this curve with the actual intensity along the arc in the visual field. Now if the real and the effective inputs are considered as wave forms, it will be seen that the effective input will lack some of the higher frequency components of the real input. The extent of this high-frequency loss is related to the degree of smoothing caused by the ommatidium, and this in turn is roughly related to the breadth of its polar acceptance curve (*4*). The exact relations are best expressed in the Fourier domain: with Parseval's theorem, the Fourier transform of the effective input is the product of the transform of the real input with the transform of the polar acceptance curve. Thus it is the highest frequency in the transform of the polar acceptance curve that determines the highest frequency in the effective ommatidial input. It is true that the breadth of the curve gives a guide to this, but the detailed shape is important, and in this connection it is worth pointing out that the Gaussian shape commonly assumed for the polar acceptance is actually impossible: its transform includes all frequencies, whereas those beyond the diffraction limit must be wholly demodulated.

So far, it has not been mentioned that ommatidia occur only at certain fixed positions separated by the interommatidial angle. This is equivalent to the height of a waveform being measured at certain points and, according to Shannon's theorem (*5*), such sampling causes no loss of information if the sample interval is less than half the shortest wavelength contained in the wave form. Now the interesting point about diffraction is that it places an absolute upper limit to the frequencies contained in the effective input: there can be no frequencies whatever above λ/d (*6*). From this it follows that it would be uneconomical for insect eyes to have interommatidial angles much less than $\lambda/2d$, and I do not think this has ever been reported. What is remarkable is that this value does seem to be approached in the central zone of the bee's eye, and in those of the other diurnally adapted Hymenoptera of widely varying eye size and ommatidial number (*7*). It is difficult to see why the insect eye obeys the dictates of the diffraction limit and Shannon's sampling theorem unless, in these cases, spatial frequencies close to the diffraction limit are passed by the ommatidia. The well-designed eyes of these Hymenoptera provide an example in which the anatomical arrangement of the ommatidia is well matched to the number of the degrees of freedom in the available input.

In other cases, especially where the eye has to work under low illumination, the polar acceptance of the ommatidia is doubtless broader than diffraction would necessitate. As Gotz (*4*) has shown, where this is so the interommatidial angle can also be greater without any information being lost. It is interesting to consider those instances where the interommatidial angle is greater than half the highest spatial frequency passed by the ommatidia, for then the high frequencies are not adequately sampled and can lead to the false appearance of spatial frequencies which were not present in the real input. These spurious components must be the ones responsible for the reversed optomotor responses in certain insects which Hassenstein (*8*) has described and others (*9*) have investigated intensively. Thus, these misdirected beetles illustrate one possible consequence of the number of ommatidia being improperly matched to the number of degrees of freedom in the effective input.

In spite of reports of broad acceptance curves and resolution beyond the diffraction limit there is no need to abandon Exner's classical description of the mode of function of the apposition compound eye, and diffraction at the ommatidial lenslet still appears to be the physical factor limiting the evolution of higher acuity in this type of eye. In some instances the number of ommatidia is well matched to the number of degrees of freedom in the effective optical input, but in others the number is too low and in these instances reversed optomotor responses to moving gratings can occur.

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10. I thank John Palka, G. Westheimer, and others for their helpful discussions. Part of the apparatus for this experiment was purchased under a Fight for Sight grant-in-aid of the National Council to Combat Blindness, Inc., New York.

31 March 1965

Sound Production by Cichlid Fishes

Abstract. *Adults of three cichlid species,* Hemichromis bimaculatus *Gill,* Cichlasoma nigrofasciatum *(Günther), and* Pterophyllum *sp., produce sounds of apparent biological significance. Both sexes of* H. bimaculatus *produce sounds, but whether both sexes in the other species produce sounds has not been established. The most intense tone frequencies in* H. bimaculatus *and* C. nigrofasciatum *lie generally between 300 and 500 cycles per second. The sound produced by* Pterophyllum *sp., however, has a broad maximum intensity around 3500 cycles per second and component frequencies over 10,000 cycles per second. Sound production appears to depend on the aggressiveness of the individual.*

Underwater sounds produced by fishes play an important role in the life of some species (*1*). Until now, however, over 95 percent of the species known to produce sound were members of either marine families or fresh-water cypriniform families. The only evidence that a fish of the fresh-water, noncypriniform family Cichlidae produced sounds was that of Bauer (*2*) who described a sound, heard outside the aquarium, made by a courting male of *Tilapia nilotica* (Linnaeus). We have now demonstrated that other species also produce underwater sounds, but the sounds are not of such intensities as to extend beyond the confines of the aquarium.

The sounds were recorded from three cichlid species, each representing a wide geographic area: *Hemichromis bimaculatus* Gill (Africa), *Cichlasoma nigrofasciatum* (Günther) (Central America), and *Pterophyllum* sp. (probably *P. scalare* C & V) (South America). Pairs and small groups of fishes were maintained and tested in 180-liter aquaria with water temperatures ranging between 25° and 27.5°C. The bottoms of the aquaria were covered with medium-sized gravel; overturned flower pots, spawning slates, and various types of vegetation were present.

The aquaria were placed at least 15 cm apart and were monitored separately with a hydrophone for various lengths of time (usually ½ to 1 hour in a single aquarium) during each of 15 recording sessions. Each species was tested in separate aquaria. To determine which sex produced sounds, one of a pair was either removed from the test situation or was placed in a separate 5-liter aquarium, set within 7.5 to 15 cm of the monitored aquarium so that visual but no acoustical mediation was allowed between the individuals. Occasionally, removal of a member of a pair resulted in complete silence (especially in *C. nigrofasciatum*). Recordings were often supplemented by observations of definite behavioral sequences being performed by only one individual while a particular sound was produced. To find what circumstances led to sound production, a glass partition was set in front of one corner of the aquarium and an individual, either conspecific or of another species, was placed behind the partition. This procedure often led to sound production, but it was not possible to determine absolutely which individual(s) produced the sounds.

The hydrophone (*3*) was coupled to a differential amplifier because of the unshielded cable of the hydrophone. The amplifier was connected to an oscilloscope for visual monitoring of the hydrophone signal, and to a stereophonic tape recorder. One channel recorded data from the hydrophone and the other channel recorded from a microphone the simultaneous observations made on monitored individuals during their reproductive, fighting, feeding, and resting periods. The observer monitored the hydrophone channel by earphones.

Because of the shortness of the pulses in regard to the tone frequency, recorded sounds were not analyzed primarily by spectrography. Instead, oscillograms were made by storascope (Wandel and Golterman) and the lengths of the single periods were measured. Spectrograms (*4*) were made when clearer information could be obtained by that means. Sound pressures were not measured as no special apparatus was available for that purpose. In the sense proposed by Fish (*5*), the sounds we recorded may be considered biological rather than mechanical, although we agree with others (*6, 7*) that these categories may well grade into each other.

Both the male and female of *Hemichromis bimaculatus* produced sounds (Table 1 and Fig. 1, *A–C*). The first, or the "Br-r-r" sound (Fig. 1, *A* and *B*), was heard most frequently and was variable among individuals. By sonagram analysis of a few sounds, we found that frequencies of greatest intensity generally became higher as the size of the individual decreased. For example, a fish 12 cm long showed a peak intensity at 250 to 350 cy/sec; another, 9 cm long, at 400 to 450 cy/sec; and another 6 cm long, at 500 to 700 cy/sec. Sonagrams must still be made on a large series of sounds, however, to establish this general correlation. The duration of a sound complex appeared correlated with aggression (that is, the more aggressive the fish, the greater the duration and time frequency of a sound).

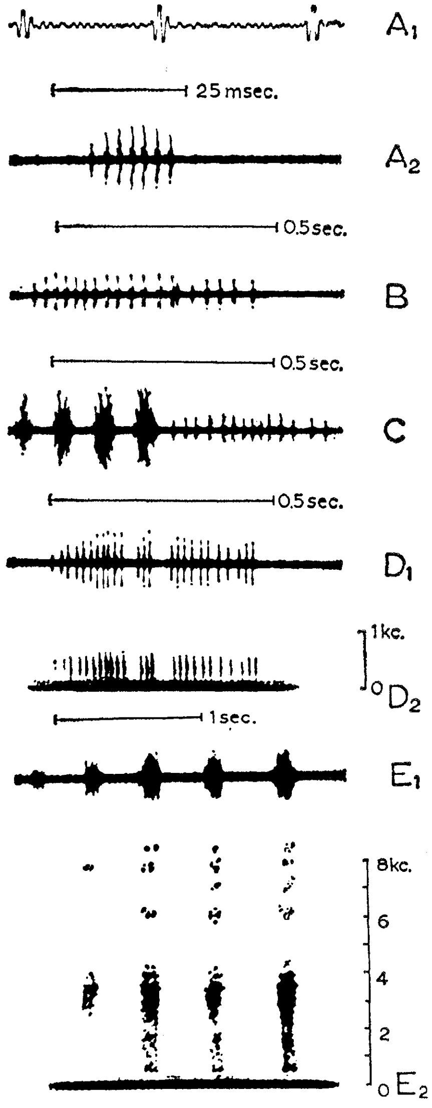

Fig. 1. Oscillograms and spectrograms of the underwater sounds produced by the test species. (A_1) Three individual pulses of the "Br-r-r" sound produced by a female *Hemichromis bimaculatus*; (A_2) The entire "Br-r-r" sound produced by a female *H. bimaculatus*; (*B*) the "Br-r-r" sound produced by a male *H. bimaculatus*; (*C*) the "Thump–Br-r-r" sound produced by a male *H. bimaculatus*; (D_1) the "Br-r-r" sound produced by a female *C. nigrofasciatum*; (D_2) spectrogram of D_1; (E_1) oscillogram of the "Tzz-tzz" sound produced by *Pterophyllum* sp.; (E_2) spectrogram of E_1.

During the parental period, the female of *H. bimaculatus* often produced a sound (Fig. 1*A*) just before attacking an intruder, although it was often difficult to determine whether the sound occurred before or after an attack, if attacks occurred in rapid series. The tone frequency of greatest intensity was around 400 cy/sec for the females and the pulse repetition rate was around 35 per second. Conspecific intruders caused more sounds to be produced than equal-sized intruders of another species. Often there was an almost 1 : 1 relation between a sound and a ram or bite on a conspecific intruder by the female. Sound production increased during egg incubation, maximum sound being produced during the development of the larvae (3 to 4 days). As the young became free-swimming, the number of sounds decreased. The female also produced sounds during courtship while aggressively "holding ground" against the male after he had attempted to bite or ram her, or had succeeded in doing so. There appeared to be little difference between the sounds heard during courtship and during the parental periods. During the latter period, females produce far more sounds than males.

Males of *H. bimaculatus* produced at least two different sounds. The first (Fig. 1*B*) was similar to that of the female, except generally deeper in tone and of longer duration. Tone frequency of highest intensity was around 330 cy/sec, the pulse repetition rate around 35 per second. Males produced sound during aggressive situations in early courtship, during the parental period, and also when their mates were returned to the tank after they had been removed for an hour. In one instance when a female had just been returned to a tank, the male produced sound synchronously with a long series of repeated dorsal fin extensions. Sound production and fin extension, however, often occurred separately. The second sound produced by the male was that of a "Thump," which was usually produced in a series of three to five and often preceded the "Br-r-r" sound (then somewhat muffled, Fig. 1*C*). Both sounds also occurred separately. The "Thump" sound appeared to have a middle frequency similar to the "Br-r-r" sound, but consisted of many more periods and was more intense. The pulse repetition rate was around 12 per second. The "Thump" sound was heard during the early stages of fighting between conspecific males (that is, approach, lateral display, and tail-beating), but no sounds were heard after the fight was once decided and as the victor followed and rammed the loser.

Table 1. Summary of tests on sound production in three cichlid species.

No. of individuals tested	Total No. of tests	Total duration of tests (minutes)	Sounds: Total No. monitored	Sounds: No. associated with aggressive response*	Sounds: No. not associated with aggressive response*
	Hemichromis bimaculatus				
Three pairs	39	515	175	134	41 †
	Cichlasoma nigrofasciatum				
Two pairs	31	510	42	38	4 †
	Pterophyllum sp.				
One pair	2	60	34		
Two groups (six each):					
(i) No aggressive individuals	1	60	0		
(ii) Aggressive individuals	1	60	10		

* Aggressive responses were lateral display, frontal display, tail-beating, circling, frontal attack, biting, and ramming. † Sounds were heard only during periods of aggression but were not directly associated with an aggressive response.

No sounds were heard from the species during nonaggressive courtship, spawning, fanning eggs, mate exchange over the eggs or young, pelvic-fin "flicking" over the young, or during feeding and normal swimming about the aquarium.

An important part of the sonic mechanism in the species may well be the swim bladder. This assumption is based on the pulse repetition rate and frequency range. No tests, however, were made to determine the sonic mechanism.

Cichlasoma nigrofasciatum did not produce sounds as frequently as *H. bimaculatus*, but this may reflect the particular laboratory conditions rather than a characteristic of the species. Sounds were not heard during fights between males; however, a fight was never held between closely matched individuals. Sounds were most often produced when a female was "holding ground" while being attacked by a male. At such times, she gave a frontal display coinciding with a "Br-r-r" sound as shown in Fig. 1*D*. The sound was similar to that produced by *H. bimaculatus* but generally was of higher frequency (middle frequency was about 480 cy/sec for a female 7 cm long) and the pulses were not emitted as rapidly (around 20 per second). The only sounds heard during the entire courtship or prespawning period were various "mechanical" sounds (for example, digging, spitting stones) or when the male attempted to bite or ram the female. Immediately after a male's first explosive attack and as he drew back for a second ram, the female would turn toward him with spread fins, and a sound similar to that shown in Fig. 1*D* would be heard. The male would then immediately halt his attack, rest for a moment, and then continue normal courtship.

When a pair of *C. nigrofasciatum* was alone in an aquarium, the male left the vicinity of the eggs shortly after spawning and returned after approximately 2 days. His aggressive return was met with a frontal display by the brooding female who bit and occasionally rammed him. Often, however, as the female began to advance toward him, her characteristic sound was heard. This was often followed by the male halting his attack and rapidly returning to his shelter. The intimidating effect of the sound on the male was strikingly similar to that seen during aggressive situations in the courtship period. Yet, if the male swam slowly toward the female, the latter would give a frontal display and a weak attack, but no sounds would be heard. Occasionally, a male would approach a nest without being noticed by the female, but eventually the female would lunge at him, making characteristic sounds which were more extended and louder than normal. If a female, tending eggs, was removed from its aquarium for a short time and then returned, no sounds were heard until she began once again "holding ground" in the face of the male's attacks. However, female aggression could be increased rapidly by removing her eggs. At such times, sound production also increased rapidly, although the eggs meant relatively little to the male at that time. When conspecific intruders were brought into the vicinity of a pair under parental motivation, far more sounds were heard than when equal-sized intruders of another species were presented. This was similar to that found in *H. bimaculatus*. No evidence was obtained that males of *C. nigrofasciatum* also produce sounds.

The close similarity of the sounds produced in *C. nigrofasciatum* and *H. bimaculatus* suggest that both species share the same basic sonic mechanism.

Sounds were also produced by adult *Pterophyllum* sp. (probably *P. scalare*) (Table 1, Fig. 1*E*) when a pair with eggs was confronted by another adult either in the same aquarium but separated by a glass partition, or in a separate aquarium set 7 to 10 cm away. The sound had a definite noise quality caused by the great number of contained frequencies. There appeared to be a broad maximum intensity around 3300 cy/sec and a major pulse repetition rate of around 6 per second. There were frequency components over 10,000 cy/sec, a frequency range certainly approaching the upper range produced by cyprinid fishes (*6*) and extending far beyond the known ranges of most, if not all, known noncypriniform fishes. Little can be stated about the harmonic characteristics of the sound except that it was richer than the sounds recorded in the other species. There appeared to be also a low-frequency pulse (around 300 cy/sec) between each of the major pulses.

This "Tzz-tzz" sound often occurred just before a parent attacked conspecific adults, but it was unclear which of the pair produced the sounds. Sound production increased while the eggs were being incubated in the nest, reached a maximum during the development of the larvae, and decreased when the young took up a free-swimming existence. Similar sounds were also heard when two equally matched individuals fought in the ritualized manner of the species. Sounds were not heard when the pair was alone with eggs, larvae, or free-swimming young, or when a group of adults swam about showing no aggression.

The frequency range strongly indicates that the sonic mechanism is of a stridulatory type, with little or no resonance.

Our observations indicate that in cichlid fishes sound production is closely correlated with aggression rather than with a particular period in the life cycle (such as during territory formation, courtship, parental periods, or feeding) as found in certain other species (*8*). Aggression can occur, however, without sound production. Schneider (*9*) found that sounds produced by various species of *Amphiprion* (family Pomacentridae) also are apparently only of an agonistic nature.

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3. The hydrophone was a crystal receiver SW51e, Atlas-Werke A. G. Bremen, developed as a listening device for use in submarines. It had the following characteristics: sensitivity, —100 db relative to 1 volt per μbar; frequency response, 30 cy/sec to 12,000 cy/sec ± 1.5 db; direction characteristic, undirected. The differential amplifier was a Tectronix 220; the tape recorder was a two-channel Telefunken 98.
4. We thank Dr. W. M. Schleidt for his help with the spectrography. The spectrograms presented in the text were produced by an apparatus described elsewhere by Dr. Schleidt [*Rohde Schwarz Mitt.* **18**, 155 (1964)].
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13 April 1965

Orientation of Ambystoma maculatum: Movements to and from Breeding Ponds

Abstract. *Migrating* Ambystoma maculatum *tend to utilize the same track on entering and leaving breeding ponds. The movements are usually accomplished at night in rain, fog, or cloudy weather when visible celestial cues may not be available. The sensory basis for the orienting ability is unknown.*

In eastern Massachusetts during March and April, the salamander *Ambystoma maculatum* migrates at night from terrestrial retreats to specific ponds for breeding and oviposition. Anderson(*1*) indicates that adult ambystomatids returning to ponds to breed may use the same tracks as they used when they first left the ponds as newly metamorphosed juveniles. My study was designed to determine whether individual adult *A. maculatum* use the same track in leaving the breeding pond as they use during migration to the pond.

As part of a larger investigation of salamander orientation, I devised a method for determining the direction from which the animals arrived at a pond and the direction in which they departed by fencing a breeding pond approximately 15 m in diameter with screenwire. The screenwire was buried from 10 to 15 cm in depth, extended 30 to 35 cm above ground, and was about 1 m from the pond border. Deep tin cans sunk along the inner and outer faces of the fence at 16 compass points (about 3 m apart) served as traps (Fig. 1). Animals moving to and from the pond encountered the fence, moved along it, and fell into the first trap encountered. Trapped animals could not escape.

The pond, which is bordered by trees (Fig. 2), is in an irregularly shaped open field. On the western, northern, and eastern sides of the field are woodlands situated from 35 m to more than 100 m from the pond. There are no obvious topographic features of the area that would influence the migration of salamanders. Some animals move uphill and others downhill to reach the pond.

Animals collected in traps on the outer face of the fence were marked and released on the other side. This process was reversed as the animals moved away from the pond. The traps were checked during March, April, and May 1964, two to three times each night and twice each day. During nights of heavy migration the traps were checked continuously. Although all traps caught animals, the majority were caught in traps located on the western, northern, and eastern borders of the pond. Most of the animals were trapped during rain, fog, or cloudiness. During 1964, 155 animals were encountered; of these, 99 were trapped only as they

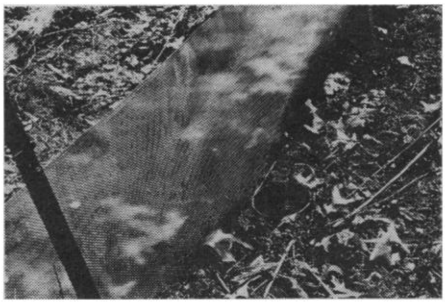

Fig. 1. A view of a trap and the fence around the pond border.

Fig. 2. A view of the breeding pond showing tree border and surrounding open field.

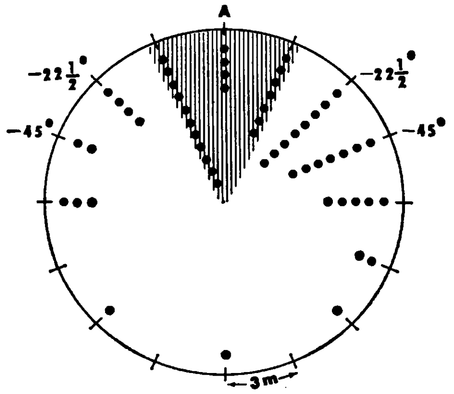

Fig. 3. Pooled data for correlation of arrival and departure directions of 56 salamanders. Point *A* represents the point where the animals were trapped on arrival (not north). The solid circles represent the departing individuals, and the shaded area includes those animals taking consistent departure headings.