PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES
Volume 1 AUGUST 15, 1915 Number 8

WEBER'S LAW AND ANTAGONISTIC SALT ACTION

By Jacques Loeb
ROCKEFELLER INSTITUTE FOR MEDICAL RESEARCH, NEW YORK

Presented to the Academy, June 26, 1915

1. In a series of papers beginning in 1900 I have shown that: (*a*) It is necessary for the normal functions of living organs and organisms that the ratio of the concentration of antagonistic ions or salts C_{I}/C_{II} of the surrounding solution be kept within certain limits; if the value of this quotient becomes either too high or too low, life phenomena become abnormal and finally impossible.[1] (*b*) The salts to be considered as antagonistic in this sense are in the first place those of univalent and bivalent metals and that therefore the most important critical quotient will generally be C_{Na+K}/C_{Mg+Ca}. (*c*) There is also an antagonism between the salts of bivalent ions such as Sr and Ca, and Mg and Ca.[2] In the following discussion the antagonism between Na and K on the one hand, and Mg and Ca on the other will be solely considered.

I further suggested that if the value of C_{I}/C_{II}, e.g., C_{Na+K}/C_{Mg+Ca} had once reached the lower limit required for the normal process of life phenomena the alternate reversible replacement of one of the two groups of ions by their antagonists in combinations with certain colloids (proteins or fatty acids) of the cells determined the alteration between activity and rest of the organs or the organisms.

This idea was carried further by Lasareff, who showed that from these data not only Nernst's law of electrical stimulation could be derived[3] but also the phenomena of vision in weak light in which the effect depends solely on the bleaching of visual purple by the light.[4]

Life phenomena as a rule take place in a medium whose composition and concentration undergoes little or no variation, such as sea water or blood serum, and the majority of organisms cannot stand any wide variation from this fixed standard. For such organisms only one value for C_{Na+K} can be considered and hence only the lower and upper limit for C_{Mg+Ca} can be determined for this value. A few organisms can stand wide variations of osmotic pressure and hence in their case the value C_{Na+K} can undergo wide variations. The question arises: How do the minimal and maximal values of C_{Mg+Ca} change when C_{Na+K} varies? It is this question which will be discussed in this paper.

2. The animals used in these experiments were the newly hatched larvae of a barnacle (*Balanus iberneus*). These larvae upon hatching are positively heliotropic and form a dense cluster on the light side of the aquarium, so that they can be collected in a pipette with comparatively little sea water. They are able to live not only in normal sea water but also in sea water which is diluted with eight times its volume of distilled water, as well as in sea water whose concentration is raised almost 50%.

When such larvae are put into a mixture of NaCl, KCl and $CaCl_2$ of the concentration and proportion of sea water, the majority will not swim but fall to the bottom of the dish. If, however, we increase the amount of $CaCl_2$ in the solution the larvae instead of falling to the bottom will swim, as they would in normal sea water, and will collect at the side of the dish nearest to or most remote from the light. Instead of adding more $CaCl_2$ we may add $MgCl_2$ or $SrCl_2$.

3. If the bivalent cations contained in the solution are of one kind only, namely either $CaCl_2$ or $MgCl_2$ or $SrCl_2$, and if they are in sufficient concentration to allow the animals to swim, the latter will do so as a rule only for about five minutes. If we wish the animals to swim permanently we must add a mixture of two bivalent cations, e.g., Ca and Mg.

In the following experiments a mixture of $CaCl_2$ and $MgCl_2$ was always used to supply the bivalent cations. This mixture contained the two cations in that ratio in which they occur in the sea water, namely 1.5 molecules of $CaCl_2$ to 11.6 molecules of $MgCl_2$. The concentration of the mixture used was $\frac{3}{8}$ grammolecular.

4. When we put the animals into a mixture of 50 cc. NaCl + KCl (no matter what concentration) they will fall to the bottom and are unable to make sufficiently vigorous swimming motions, although they may live in such a solution for a day or longer. Various concentrations of the mixture of NaCl + KCl (in the proportion in which these salts exist in the sea water) were prepared and it was ascertained what was the minimum amount of $CaCl_2$ + $MgCl_2$ necessary to induce all (or practically all) the animals to make normal swimming movements and to collect in a dense cluster at the window side (or the opposite side) at the surface of the dish.

The absolute value of Ca + Mg required was not always identical for the same concentration of NaCl + KCl in different experiments; this was probably due to differences in temperature or in illumination or in the condition of the larvae. It was, therefore, necessary to compare only experiments made simultaneously with the same material. As a rule two sets of experiments were made simultaneously for two different concentrations of NaCl + KCl; the two concentrations of NaCl + KCl were usually chosen in the ratio of 1:2 or 1:4.

Table I gives some of the results. The figures for CaCl + $MgCl_2$ indicate the number of cc. $\frac{3}{8}$ m $CaCl_2$ + $MgCl_2$ required to just allow

TABLE I

MINIMAL AMOUNT OF $CaCl_2$ + $MgCl_2$ REQUIRED TO ALLOW THE LARVAE TO SWIM IN 50 CC. (NaCl + KCl) OF THE FOLLOWING CONCENTRATIONS

NUMBER OF EXPERIMENT	CONCENTRATION NaCl + KCl	CC. OF 3/8 M $CaCl_2$ + $MgCl_2$ REQUIRED	VALUE OF $\frac{C_{Na+K}}{C_{Mg+Ca}}$
I	m/16 m/8	0.3 0.4 to 0.5	27.8 37.0
II	m/8 m/4	0.5 0.9 to 1.0	33.3 35.1
III	3/16 m 3/8 m	0.7 1.3	35.7 38.5
IV	m/8 m/2	0.5 1.8 to 1.9	33.3 36.0
V	m/4 m/2	0.8 to 0.9 1.6 to 1.7	39.2 40.3
VI	5/16 m 5/8 m	0.9 1.7	46.3 49.0
VII	3/16 m 6/8 m	0.6 2.4	41.7 41.7

all the animals to swim and to collect in a dense heliotropic cluster; a diminution of this quantity by 0.1 cc. resulted, as a rule, in a diffuse and incomplete collection while with a further diminution by 0.1 cc. only a small percentage of larvae rose to the suface. The endpoint or threshold according to our criterion was therefore usually sufficiently sharp to allow different unbiased observers to select the same dish as representing the threshold in a series.

It was necessary to wait four hours or still better a day, before the final decision was made, as in the very weak as well as in the strong solutions the larvae fall first to the bottom and will not rise until after some hours.

Other experiments gave similar results.

If we select for comparison the experiments with the moderate concentrations (between m/8 and m/2 NaCl + KCl) *we find that the value of* C_{Na+K}/C_{Mg+Ca} *varies little around 35.0 or in other words that the concentration of CaCl + MgCl required increases in direct proportion with the concentration of NaCl + KCl;* as far as the degree of accuracy of these experiments permits it to be stated. In concentrations above m/2 NaCl the animals will usually not all rise or if they do they soon fall to the ground again and this makes the determinations of the endpoint difficult. The value of $MgCl_2$ + $CaCl_2$ to be added to m/16 NaCl is higher than the theory demands and therefore the law does not hold strictly in this case. *The law of direct proportionality found for moderate concentrations is therefore Weber's law.* As is well known, Weber's law is not strictly correct for very low or very high intensities and the deviation is in the same sense as in our experiments, namely as if the weakest concentration tried were stronger than it actually is.

TABLE II

MAXIMAL AMOUNT OF $CaCl_2$ + $MgCl_2$ WHICH ALLOWS THE LARVAE TO SWIM IN 50 CC. (NaCl + KCl) OF THE FOLLOWING CONCENTRATIONS

CONCENTRATION NaCl + KCl	MAXIMAL AMOUNT OF $CaCl_2$ + $MgCl_2$	VALUE OF $\frac{C_{Na+K}}{C_{Mg+Ca}}$
50 cc. m/16 NaCl + KCl	> 5 cc. 3/8 m $CaCl_2$ + $MgCl_2$	1.67
50 cc. m/8 NaCl + KCl	> 8 cc. 3/8 m $CaCl_2$ + $MgCl_2$	2.08
50 cc. m/4 NaCl + KCl	>14 cc. 3/8 m $CaCl_2$ + $MgCl_2$	2.38
50 cc. m/2 NaCl + KCl	>25 cc. 3/8 m $CaCl_2$ + $MgCl_2$	2.67

5. According to the writer's theory the swimming motions should also cease when the value of C_{Na+K}/C_{Mg+Ca} falls below a certain limit. It is more difficult to determine this endpoint than the other one, since with an increasing concentration of Ca + Mg the percentage of the larvae able to swim diminishes very gradually.

When the larvae are put into solutions with an excess of $CaCl_2$ + $MgCl_2$ they all swim at first but in a few minutes they fall to the bottom though they will live for a long time. The power of rising to the surface and forming a permanent dense heliotropic cluster no longer existed when more than the following quantities of 3/8 m $CaCl_2$ + $MgCl_2$ were added to 50 cc. of NaCl + KCl (Table II). The final observations were usually taken after two days.

Considering the difficulty in getting a sharp endpoint, these values are in good agreement with Weber's law of proportionality. It is, therefore, apparent that the upper limit of the value C_{Na+K}/C_{Mg+Ca}, which just annihilates the power of free swimming motions, remains also approximately constant, namely about 2, if the value of C_{Na+K} varies. Attention should be called to the fact that this value seems to rise slowly with the concentration of NaCl + KCl.

6. It is occasionally stated that the bivalent cations are the stimulating ions. This can be disproved if we prepare solutions of $MgCl_2$ + $CaCl_2$ in m/2 cane sugar or m/2 glycerine. It is impossible to induce the larvae to swim in such solutions. Neither can we induce them to swim if we add NaCl + KCl to a m/2 cane sugar or glycerine solution. This is in harmony with the law that the normal activity is only possible if the value of the quotient C_{Na+K}/C_{Mg+Ca} keeps within certain limits, but contradicts the idea that Ca or Mg stimulate the animals into activity.

7. It has been stated that in a m/2 solution of NaCl + KCl + $CaCl_2$, in the normal proportions, none or few of the larvae can swim, but that on addition of either more $CaCl_2$ or $MgCl_2$ or both the larvae will swim. We can bring about the same effect if we add instead of $MgCl_2$ or more $CaCl_2$ simply some alkali, e.g., 0.8 cc. N/100 NaOH or 0.5 cc. m/10 $NaHCO_3$ to 50 cc. of the solution of NaCl + KCl + $CaCl_2$. The larvae will after some time rise to the surface and gather permanently in a cluster although no $MgCl_2$ is present. This fact brings these phenomena into a close parallel with the phenomena of fertilization. I have shown that the eggs of sea urchins and other marine animals cannot be fertilized in a mixture of NaCl + KCl although the sperm remains active for a long time in such a solution; that the addition of $CaCl_2$ allows the fertilization of a few eggs, but that the addition of either $MgCl_2$ or NaOH (or $NaHCO_3$) may allow all the eggs to be fertilized.[5] This is mentioned to indicate that the phenomena discussed in this paper are of a wide biological application.

Summary. I had formerly shown that the normal functions of an organism are only possible if the value C_{Na+K}/C_{Mg+Ca} remains with certain limits *A* and *B*. In this paper this value has been investigated in an animal which stands wide variations of C_{Na+K} and it was found that the values *A* and *B* remain approximately constant if C_{Na+K} changes. This fact is the expression of the Weber-Fechner law. Since this law underlies many phenomena of stimulation it appears possible that changes in the concentration of antagonistic ions or salts are the means by which these stimulations are brought about, as suggested in my ion-protein theory and by the investigations of Lasareff.

---

[1] Loeb, *The dynamics of living matter*, New York, 1906. Physiologische Tonenwirkung, *Oppenheimer's Handbuch*, Vol. 2, Jena, 1909.

[2] Loeb, *Amer. J. Physiol.*, **3,** 434 (1899); **6,** 411 (1902); and *J. Biol. Chem.*, **1,** 427 (1906).

[3] Lasareff, *Arch. ges. Physiol., Bonn,* **135,** 196 (1910).

[4] Lasareff, *Arch. ges. Physiol., Bonn,* **154,** 459 (1913).

[5] Loeb, *Science,* **40,** 316 (1914); *Amer. Nat., Boston,* **49,** 257 (1915).

THE POLARIZED FLUORESCENCE OF AMMONIUM URANYL CHLORIDE

By E. L. Nichols and H. L. Howes

PHYSICAL LABORATORY, CORNELL UNIVERSITY

Read before the Academy, April 20, 1915. Received June 2, 1915

The remarkable fluorescence spectrum of ammonium uranyl chloride ($UO_2Cl_2 2NH_4Cl + 2H_2O$), which has been described in a recent paper read before the American Physical Society, consists of several equidistant groups of bands. Each group contains five nearly equidistant bands, *b*, *c*, *d*, *e*, and *a* (fig. 1) and the spacing repeats itself with such precision in successive groups that the homologous bands, b_1, b_2, b_3,—c_1, c_2, c_3 (see fig. 2) form series having a common and constant frequency interval.

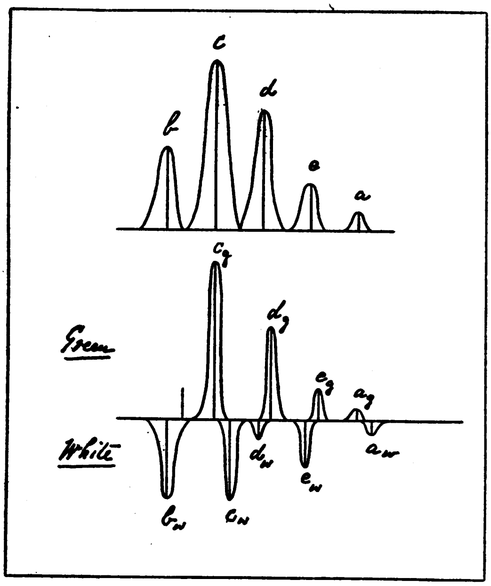

FIG. 1

Observations at the temperature of liquid air show that these bands are really doublets, unresolved at +20° but separated at low temperatures; a dim companion of the band as observed at +20° increasing greatly in brightness as the temperature falls while the dominant member becomes relatively feeble or in some instances disappears altogether. At low temperatures, as is usual with the uranyl compounds, all the bands are very narrow so that overlapping components which are entirely indistinguishable at the tempera-