Tone Perception in Gammarus pulex.

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The proof of the existence of a restricted tonal sense in any animal would be of great interest. The present paper offers evidence of the occurrence of this phenomenon in the Gammarids. Though it must be admitted that the number of animals which responded to the tests was small, the response, when it occurred, was so definite and unmistakable that a description of the results seems desirable. My attention was first directed to the matter by Miss Margaret Cussans, who was engaged at the time in working out, at my suggestion, the circulation of *Gammarus pulex* on the living animal under the microscope. We then noticed that this species responded only to the bass note of the College chime, which, giving on examination 240 vibrations per second, therefore corresponded to the B below middle C of the pianoforte.

In the first place it must be noted that the animal responds (in water) only when imprisoned in the compressorium or live box. This makes the case the more interesting, since if the reaction had not been observed by the merest accident, the same experiments might have been conducted on the animals in their natural surroundings with absolutely negative results. They are compressed only so much as to prevent wandering, whilst leaving their appendages quite free. They may then be kept under observation on the stage of the microscope. I had a special live box constructed so as to permit a gentle stream of water being passed continuously through it. This prevents asphyxiation, and allows a single specimen to be experimented with for a longer period than would otherwise be possible. It is, of course, inevitable that the vibrations should be conveyed to the animal by the medium in which it finds itself, and in this sense it is impossible to postulate true audition (as usually understood) in any true aquatic species. The factor to eliminate here is clearly the specific period of the medium itself, the energetic vibration of which, in response to its own note, may vitiate the result of the experiment. For this reason I used three types of live box and microscope, without, however, any difference in the results being noticed. Further, the fact that the response is only evoked by a limited range of tone, and then without reference to any specific forced or sympathetic vibration of the surrounding medium, intimates that the stimulus is associated with a definite physiological status of the animal itself, since even if the box were

an essential factor in the success of the test, we should still leave unexplained the differential response. It is, however, easy to show that the box itself, owing to its small size and heavy construction, is ill adapted for the transmission of vibrations, and is certainly the last means one would adopt to transmit aerial vibrations freely to the animal.

Tested with the trombone under the conditions of many of the following experiments, both by means of the optical lever and by polarised light, two of the live boxes showed no traces of strain in the latter case, and in the former only an extremely slight vibration to the G, F sharp, and F below middle C.

The animal having been placed in the live box, and the current of water started, the whole was then transferred to the stage of the microscope, and the following three tests applied:—

(1) On a specially prepared physical table, constructed of alternate layers of sawdust and three massive cast iron slabs,* which served to filter off vibrations from the ground, and to ensure that any response observed was due to a stimulus conveyed through the atmosphere, *i.e.* was a true auditory and not a tactual reaction. Judged by the mercury test this table was quite efficient.

(2) On an elongated rectangular resonator provided with a sliding piston. Here the rationale of the piston is to make it possible to eliminate the factor of the specific note of the resonator itself (a point of obvious importance), and I may as well state at once that the position of the piston never appeared to affect the results in the least. For example, a female tested on the resonator responded equally well to middle B flat whilst the length of the resonator was being reduced from 135 to 30 cm. I should also observe here that the bell of the trombone was usually placed near the open end of the resonator, but not, of course, touching it.

(3) On an organ reed, made to my instructions, which gave at least two good octaves, one above and the other below middle C. This was effected by means of a sliding piston and an adjustable lip, and was much more satisfactory than the makers anticipated that it would be.

In the cases of 1 and 2, a B flat or tenor trombone was employed to provide the stimulus, and it was generally found necessary to produce a *ff* note. I have observed, for example, that a crescendo note is only responded to when the louder portion is reached.

The intervals mentioned in this paper are those of the harmonic chromatic scale of C major.

The responses which the animal makes to sound are of two kinds, and

* My colleague, Prof. G. J. Burch, F.R.S., kindly suggested this to me.

although there can be no doubt as to the genuine character even of the first, it is only to the second that I have considered it safe to attach any importance. In the one case the first antennæ are observed to give a distinct neurotic flicker, but in the other they are rapidly and powerfully flexed, being bent right underneath the body, and carrying the passive second pair of antennæ before them. In both cases it is important to note that we have to do with a definite *physiological* response, which unquestionably supervenes as the result of the stimulus, and is not a merely physical effect such as Hensen observed in the auditory setæ of the Decapod Crustacea, which effect has since been shown to have no *necessary* auditory significance. In my earlier experiments no record was, unfortunately, made of the sex of the specimens employed. This was, however, done in the later work, but no difference between the sexes was observed. In a very few cases the response was of a character different from either of those just described, the anterior antennæ being only partially flexed at the first stimulus, and, instead of returning to the *status quo*, becoming more and more flexed with each successive stimulus, until they finally reached a position similar to that attained by the one flexure in the case of the second type of response above. Tested dry out of water directly on the resonator, and on the organ pipe, some individuals showed very distinct signs of disturbance to notes immediately above and below middle C, but they did not hop.

In *Gammarus* the auditory function is generally supposed to be located in the first antennæ, and, that this is so, is proved by the following experiments. Four pairs *in copula* were separated, and two of each sex had either the first or the second pair of antennæ removed. This is easily done by holding the animal down with a camel's hair brush and detaching the antennæ with a sharp needle or a very fine pair of forceps. The blood at once clots over the wound, leaving a characteristic black scar. Both males and females on the resonator responded to middle B flat after removal of the second antennæ, in some cases only to the B flat, and in one case markedly to the B flat, and less so to a few semitones below it. On no occasion, however, was the slightest response observed after the first antennæ had been removed. A female minus the second antennæ was tested on the physical table, and responded distinctly to B flat when the bell of the trombone was not more than 6 inches from the microscope, but failed to respond when the bell was withdrawn to 18 inches. All the above individuals were tested again 10 days after the operation (except one female which had died), and whilst there was still no response whatever from those without the first antennæ, those with these appendages only responded in two cases, and then but slightly.

Fatigue appears to play an important part in the results of the experiments,

and this I have noticed a number of times. For example, a specimen in the live box placed on the resonator responded very markedly to B flat five successive times. Transferred then to the physical table it responded energetically to B flat the first time, not so distinctly the second time, slightly the third time, very distinctly the fourth time, and slightly the fifth time. Replaced now on the resonator, it no longer responded either to B flat or A flat. As it seemed possible that the shock of compressing the animal in the live box and testing it at once might affect the results, I tried the effect of several hours' imprisonment in the live box before applying the stimulus. I could not, however, persuade myself that there was any appreciable difference. For example, a female was placed in the live box, and the current of water started at 11 A.M. The heart beat was then 210 per minute.* Tested on the resonator first at 135 cm. and then at 85 cm. at 2.30 P.M., when the heart beat was 240 per minute, it responded quite well at first, but then failed to respond on the physical table, and afterwards on the resonator.

A typical, successful experiment may be described as follows: A male was tested on the resonator (but without the water current) with the chromatic scale up and down from middle B flat. Between every two notes the B flat was sounded in order to make it certain that a negative result was not due to fatigue or other causes. The response to B flat was very energetic, the first antennæ making a sudden and rapid downward sweep under the body, carrying the second antennæ with them. There were also responses, but not so well marked, down to the A flat, and slight doubtful responses three semitones below that again, but no more. In all cases, however, there was a quite perceptible difference between the response to the alternative B flats and the other notes of the scale. On the animal showing signs of fatigue the alternative B flat chromatic scale was repeated, but now there was only a response to the B flat. Tested to an octave above the middle B flat, there was only a slight response to the upper three semitones, but in no respect was it at all striking. Transferred now to the physical table the animal responded simply to the B flat, and then only when the bell of the trombone was quite near the microscope. This, however, must have been due to fatigue, as no better result was elicited when the experiment was subsequently tried on the resonator. In another case a male was tested on the resonator and with running water with the alternative B flat chromatic scale, a quarter of a minute rest being allowed between successive notes. The response to B flat was quite undoubted, to A natural very slight, and to A flat scarcely perceptible, but there was no further response down to F, at

* Miss Cussans states that the heart beat ranges from 120 to 130 per minute.

which time, the animal failing to respond even to the B flat, the experiment was brought to a conclusion.

A large number of specimens were tested with a view to ascertaining whether the sensitiveness to middle B flat was of general occurrence. For example, a male placed on the resonator responded moderately to A flat at the first stimulus, but very slightly if at all to the same note the next four times. Tried then with B flat and A flat sounded alternately, five times each, there was always a response to the B flat, quite distinct if not very well marked, but none at all to the A flat. The subordinate notes may be eliminated by gradually withdrawing the trombone to a distance. Thus a male on the resonator responded quite well when the bell of the instrument was 4, 7, and 10 inches from the mouth of the resonator, but did not respond at all after the foot had been passed. In another case there was a marked response when the bell was a foot away, and even slight responses at $1\frac{1}{2}$ and 2 feet, but none beyond the latter distance. In a female, with the bell at a foot, there was a marked response to B flat, and only a slight one to A natural. Again, a female tested on the physical table responded distinctly to B flat at 4 inches, slightly at 8 inches, but distinctly again at 12 inches, and at 2 feet not at all. Returning now to 4 inches there was a well-marked response, and immediately at 2 feet a slight response.

A specimen in a remarkable condition of hyperæsthesia was encountered on one occasion. In the first experiment the chromatic scale was played with one minute rest between successive notes, but it should be pointed out that at first the animal also responded to the slightest tap on the resonator, the only individual which has done this. It was a male, and we tried it first on the resonator at 135 cm., and with the current of water. The result was as follows: To middle B flat and A natural there were at once very striking and emphatic responses; to A flat and G, rather less; to F sharp, F, E natural, and E flat, well-marked responses; to D natural, D flat, and C, not so well marked. We now repeated the same scale, but only allowed sufficient time between each note for the antennæ to straighten out. It responded in the same way to every note as before, but not so vigorously. Tested with the chromatic scale up from middle B flat, and with the same minute intervals, we found: B flat and B natural, well marked; C, less; D flat, very slight, *but responded well to the middle B flat immediately;* D natural and E flat, slight, but only slight to the B flat also; E natural, slight, but a better response to the B flat; F, very slight, but a much better response to the B flat. In the latter experiment the animal was, I think, probably becoming fatigued, and thus did not respond as well as it might

have done at first. We now stopped the water current for a time, in the expectation of getting at the fundamental note of the animal by eliminating the subordinate tones. It still responded, but very slightly, to all the notes as before, but was unquestionably more sensitive about B flat and A flat.

I am, of course, aware that most of the preceding experiments may be interpreted as either tactual or auditory reactions, and, if it is possible at all to distinguish these two phenomena in the lower aquatic animals, the fact that they are not *necessarily* auditory does not justify one in concluding, as some recent observers have done, that they are therefore tactual. In the case, however, of the experiments conducted on the physical table, it is, to my mind, difficult to deny a true auditory sense to *Gammarus*. But this sense (whatever its nature) seems to be extremely restricted, and only a few tones appear to be appreciated.

A Physiological Effect of an Alternating Magnetic Field.

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Down to the present time it has been held by all physicists and by all physiologists that magnetism produces no physiological effect either on the human subject or on any living organism. Many persons have looked for such effects. Lord Lindsay (now the Earl of Crawford), assisted by Mr. Cromwell F. Varley, constructed many years ago an enormous electro-magnet,* now in the Observatory at Edinburgh, so large that it would admit between its poles the head of any person who wished to test whether a strong magnetic field would have any sensible effect. Nothing whatever was perceived as the result.

I have, however, recently succeeded in demonstrating a real physiological effect due to magnetism. Some six years ago, when experimenting with an alternating electro-magnet which had been constructed for showing Prof. Elihu Thomson's well-known experiments on the repulsion of copper rings, I observed a faint visual effect when my forehead was placed close to the magnet.

Recently, incited thereto by finding Lord Kelvin's mention of the negative

* See Lord Kelvin's 'Popular Lectures and Addresses,' vol. 1, p. 261.