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Pressure Sensitivity of an Amphipod

Abstract. The responses of an intertidal amphipod indicate an ability to perceive rapid pressure changes of less than 0.01 atm. The interaction of rate of change of pressure and total difference in pressure implies a rapid accommodation as well as a threshold. Evidence suggests that the sensory mechanism may not involve compressibility of a gas.

It has long been recognized that changes in hydrostatic pressure, in the range of hundreds of atmospheres, can have marked, and often lethal, effects on organisms (*1*). Recently, Hardy and Bainbridge (*2*) described controlled experiments in which decapod larvae slowly swam upward after much smaller increases of hydrostatic pressure: 500 to 2000 mb (*3*). The response continued for more than an hour. Two other recent papers have claimed that planktonic invertebrates, including representatives of several phyla, may be sensitive to changes in hydrostatic pressure as small as 10 mb. Knight-Jones and Qasim (*4*) described a "negative geotaxis" associated with pressure increase, and a general decrease in activity associated with pressure decrease. Baylor and Smith (*5*) stated that the organisms they examined swam upward the appropriate distance to compensate for pressure increase, and downward to compensate for pressure decrease. Neither of these reports described the experimental methods used to determine the presumed thresholds.

This preliminary report (*6*) deals with the brief but sharp increase in activity shown by a benthic intertidal amphipod, *Synchelidium* n. sp. (*7*), in response to small changes in hydrostatic pressure. The experimental equipment consisted of: a 250-cm^3 observation flask, containing about 300 amphipods, attached to a 50-cm^3 syringe by 6 m of 3-mm (inside diameter) plastic tubing, the entire system being filled with seawater, except for a 5-cm^3 airspace in the flask; a transducer-type pressure gauge (Statham model PM 6 TC, ± 1 lb/in.^{2} full range) connected directly to the flask by a glass Y-tube; a 30-cy/sec amplifying recorder (Gilson Medical Electronics, "Mini-polygraph") with one pen connected to the transducer and a second pen to an event-recording line leading from near the flask. The observation chamber, pressure gauge, and an observer were in a room where a high noise level was maintained; the recorder and the syringe through which pressure changes were applied were in a separate, adjacent room. The observer thus had no auditory or visual cue to the timing of pressure changes, other than the behavior of the animals. The large number of amphipods was used in order to allow more precise differentiation between the normal, average activity pattern of the animals and the increased activity associated with pressure changes.

Pressure on the system was changed either by placing (or removing) small weights on a platform atop the syringe plunger, producing an almost instantaneous pressure change; or by mechanically raising the open syringe up an inclined ramp at a rate that could be adjusted as desired. The air space in the flask is not essential to the response of the amphipods; they reacted similarly when the system was completely filled with water. It did serve, however, to considerably cushion the pressure change, eliminating large overshoot and rebound with the first method, and producing a much smoother pressure record with the second method.

The observer was notified that a recording had been started; at sometime within the next 60 seconds, the timing being determined by a number selected from a table of random numbers, the operator changed the pressure on the system. When, and if, the observer noted a marked change in the behavior of the amphipods, his signal depressed the event-recording pen of the recorder.

Several considerations make it appear unlikely that the observed response was due to a pressure-correlated sound stimulus: (i) The behavior of the animals when subjected to a wide variety of shock and noise stimuli, in the absence of pressure changes, indicates that this species is relatively unresponsive to all sounds tested, including loud, strong blows on the syringe. (ii) The absence of the air space in the experimental system, which should have altered the sound transmissive characteristics, had no noticeable effect on the response. (iii) The same type of response was obtained when the open syringe was raised carefully by hand, either with or without the airspace in the flask, a procedure presumably avoiding any high-frequency mechanical shocks associated with other methods. (iv) There is no known mechanical peculiarity of the system which could account for a sound stimulus present during prolonged linear pressure increases and absent during briefer increases (Table 1).

Table 1. Responses to slow, linear pressure increases: av. rate, 2.8 mb/sec (2.6 to 3.1); percentage of time at atmospheric pressure, 61 and 77; three "spontaneous activity" records. For ΔP, ΔP_T, and T, see Fig. 1*B*.

ΔP (mb)		Responses		T (sec)	
Av.	Range	Positive	None	Av.	Range
		Large increases (final $\Delta P > 35$ mb)			
41.8*	27–51*	19	1	14.4	9.4–17.7
		Small increases (final $\Delta P < 25$ mb)			
18.7	18–21	0	19		

* ΔP_T

The system has been carefully examined for the possibility of some pressure-correlated visual cue to the animals; none has been found.

The most evident response to pressure change is the sudden onset of a rapid scrambling and darting by the amphipods, which are otherwise far less active, predominantly resting on the bottom of the flask. The reaction occurs whether the pressure is increased or decreased, but is much stronger after pressure increase. With slow rates of pressure increase, the sudden burst of activity is preceded by a brief reduction of the slight normal movements of the animals. This decreased activity is less easily discerned, however, and the criterion for pressure response will here be restricted to the sudden pronounced increased activity. Rough estimates of the duration of increased activity associated with pressure change ranged from about 5 seconds for an increase of 10 mb, to about 15 seconds for an increase of 100 mb.

Small bursts of spontaneous activity occasionally occurred in the observation flask; signals denoting an apparent response to pressure at a time prior to

Table 2. Threshold for observable reaction to rapid pressure increases: t, 0.6–0.9 sec; percentage of time at atmospheric pressure, 86 and 92; one "spontaneous activity" record. For ΔP, T, and t, see Fig. 1*A*.

ΔP (mb)	Responses		T (sec)	
	Positive	None	Av.	Range
	Initial threshold			
6–8	6	4	1.7	1.0–2.3
8–15	5	1	1.3	1.0–1.7
15–20	4	0	1.1	1.1–1.2
	Final threshold			
6–8	0	5		
8–10	1	4	2.0	
10–15	8	4	1.9	1.5–3.0
15–20	5	0	1.6	1.4–1.8

the actual pressure change were designated as "spontaneous activity" records. These errors were made only when dealing with the weak responses near threshold level. Rapid pressure changes of more than 30 mb are associated with such an emphatic response that it cannot be confused with spontaneous activity. The decision that there has been a "sudden increase in activity" is, of course, subjective; the precision in timing relative to the randomly timed pressure changes, the reproducibility of results, and the low frequency of "spontaneous activity" records suggest, however, that activity changes associated with pressure changes are great enough to provide an objective basis for study of the phenomenon.

Pressure increases during the "active" phase of the animal's endogenous tidal rhythm (*8*) result in some increase in the number of upward-swimming animals, after the rapid scrambling on the bottom of the flask, a result similar to the "negative geotaxis" referred to by Knight-Jones and Qasim (*4*). This feature is not conspicuous during the "inactive" phase of the rhythm, even with large pressure increases, and has not been observed after pressure decreases at any time. Those animals which swim upward rise a distance of only 2 to 5 cm, regardless of the magnitude of the pressure increase; these benthic amphipods do not appropriately "compensate" in the manner described by Baylor and Smith (*5*) for planktonic organisms.

Tracings from typical experimental records are shown in Fig. 1. More than 50 experiments have been conducted with rapid pressure changes of 25 to 50 mb (Fig. 1*A*) with 100 percent positive responses and no "spontaneous activity" records.

Tables 1 and 2 summarize a representative set of experiments with pressure increase performed on 13 September 1960 from 9 A.M. to 1 P.M. during the "inactive" phase of the amphipod's tidal rhythm. The same group of animals was used throughout, with a minimum of a 1-minute interval between trials. The initial threshold experiments of Table 2 preceded the experiments in Table 1; the final threshold experiments followed them. The initial pressure, in all cases, was atmospheric ± 10 mb. The percentage of recorded time at atmospheric pressure is an index of the time during which "spontaneous activity" records were possible. Any responses to stimuli not associated with pressure changes would be expected to be distributed more or less evenly over the entire period of observation.

Table 2 indicates that the initial threshold for observable reaction was at least as low as 7.0 mb. Similar experiments with other freshly collected animals have shown positive responses down to a pressure increase of 5.1 mb. As a determination based on an overt reaction, this value should be regarded as only an estimated upper limit of true threshold.

Table 2 also indicates that the threshold to rapid pressure changes had increased during the experiments, to a value greater than 8.0 mb, but less than 15.0 mb. The increase in apparent threshold may be related to sensory fatigue from the intervening series of larger pressure increases. Control experiments indicated that reduced oxygen tension and other factors associated only with the experimental confinement did not measurably increase threshold.

Table 1 indicates that the response of the amphipods is dependent on both the total change and the rate of change of pressure. The large and small pressure increases of this series were presented in a random sequence. At a rate of change of about 2.8 mb/sec, an accumulated pressure difference of 18 to 21 mb did not evoke the response ("small increases"), compared with positive responses to less than 10 mb given rapidly (Table 2). The same rate (2.8 mb/sec), continued for 10 seconds or more, reproducibly induced response ("large increases"). The nature of the interaction of rate of change of pressure with total change of pressure is similar, at least superficially, to the properties of other better-known sensory systems.

The time between the start of pressure increase and the observation of a response (T) has a far greater range in Table 1 than in Table 2. In part, this is due to the fact that there was a significant trend ($p < .001$) for the value of T to increase during the course of the experiments. The trend may be another aspect of the sensory fatigue suggested by a comparison of initial and final thresholds (Table 2). In addition to this trend, however, the timing of *sequential* positive responses was also less precise than with rapid pressure changes. The difference in the value of T for successive responses averages 2.4 seconds (ignoring sign), which is greater than the entire range in Table 2. With slow pressure changes, interindividual variability in both the threshold pressure difference and the accommodation rate could contribute to a less sharp and coordinated response in a population; these factors would not alter the timing of initial response to rapid pressure changes.

While a gas-containing organ seems the most likely basis for a pressure-responsive sensory mechanism, there is, so far, no evidence for the presence of such an organ: (i) Extensive micro-

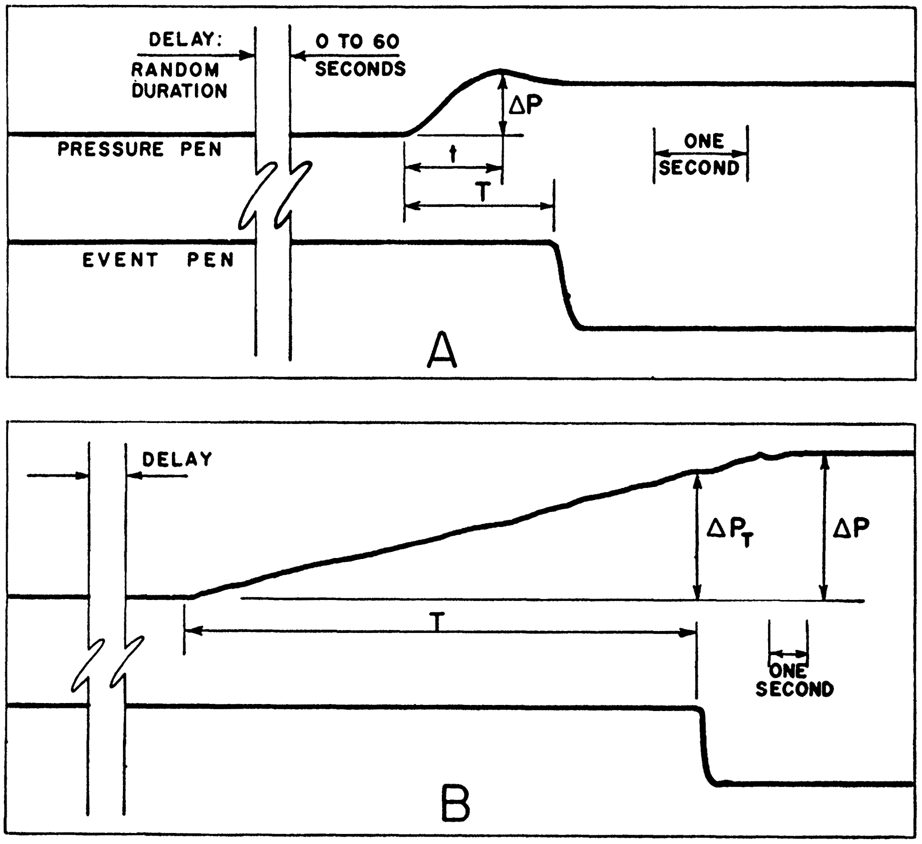

Fig. 1. Tracings of records from typical experiments. *A*, rapid pressure change; *B*, slower, linear rate of change. Symbols as used in Table 1.

scopic examination of the animals has not revealed any visible gas bubble. (ii) Upon evacuation of a flask of amphipods in sea water, any gas contained in a flexible organ might be expected to greatly expand and thus increase the buoyancy of the animals, but no change in buoyancy was observed on evacuation. (iii) After the animals were maintained at several atmospheres (about 4000 mb) for 10 minutes, they showed an activity response to pressure increases of as little as 30 mb above the 4000-mb level, even though one might expect a marked reduction in the size of a contained gas bubble, due to both compression and solution of the gas in the animal's tissue fluids, with probably an accompanying larger loss in sensitivity to pressure changes than that observed.

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6. This work was performed during the tenure of a National Science Foundation predoctoral fellowship. Experimental work was supported by National Science Foundation grant No. G-7141 to Dr. E. W. Fager. I wish to express my sincere thanks to my scientific adviser, Dr. E. W. Fager, for much helpful discussion and encouragement with the work. Thanks are also due to Richard Ford and Nancy Enright for their time as observers and operators in the experimental work, to Frank Snodgrass and James Snodgrass for help with instrumentation, to Dr. Robert Arthur for a helpful discussion of methods, and to a large number of other friends for valuable comments and discussions.
7. This small oedicerotid amphipod, which is abundant on the intertidal beach at Scripps Institution of Oceanography, La Jolla, California, was identified by Dr. Clarence Shoemaker (deceased) and will be formally described by Dr. Thomas E. Bowman in a forthcoming monograph on the genus. It differs from two other undescribed species of the genus found in the La Jolla area in the following conspicuous morphological characters: the first and second antennae of the mature male are roughly 80 and 95 percent, respectively, of the length of the cephalothorax; those of the female are roughly 45 percent each; comparable values for the other two species are about 50 and 220 percent for the male and 35 percent each for the female. The second and third uropods, in both sexes, are roughly 65 and 35 percent, respectively, of the length of the first uropod, compared with 80 and 65 percent for the other two species. The bulk of the adult population of this species is in the uprush zone of the beach at La Jolla; of the other two species, which are much less abundant, one ranges from low intertidal to depths of about 3 m, and the second is usually taken deeper than 5 m.
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12 October 1960

Primate Taxonomy and Oreopithecus

W. L. Straus, Jr., and M. A. Schön have reported their findings on the cranial capacity of *Oreopithecus bambolii* (*1*). The abstract from this report reads: "From a plaster reconstruction of the skull of the August 1958 skeleton, the cranial capacity of *Oreopithecus bambolii* has been estimated as falling between 276 and 529 cubic centimeters, thus within the ranges of variation of both orangutan and chimpanzee. In cranial capacity, therefore, and probably in body-brain ratio as well, *Oreopithecus is a hominoid*" (italics mine).

The authors explain that after Hürzeler's recent revaluation it seems evident that *Oreopithecus* is a member of the superfamily Hominoidea, which comprises the families Pongidae (anthropoid apes) and Hominidae (man and his immediate forerunners).

Three letters appeared last year in *Man* (*2, 3*). Their titles clearly indicate the worry of anthropologists about the thorny problem of the taxonomy of our probable or possible ancestors.

Before *Oreopithecus* "revalued"—as Huxley would most likely say—came into the picture, Simpson's (*4*) creation of the superfamily Hominoidea appeared convenient, and thus the term has been widely used. We had "hominoid," "hominid," and "pongid" equated, as the adjectival forms of the zoological groups Hominoidea, Hominidae, and Pongidae. As Wells (*2*) has commented, "This nomenclature commits us to the view that man is more directly linked in origin with the anthropoid apes than with the other Old World primates (Cercopithecoidea). Although this conception is both plausible and widely held, Straus (1949) (*5*) has argued persuasively for the alternative view that the Hominidae arose from stem Catarrhines too primitive to be classified as anthropoid apes even in the broadest sense. On this view, the Catarrhina (*sensu* Hemprich, 1820) would form a natural unit with three co-ordinate subdivisions: Cercopithecidae, Pongidae and Hominidae; *the Hominoidea of Simpson would then be an arbitrary grouping. Nevertheless, at this stage anyone who proposes to use the term 'hominoid' in any other sense than that adopted by Le Gros Clark* (*6*) *must define its meaning very carefully*" (italics mine).

But thus far, although several ancestors of the Pongidae had been discovered corresponding to pre-Pleistocene chronology, hominids going beyond Pleistocene dating were unknown. Le Gros Clark could say in 1955 (*7*), "Similarly, the fossil Hominoidea of Miocene age may appropriately be called 'primitive anthropoid apes,' even though they had not acquired all the specialized features which are accepted as characteristics of the anthropoid apes of today."

That is, the use of the term hominoid "in any other sense than that adopted by Le Gros Clark" (*2*) seems to me, in the light of the recent *Oreopithecus* discoveries, as somehow unfitting. One may ask, Is this Upper Miocene primate a "hominoid" or a "primitive anthropoid ape," considering that he is classed under the superfamily Hominoidea? Then would *Proconsul* also be a "hominoid," and *Limnopithecus* another?

I believe that, as has been stated by several authors, while it was appropriate—in spite of Straus (*5*)—to create a superfamily which would encompass the two families Pongidae and Hominidae, it was unwise to give it a name which refers exclusively to one of them, and to that carrying a deeper emotional charge.

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17 October 1960

Dr. Santiago Genovés objects to the use, by myself and M. A. Schön (*1*), of G. G. Simpson's term, Hominoidea (and its adjectival and substantival derivative, "hominoid") to denote a superfamily comprising the families Pongidae (anthropoid apes) and Hominidae (man and his immediate forerunners). Consequently, he disapproves of our classification of *Oreopithecus* as a hominoid. In this, he is tilting with a windmill.

My paper of 1949 (*2*) has been cited by Genovés in his argument against use of the terms Hominoidea and hominoid. The implication is that my present acceptance of Simpson's definition of a superfamily Hominoidea contravenes my earlier views respecting man's ancestry, for this superfamily associates the anthropoid apes and man, with the Old World monkeys excluded as a separate catarrhine superfamily,