

ences, as well as a quantifiable assessment of statistical significance.

The analysis revealed that in the case of occipital recordings, none of the four subjects showed any significant difference related to the context of the ambiguous stimulus: that is, none of the rotated eigenvectors were differentially loaded on "B" and "13" wave forms. In the case of frontal recordings, three of the four subjects showed differential loadings on one or more factors. The subject with simultaneous recordings for occipital and frontal locations showed significantly different loadings on recordings from the frontal location and no difference in the occipital recordings.

Figure 2 shows an example of the eigenvectors extracted from frontal recordings for one subject, together with the "B" and "13" wave forms averaged over all experimental sessions. In this case, four factors accounted for more than 85 percent of the total variance. Only factor 2 (f2), which begins 160 msec after stimulus presentation, is differentially loaded on "B" and "13" ($U = 0$, $P < .002$). Frontal recordings for two other subjects also showed differential loading on a similar factor temporally located on this part of the wave form ($U = 0$, $P < .002$; $U = 1$, $P < .004$). This suggests that the most significant difference between "B" and "13" wave forms occurs in the late components, starting 160 msec after the stimulus. In addition, one frontal recording subject had a significantly different loading on a second factor which accounted for 5.9 percent of the variance ($U = 0$, $P < .002$). This factor (f4) was temporally located between 100 and 140 msec after stimulus presentation. Comparable factors in two other frontal recording subjects also showed a trend in this direction ($U = 8$, $P < .066$; $U = 7$, $P < .047$).

There was no significant difference between the reaction time to a "B" or a "13" over all subjects. This suggests that the observed differences in the wave forms cannot be accounted for by differences in the arousal level or attention of the subjects. Differences due to corneoretinal potentials are improbable since they were almost eliminated by the procedure described earlier, and it appears unlikely that differential eye movements would occur in response to a 10- μ sec flash of the same stimulus in the two different contexts.

Our results demonstrate that late components of the evoked potential wave form, recorded from the frontal

areas of the brain, reflect neural activity correlated with the meaning of the stimulus. No such differences can be detected from the visual cortex. Begleiter *et al.* (9) also reported meaning-correlated changes in VEP's recorded from the vertex but not from occipital locations. They recorded the evoked potential in response to a medium-intensity flash presented several seconds after an auditory stimulus that was predictive of a bright flash or of a dim flash. They found that late components of stimulus-locked potentials recorded from the vertex changed as a result of these two different temporal contexts. These findings suggest that the visual cortex may be concerned with the representation of the physical characteristics of the stimulus, but the frontal areas may be more involved in the subsequent representation of meaning.

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Gastric Brooding: Unique Form of Parental Care in an Australian Frog

Abstract: *The recently described leptodactylid frog Rheobatrachus silus of Queensland, Australia, exhibits a unique form of parental care. The female carries embryos and young in the stomach, propulsively ejecting the juveniles.*

Although most frogs play no active role in ensuring the survival of their offspring, a number have independently evolved quite elaborate forms of parental care. These range from the transport of eggs or tadpoles by one of the parents to the formation of dermal or subdermal pouches in which the embryos undergo their entire development. Because some of the life cycles are so bizarre, they have been cited widely in the popular and scientific literature. Here we report a unique type of parental care exhibited by the Australian leptodactylid frog *Rheobatrachus silus*: transport and brooding of larvae and juveniles in the stomach of the female frog.

Rheobatrachus silus is an aquatic, stream-dwelling frog recently discovered near Brisbane, Queensland, Australia (1). This monotypic leptodactylid genus is morphologically unlike any other in Australia, and in its general body form it resembles the African pipid *Xenopus*, maintained in laboratories throughout the world.

1. E. R. John, R. N. Herrington, S. Sutton, *Science* **155**, 1439 (1967).
2. H. G. Vaughan and R. C. Hull, *Nature (Lond.)* **206**, 720 (1965); T. Shipley, R. W. Jones, A. Fry, *Science* **150**, 1162 (1965); M. Buchsbaum and J. Silverman, *Psychosom. Med.* **30**, 12 (1968); D. Regan, *Nature (Lond.)* **210**, 1056 (1966); J. D. Wicke, E. Donchin, D. B. Lindsley, *Science* **146**, 83 (1964).
3. E. Donchin, *IEEE (Inst. Electr. Electron. Eng.) Trans. BioMed. Eng.* **13**, 131 (1966).
4. H. Begleiter and A. Platz, *Science* **166**, 769 (1969); H. Begleiter, M. M. Gross, B. Kissin, *Psychophysiology* **3**, 336 (1967).
5. S. Sutton, M. Braren, J. Zubin, *Science* **150**, 1187 (1965); R. M. Chapman and H. R. Bragden, *Nature (Lond.)* **203**, 1155 (1964); E. Garcia-Austt, J. Bogacz, A. Vanzulli, *Electroencephalogr. Clin. Neurophysiol.* **17**, 136 (1964); W. Grey Walter, R. Cooper, V. J. Aldridge, W. C. McCallum, A. L. Winter, *Nature (Lond.)* **203**, 380 (1964); M. Haider, P. Spong, D. B. Lindsley, *Science* **145**, 180 (1964); H. Davis, *ibid.*, p. 182; M. M. Gross, H. Begleiter, M. Tobin, B. Kissin, *Electroencephalogr. Clin. Neurophysiol.* **18**, 451 (1965).
6. E. J. Gibson, H. Osser, A. D. Peik, *J. Verb. Learn. Verb. Behav.* **2**, 142 (1963).
7. At the digitizing rate of 500 points per second, only one channel of data could be collected by using the available computer memory. By reducing the rate to 250 points per second, it was possible to collect both channels simultaneously in the final subject.
8. W. C. McCallum and W. Grey Walter, *Electroencephalogr. Clin. Neurophysiol.* **25**, 319 (1968).
9. H. Begleiter, B. Porjesz, C. Yerre, B. Kissin, *Science* **179**, 814 (1973).

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Evidence of the brooding habits was first obtained on 23 November 1973, when an adult frog collected 19 days previously was about to be transferred from one aquarium to another. This individual was of unusually large girth, the lateral surfaces appearing particularly distended. After rocks and other material had been removed from the original aquarium the frog swam haphazardly, seeking the sort of refuge beneath which it had normally hidden. It then rose to the surface of the water and, after compression of the lateral body muscles, propulsively ejected from the mouth six living tadpoles. Three of them were immediately preserved; one is shown in Fig. 1a.

In the new aquarium the frog spent most of its time drifting passively in a vertical position, with the arms and legs extended and the head so oriented that the eyes and nostrils remained above the surface of the water. This pose proved ideal for direct observation, for when the frog drifted near the glass, the abdominal region was

clearly visible. The occasional movements of additional young adpressed against the body wall could be readily seen.

On 11 December 1973 (37 days after capture and 18 days after the disgorgement of the tadpoles), a juvenile frog was found swimming in the aquarium with the adult. Two days later two more juveniles were found, and it was decided to preserve the adult in the hope of finding other juveniles in situ. However, when the adult was grasped by the hind limbs, it underwent extreme dorsiflexion, simultaneously elevating the head and opening the mouth widely. Eight juvenile frogs were then propulsively ejected in groups of two or three in no more than 2 seconds. Two further juveniles were ejected after a few minutes and, 30 seconds after the frog had been transferred to preservative, three more were disgorged similarly. Of the 16 juveniles, three were preserved; one is depicted in Fig. 1b. Their snout-to-vent lengths ranged from 12.5 to 13.0 mm.

Of the tadpoles obtained on 23 November, three were preserved, two were transferred to a separate tank for observation, and one was left with the parent and an accompanying adult male. This last tadpole disappeared without trace, so we are uncertain whether it was taken by the parent or devoured by the second adult. Thus the total number of progeny held by the parent is uncertain, being either 21 or 22.

Postmortem examination of the adult frog revealed that it was a female with a snout-to-vent length of 45.8 mm. Other than those in the abdominal region, there were no anatomical modifications relevant to the habit of parental care. The abdominal cavity was noteworthy only in that the stomach was exceptionally large and thin-walled, and occupied a medial rather than the customary sinistral position. The ileum was convoluted but short, and the rectum was not empty. The muscles surrounding the lateral and ventral borders of the abdominal cavity were exceptionally thin, presumably a consequence of their recent gross and prolonged distension. Other specimens of this species deposited in the collection of the South Australian Museum lacked these modifications.

The tadpoles constitute an unusual morphological type. The existence of large yolk reserves in the abdomen at such an advanced stage of development is indicative of macrolecithal ova, and we assume that the internal food re-

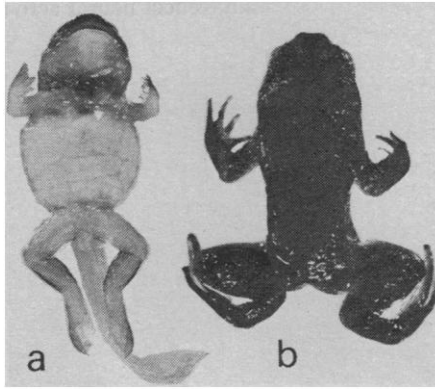


Fig. 1. Progeny of *Rheobatrachus silus*: (a) tadpole disgorged by adult and (b) juvenile frog disgorged by same adult 18 days later. [Photographs: D. N. Caville]

serves are adequate for the entire period of development. In such a situation, persistence of a tail appears superfluous because, in frogs in which the larval stages are passed on land within the vitelline membranes (such as *Asterophryne* and *Sphenophryne* microhylids and many New Guinea ranids), the tail is usually rudimentary. The tail of *R. silus* is large, and is unusual in having flexure of the posterior half. In this respect, *R. silus* tadpoles are similar to those of *Rhinoderma darwini* of Chile (2), which are carried in the enlarged vocal sac of the male frog.

In water, the disgorged tadpoles of *R. silus* appeared quite out of their element and survived for only 2 days. Most of the time they were inactive, either floating on the surface of the water or lying at the bottom of the tank. When gently prodded, they would swim rapidly, either horizontally or downward. Swimming upward appeared to require a great deal of effort, and the tadpoles were often unsuccessful. Swimming entailed vigorous movements of the tails and limbs.

The form of parental care exhibited by *Rheobatrachus silus* is completely without parallel among vertebrates. There are many fish species, representing numerous genera and several families, in which males or females take eggs into their mouths and transport them about. However, the eggs are not swallowed (3), but are retained in the buccopharyngeal cavity (oral incubation). Many anurans become involved in the protection of their eggs, but there are few species that transport their young (4). *Rheobatrachus silus* is unique in regard to the major physiological and behavioral adaptations of the assumed parent. For example, we

assume that there is total inhibition of gastric secretions and digestive processes. It is implicit that the control mechanism for the inhibition is under the influence of reproductive hormones, for an intimate interaction is required. Anurans vary in the mechanism of control of gastric secretions, but the case of *R. silus* appears to substantiate evidence that there is hormonal control in some species (5).

The behavioral adaptation of failing to feed is a matter of necessity, not simply because of the inability to digest, but because of the incredible demands on the potential capacity of the stomach in which the young are retained. Although the existence of stretch receptors in the stomach of anurans comparable to those in mammals (6) has yet to be demonstrated, evidence of the experience of satiation in one *Bufo* species can be inferred from the way in which the size of the food item selected is associated with the volume of food previously ingested by the individual (7).

Salthe and Duellman (4) indicated that most examples of anuran parental care occur in the Neotropical region. However, they did not list *Assa darlingtoni* (8), which occurs in cool, montane rain forests bordering Queensland and New South Wales. The male of that species was discovered to carry tadpoles in subdermal, inguinal pouches (9). The habit of parental care reported here for the recently discovered species *R. silus* bears testimony to the probable existence of major gaps in the current knowledge about vertebrates.

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References and Notes

1. D. S. Liem, *Mem. Queensl. Mus.* 16, 459 (1973).
2. G. K. Noble, *Ann. N.Y. Acad. Sci.* 30, 31 (1927).
3. C. M. Breder and D. E. Rosen, *Modes of Reproduction in Fishes* (Natural History Press, New York, 1966).
4. S. N. Salthe and W. E. Duellman, in *Evolutionary Biology of the Anurans*, J. L. Vial, Ed. (Univ. of Missouri Press, Columbia, 1973), pp. 229-249.
5. W. G. Reeder, in *Physiology of the Amphibia*, J. A. Moore, Ed. (Academic Press, New York, 1964), pp. 99-149.
6. A. S. Paintal, *J. Physiol. (Lond.)* 126, 255 (1954).
7. H. Heatwole and A. Heatwole, *Copeia* 1968, 692 (1968).
8. M. J. Tyler, *Zool. Meded. R. Mus. Nat. Hist. Leiden* 47, 193 (1972).
9. I. R. Straughan and A. R. Main, *Proc. R. Soc. Queensl.* 78 (No. 2), 11 (1966).

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