile values were  $>0$ , indicating that during L-proline stimulation, the activities of the least active fish were also increased.

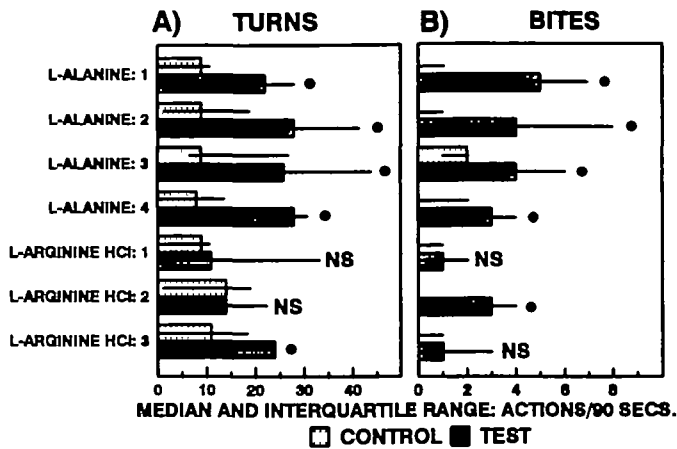
In the second group of tests, the stimulatory effectiveness of eight different low molecular compounds to induce swimming and biting behaviors was compared at two different concentrations. At estimated contact concentrations of 0.003–0.03 mM, L-proline, L-alanine, L-arginine HCl, glycine, betaine and L- $\alpha$ -amino- $\beta$ -guanidino propionic acid (AGPA) released a significantly greater (2-fold) increase in the number of turns  $>90^\circ$  than did water controls (Figure 2A). The effectiveness of the amino acids tested at different contact concentrations in releasing biting activity was, however, rather inconsistent. At the higher concentrations (0.3–3.0 mM for most compounds and 0.03–0.3 mM for L-AGPA, L-leucine and L-norvaline) tested, only L-proline, L-alanine, L-leucine and L-norvaline released a significantly larger number of turns than did water controls (Figure 2B). At micromolar concentrations L-proline, L-alanine and L-leucine released significantly more bites than did controls (Figure 3A). L-proline, L-alanine, L-leucine and L-norvaline were effective in releasing biting activity at 0.3–3.0 mM



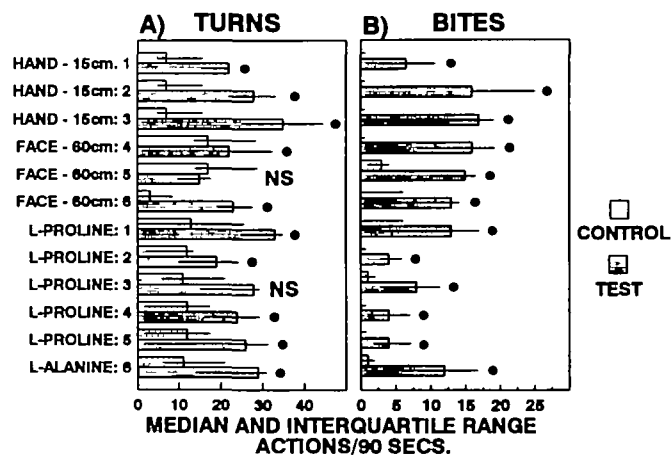
**Figure 3** The effectiveness of different compounds in releasing biting/snapping behavior at low (A) (0.003–0.03 mM) and high (B) (0.3–3.0 mM, 0.03–0.3 mM only for those indicated by an asterisk) stimulus concentrations. The same 11 fish were tested in panels (A) and (B). AGPA, L- $\alpha$ -amino- $\beta$ -guanidino propionic acid.

concentrations. The increase in swimming activity in response to the effective amino acids was always more than twice that of controls. L-proline and L-alanine (0.3–3.0 mM) also released a significantly greater number of bites, which usually occurred within 15 s after the onset of the swimming activity, than did water controls (Figure 3B). AGPA (0.03–0.3 mM) was a relatively ineffective stimulus behaviorally, whereas L-leucine and L-norvaline were highly stimulatory, at least at the higher concentration tested (Figures 2 and 3). Biting responses to L-proline at 0.3–3.0 mM contact concentrations were by far the most consistent response to any of the chemicals tested (Figure 1B). When tested successively (during four repetitions), 0.3–3.0 mM contact concentrations of L-alanine were a more consistent stimulus in releasing swimming (Figure 4A) and biting (Figure 4B) behaviors than was L-arginine HCl.

In response to a conditioned visual stimulus (i.e. either the hand or face of the laboratory technician at a 20–60 cm distance from the aquarium) and in the absence of chemical stimulation, food search activity of rainbow trout was increased to the same level as that released by 0.3–3.0 mM L-proline and L-alanine (Figure 5A). The visual and chemical stimuli were presented successively. The visual stimulus preceded or was followed by the chemical stimulus. The increase in search activity after L-proline stimulation was more consistent than that after visual stimulation. In contrast, the number of bites during the intermittent visual stimulation (animals mostly bit towards the presented hand)



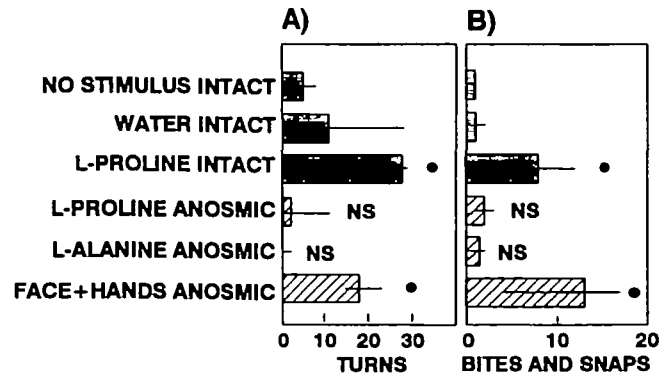
**Figure 4** Comparison of the effectiveness of L-alanine and L-arginine in releasing turning  $>90^\circ$  (A) and biting (B) behaviors. Contact concentrations 0.3–3.0 mM. Numbers adjacent to each stimulus indicate different tests with 11 fish each. For Figures 4 and 5, swimming (A) and biting (B) behaviors were counted during the video replay of the same experiments with 11 fish.



**Figure 5** Comparison of turning (A) and biting (B) responses to visual and amino acid stimuli. Contact concentrations 0.3–3.0 mM.

was greater than that during L-proline stimulation. More than 10 median number of bites occurred after visual stimulation with the conditioned visual stimulus (Figure 5B). The potency of L-proline in releasing biting behavior was usually less than that of the conditioned visual stimulus alone.

In a final series of experiments, anosmic rainbow trout were tested for their responsiveness to chemical and visual stimuli 5 months subsequent to the bilateral removal of their olfactory organs. The behavioral responsiveness of these anosmic rainbow trout, except for those actions controlled by olfaction, recovered within 1 month of the surgery.

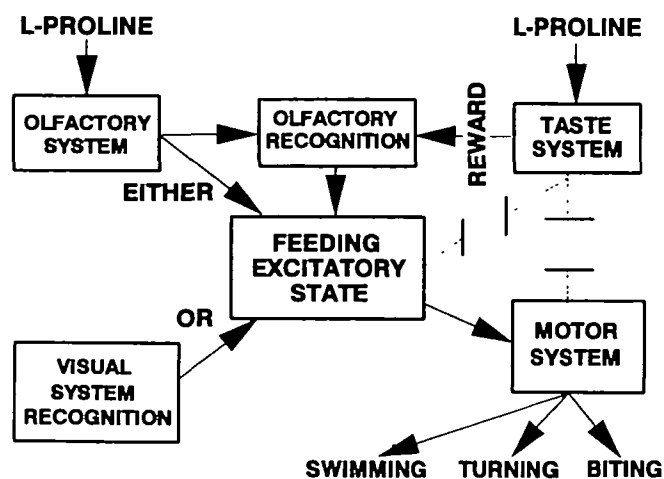


**Figure 6** Comparison of turning (A) and biting/snapping (B) behavior to visual and chemical stimuli in intact ( $n = 11$ ) and anosmic rainbow trout ( $n = 9$ ).

Anosmic rainbow trout responded with swimming and biting to visual, but not to amino acid, stimulation (Figure 6). Swimming activity was completely absent subsequent to stimulation with L-proline and L-alanine, whereas swimming activity to visual stimulation was unaffected (compare with Figures 5A and 6A). Similarly, biting activity during visual stimulation was not significantly reduced in anosmic rainbow trout compared with intact animals, whereas biting activity was not released after chemical stimulation in anosmic rainbow trout. The small spontaneous bites which occurred infrequently in anosmic rainbow trout were unrelated to chemical stimulation and were also not as large as those released by olfactory stimulation in intact rainbow trout.

## Discussion

Although feeding excitation within the central nervous system (CNS) of rainbow trout is primarily initiated following either appropriate visual or olfactory stimulation, visual control is predominant in the control of feeding behavior (Figure 7). In addition to learned visual identification of food, visual control of feeding behavior provides immediate directional and distance cues, whereas olfaction indicates, at least initially, only the presence and possibly the identity of the chemical stimulus. In the present experiments when feeding behavior was released by only visual stimuli (e.g. the experimenter), rainbow trout searched for food and snapped/bit even in the absence of chemical feeding stimuli. The snapping and biting behaviors are an innate part of ongoing feeding behavior. Even channel catfish, which have exquisite senses of both taste



**Figure 7** Postulated release of feeding behavior by visual, olfactory and taste stimuli

and smell, respond with swimming and turning behavior to conditioned visual stimuli (T. Valentinčič, unpublished data).

The present results clearly showed that unlike channel catfish, where both food search and ingestion can be released by taste stimuli alone (Bardach *et al.*, 1967; Valentinčič and Caprio, 1994b), olfaction is essential in adult rainbow trout for the release of feeding behavior by chemical stimuli (Figure 6). Although taste alone can release food search and biting in catfish, olfactory input is essential for discrimination among chemicals (Valentinčič *et al.*, 1994a,c). The present report clearly shows that in the absence of visual stimuli, a functioning olfactory system is obligatory for food search and biting/snapping behavior in adult rainbow trout (Figure 7). There was no generalized depression of the feeding behavior of rainbow trout following bilateral removal of the olfactory organs since animals responded to visual stimuli with the complete sequence of feeding motions. In addition, prior behavioral studies indicated that active feeding responses occurred subsequent to bilateral olfactory organ removal in catfish (Valentinčič *et al.*, 1994) and to bilateral olfactory bulb ablation in goldfish (Hoyk *et al.*, 1993).

Rainbow trout were tested behaviorally with amino acid stimuli at concentrations above their electrophysiologically determined olfactory (0.01  $\mu$ M; Hara, 1973) and taste (0.1  $\mu$ M; Marui *et al.*, 1983) thresholds for these chemicals. However, after bilateral removal of their olfactory organs, the fish did not respond to amino acids with either searching or biting activities (Figure 6), indicating the essential requirement of the olfactory system in feeding behavior in

this species. The biting/snapping behavior released by amino acids in intact rainbow trout occurred only during search swimming behavior. The small spontaneous bites observed in anosmic rainbow trout were apparently random and independent from taste stimulation. The mechanisms for promoting excitation within the CNS to release both feeding and reflexive biting/snapping behaviors by gustation alone apparently do not exist for adult rainbow trout which have a much reduced facial taste system in comparison with catfish (Atema, 1970).

The hypothesis that the more stimulatory amino acids to the taste system are concurrently detected by olfaction and are recognized by the animal was tested. If olfaction alone was responsible for promoting feeding excitation in the adult rainbow trout, a reasonable expectation would be that the most stimulatory odorant would also be the most effective stimulus in releasing feeding behavior. However, L-proline, the most potent taste stimulus (Marui *et al.*, 1983), but a relatively poor olfactory stimulus (Hara, 1973), was the most effective stimulus tested at releasing swimming and biting behavior in adult rainbow trout. L-Proline was a more effective feeding stimulus than some of the highly stimulatory odorants for rainbow trout. L-Alanine, which is highly stimulatory to both chemosensory systems (Hara, 1977; Marui *et al.*, 1983), was also effective at releasing feeding activity. In contrast, L-arginine, a highly effective olfactory stimulus (Hara, 1973), but non-stimulatory to the taste system at the concentrations tested (Marui *et al.*, 1983), was rarely effective behaviorally in spite of its high olfactory potency (Figure 4). Since L-arginine is not detected at low concentrations by the taste system of the rainbow trout and therefore is not part of the food reward, it did not become an olfactory conditioned stimulus for feeding behavior. Due to the narrow tuning of the taste system of adult rainbow trout (Marui *et al.*, 1983; J. Kohbara and J. Caprio, unpublished data), few amino acids (e.g. L-proline, L-hydroxyproline, L-leucine, L-alanine, L-phenylalanine) can provide such a rewarding chemical taste experience that could act as a reinforcer of feeding behavior subsequent to the intake of food containing these stimuli.

The sequential events of feeding behavior which follow food searching behavior are food intake, intra-oral evaluation, mastication, swallowing, ejection and regurgitation. A previous report indicated that intra-oral evaluation, retention and swallowing behaviors of rainbow trout were best released by proline, leucine, phenylalanine and alanine (Jones, 1989). Cotton pellets containing any of these amino

acids were retained for longer periods of time than were control pellets. A major finding of the present experiments indicates that the same stimuli which promoted the sustained retention of amino acid-soaked cotton pellets within the mouth of rainbow trout also releases swimming, turning and biting behaviors in this species. However, dependent upon the state of the animal, the same compounds that release feeding can also release escape behavior (Valentinčič and Caprio, 1994a). L-Alanine, L-serine, L-histidine and L-threonine, some of the more stimulatory olfactory stimuli determined electrophysiologically for rainbow trout (Hara, 1973), were reported to trigger escape (i.e. avoidance) behavior in coho salmon (Rehnberg *et al.*, 1986). Coho salmon avoided ('escaped' in ethological terms) the arm of the Y maze that contained these amino acids; however, behavioral testing of the salmon began within 10 min of their being transferred to the maze, a time too short for the fish to have acclimated to their new environment. In such conditions, fear and escape behavior inhibit all other behavior patterns, including feeding. It is possible that escape behavior to a novel amino acid stimulus was observed in the Coho study, rather than particular amino acids acting as specific escape stimuli. For example, in the present experiments, L-alanine released food search and biting/snapping behaviors in rainbow trout which had been acclimated to their surroundings for weeks.

## ACKNOWLEDGEMENTS

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## REFERENCES

- Atema, J. (1971) Structures and functions of the sense of taste in the catfish, *Ictalurus natalis*. *Brain Behav Evol*, **4**, 273–294.
- Bardach, J.E., Todd, J.H. and Crickmer, R. (1967) Orientation by taste in fish of the genus *Ictalurus*. *Science*, **155**, 1276–1278.
- Caprio, J. (1978) Olfaction and taste in the channel catfish. an electrophysiological study of the responses to amino acids and derivatives. *J Comp Physiol. A*, **123**, 357–371.
- Davenport, C.J. and Caprio, J. (1982) Taste and tactile recordings from the ramus recurrens facialis innervating flank taste buds in the catfish. *J. Comp. Physiol. A*, **147**, 217–229.
- Hara, T.J. (1973) Olfactory responses to amino acids in rainbow trout, *Salmo gairdneri*. *Comp. Biochem. Physiol. A*, **44**, 407–416.
- Hara, T.J. (1977) Further studies on the structure–activity relationships of amino acids in fish olfaction. *Comp Biochem Physiol. A*, **56**, 559–565.
- Hoyk, Z., Lago-Schaff, T., Zippel, H.-P., Fuzesi, G. and Halasz, N. (1993) Fast regeneration of the olfactory tract in goldfish: fine structure and behavior. *J. Hirnforsch.*, **34**, 461–465.
- Jones, K.A. (1989) The palatability of amino acids and related compounds to rainbow trout, *Salmo gairdneri*, Richardson. *J. Fish Biol.*, **34**, 149–160.
- Kanwal, J.S. and Caprio, J. (1983) An electrophysiological

- investigation of the oro-pharyngeal (IX-X) taste system in the channel catfish, *Ictalurus punctatus*. *J. Comp. Physiol. A*, **150**, 345–357.
- Kohbara, J., Michel, W. and Caprio, J. (1992) Responses of single facial taste fibers in the channel catfish, to amino acids. *J. Neurophysiol.*, **68**, 1–15.
- Lindstedt, K.J. (1971) Chemical control of feeding behavior. *Comp. Biochem. Physiol.*, **39A**, 553–581.
- Marui, T., Evans, R.E., Zielinski, B.S. and Hara, T.J. (1983) Gustatory responses of the rainbow trout (*Salmo gairdneri*) palate to amino acids and derivatives. *J. Comp. Physiol. A*, **153**, 423–433.
- Rehnberg, B.G. and Schreck, C.B. (1986) The olfactory L-serine receptor in coho salmon: biochemical specificity and behavioral response. *J. Comp. Physiol. A*, **159**, 61–67.
- Valentičič, T. and Caprio, J. (1994a) Chemical and visual control of feeding and escape behaviors in the channel catfish *Ictalurus punctatus*. *Physiol. Behav.*, **55**, 845–855.
- Valentičič, T. and Caprio, J. (1994b) Consummatory feeding behavior in intact and anosmic channel catfish *Ictalurus punctatus* to amino acids. *Physiol. Behav.*, **55**, 857–863.
- Valentičič, T., Wegert, S. and Caprio, J. (1994) Learned olfactory discrimination versus innate taste responses to amino acids in channel catfish, *Ictalurus punctatus*. *Physiol. Behav.*, **55**, 865–873.

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