Physiology of Protoplasmic Movement.¹

By

Prof. Dr. Th. W. Engelmann,
in Utrecht.

I. Introduction.

Living protoplasm possesses in very many instances the inherent property of moving with a rapidity which is perceptible with the aid of the microscope.

The movements, which show themselves by a change of form and internal arrangement of the protoplasmic masses while the volume remains apparently unchanged, may be also artificially produced or influenced by what are called stimuli.

The existence of these movements is an intrinsic part of the general conditions of life.

In this they agree with muscular and ciliary movements, with which, indeed, they are closely connected by numerous transitional forms. They must be classed with both the latter varieties of organic movement as phenomena of contractility.

The special character of protoplasmic movements lies in this, that the particles of the contractile mass move, as a rule, not in relation to any fixed position of equilibrium, but can change their arrangement and position (and this apparently voluntarily) as do the moving particles of a fluid substance. Further, the impulse to such movements does not normally come from without, but originates in the moving particles.

¹ Translated from Hermann's 'Handworterb. der Physiologie,' by A. G. Bourne, B.Sc.
PROTOPLASMIC MOVEMENT.

themselves. Protoplasm thus possesses, not only contractility and irritability, but also automatism.

Protoplasm, in accordance with its low stage of organisation, unites in itself the three properties which are usually divided between histologically differing elements—in the case of ciliary organs between the protoplasm and the cilia, in the case of muscular organs between the ganglia, the nerves, and the muscles themselves.

With this agrees its remarkably wide distribution in animal and vegetable organisms, its prevalence among the lowest forms of life in both kingdoms, as well as among embryonic or, above all, young cells, and in the same way the absence of a more complicated anatomical structure.

Sharply defined limits between protoplasmic movements and those of other organic structures cannot be drawn. As exhibiting movements transitional between protoplasmic and muscular movement may be instanced the body-substance of numerous Infusoria, the superficial sarcode of Sponges, embryonic muscle-cells of higher forms, endothelial cells of many, more especially young, blood-capillaries, &c. Pigment cells, which are contractile under the influence of a nerve impulse, found in the skin of Crustacea, Fishes, Amphibia, and Reptiles, may be also mentioned in this connection. Transitions from protoplasmic to ciliary movement, or more especially in the other direction, have been observed by De Bary and others in the spores of Myxomy-

Protoplasmic movement, properly so called, is to be distinguished from the changes of external form and internal arrangement of the protoplasm which occur during growth and reparation, segmentation, fertilization, &c., of cells, principally by its greater rapidity and its non-relation to all growth and reproduction. But here, again, there is no sharp limit, as shown, for instance, in the phenomena of fission among Protamœbae, Amœbae, and colourless blood-corpuscles, and the increasing internal movements preparatory to spore formation, which occur in the cells of many Algae and Fungi.

Historical.—The oldest description of a protoplasmic movement which I have been able to come across is by Rösel von Rosenhof.

The small "Proteus" which this excellent observer described and figured in the year 1755 was a large freshwater Amœba. Rösel distinguished between a richly granular interior and a hyaline peripheral portion ("ein zartes äusseres Häutlein), figured the unceasing changes of shape, the assumption of the spherical form in consequence of mechanical excitation, and the phenomenon of fission; this latter, by-the-bye, the first direct observation of a cell-division. Following close upon this, twenty years later, comes Bonaventura Corti's celebrated

2 'Jenaische Ztschr.,' iv, p. 87, 1868.
3 Ibid, v, p. 543, 1870.
4 'Entwickelungsgeschichte d. Siphonoph.,' pl. vi, fig. 36; pl. xiv, fig. 93, Utrecht, 1869.
7 Rösel von Rosenhof, 'Der monatlich herausgegebenen Insectenbelustigungen,' dritter Theil, pp. 621—623, pl. ci, figs. a—w., Nürnberg, 1755. The "Proteus" described shortly previous to this by Baker, is Trachelocerca color, a holotrichous Infusorian.
8 B. Corti, 'Osservazioni microsc. sulla Tremella e sulla circolazione del fluido in una pianta acquajola,' Lucca, 1774.
description of the rotation of the "cell-sap" in Characeae. The wide distribution of the phenomenon in vegetable cells was specially demonstrated in the first third of this century through the observations of Meyen ("Vallisneria, Hydrocharis," 1827), Robert Brown ("Staminal Hairs of Tradescantia," 1831), Amici, and others. Of the highest importance was Dujardin's description of a shapeless contractile body-substance in many lower organisms (Rhizopods, Infusoria, Polyps, &c.). His observations upon this substance, which he called Sarkode, and its movements are even to-day of actual importance. He was the first to observe the granular streaming in the pseudopodia of Rhizopods. Soon phenomena of movement were discovered in the cells of higher animals which resembled those of sarcode in a remarkable way (Limax eggs, Dujardin 1837; Planarian eggs, v. Siebold 1841; colourless blood-corpuscles, Wharton Jones 1846; and others). Ecker showed (1849) the connection between the various "organised" (muscles, ciliary hairs) and the "unorganised" contractile substances of animals, and a year later (1850) Ferd. Cohn expressed his opinion, and supported it with good reasons, that the actively motile substance of vegetable cells, which since 1846 (H. von Mohl) has been distinguished as protoplasm from cell-sap,"and the contractile substance and sarcode of the zoologists, if not identical, were in the highest degree analogous structures."

That it was not, as had till then under the influence of the older cell-theory been supposed, the cell membrane which effected the contractions of animal cells, but the so-called cell contents was proved by Donders. 1

5 F. C. Donders, "Form, Mischung und Funktion der elementaren Gewebs-
The actual identity of animal and vegetable protoplasmic movement has been since then more closely proved through the morphological and physiological investigations of Max Schultze,¹ Unger,² De Bary,³ Haeckel,⁴ and Kühne;⁵ and a more complete knowledge of the movement and its manifold conditions has been afforded by these authors as well as by Naegeli, Brücke, Heidenhain, Cienkowsky, Hofmeister, and others. The wandering of amœboid cells in animal tissues, brought into general notice by von Recklinghausen ⁶ (1863), and the importance of this for many physiological and pathological events in animal organisms was shown by this author, and by Stricker, Cohnheim, and others.

II. PHYSICAL AND CHEMICAL PROPERTIES OF CONTRACTILE PROTOPLASM.

Contractile protoplasm appears optically as a homogeneous, transparent, almost always colourless mass, with a higher theile in Zusammenhang mit ihrer Genese betrachtet,” 'Ztschr. f. wis. Zool,' iv, p. 249, 1852 (translated from the ‘Nederl. Lancet,’ Derde, ser. i, pp. 84, et seq., 1851—52).


² W. Kühne, ‘Untersuchungen über das Protoplasma und die Contractilität,’ Leipzig, 1864; also ‘Arch. f. Anat. and Physiol.,’ 1859, pp. 564, 748.


refractive index than water but lower than oil. In some cases, as, for instance, where it has the form of thick fibres or skin-like layers with a prevailing movement in one direction (pseudopodia of Actinosphœrium Eichornii, cortical protoplasm of Stentor), it is distinctly doubly refracting, and, indeed, as in the case of muscles and cilia, with a single positive axis, the optical axis coinciding with the direction of the movement. 1

Different portions of one and the same protoplasmic mass may have different refractive powers. In the case of naked amœboid protoplasm the more superficial layers are more highly refractive than the deeper: in the pseudopodia of Actinosphœrium and many Rhizopods a strongly refracting axial layer may be distinguished from the remainder. During the movements the refractive power of the same portion usually changes to a considerable extent.

With regard to its mechanical properties, protoplasm may present a greater or less degree of fluidity, does not mix with water, and is capable of swelling up; it presents great cohesive power, great extensile power, trifling elasticity and a tendency to take on the form of droplets. These properties vary, however, not only for different varieties of protoplasm, but at different spots of the same protoplasmic mass, and often differ even in the same spots within short intervals of time. With naked amœboid protoplasm the superficial layer is firmer than the central mass and may even permanently or temporarily pass into a strong membrane. As a general rule, no such membrane exists so that solid particles can be taken in by the outer layer of the body at any chosen spot, as may be easily observed by feeding with coloured particles (indigo, carmine, &c.). 2 In many cases the central mass is the firmer, the superficial portion being very soft and often quite sticky (pseudopodia of many Rhizopods, Actinosphœrium, &c.).

Protoplasm almost without exception contains certain bodies

1 Arch. f. d. Ges. Physiol., xi, p. 449 and 454, &c., 1875.
which play a passive rôle with regard to the movement. Setting aside as of casual occurrence solid particles which have been taken in from without and nuclear structures, they—namely, the granules and vacuoles contained in the protoplasm—are generally of exceedingly minute size. The granules may be very numerous, but on the other hand they may be of very sparse occurrence. The majority of the granules are albuminous, some are of a fatty nature while others are inorganic (e.g. carbonate of lime, in certain Myxoplasmodia). Occasionally coloured particles are present (many Myxomy-etes, Protamœba aurantiaca, &c.).

Very commonly the granules occur exclusively in the central portions of the protoplasm. In this case a fairly thick glass-like outer layer or skin devoid of granules may be distinguished from a granular and therefore opaque central mass (this is specially distinct in Amœbæ and Myxoplasmodia). These two may appear to be very sharply separated from one another during actual movement, although they are continually becoming mixed and separated again.

Where the granular protoplasm becomes drawn out into very thin threads (pseudopodia of Rhizopods, Radiolaria, &c., the thread-like networks of Noctiluca, numerous vegetable cells) the granules often project beyond the superficial layer. Indeed, in such cases they often exist chiefly in the superficial layer. Foreign particles moreover easily get stuck to the outer layers of naked protoplasm, and are then moved along in the same way as the true granules (Rhizopods, Oscillatoria, Diatoms, &c.).

The densely granular portions of the protoplasm appear as a rule to possess less cohesion than those which are devoid of granules. The granular central mass of Myxoplasmodia and Amœbæ often flows within the firmer superficial layer like a fluid emulsion in a bladder. Not unfrequently the granules exhibit irregular shaking, dancing movements, apparently quite similar to those exhibited by the smallest particles suspended in a thin fluid (Brownian molecular movement). This is the case for instance in the endoplasm of Vorticellæ, in the interior
of many Myxomycetes, and in the protoplasm of numerous vegetable cells. Special vacuoles filled with fluid in which such movements take place are by no means always or even frequently to be discovered. The whole plasma appears rather to have little more cohesion than a thin fluid at such spots. At the surface of very thin protoplasmic threads the extent to which the granules move is greater than in the more hyaline axis. Such fibres, moreover, very easily flow together, forming "sheets" like ordinary mucous threads, while the hyaline layer surrounding protoplasmic masses does not readily do so.

That the flowing together does not, or at least does not always, depend only upon the prior cohesive power of the substance is well shown in that the pseudopodia of different individual Rhizopods,¹ as well as the processes of plasmodia belonging to different species ² never fuse with one another.

Doubtless the above-cited differences in cohesive power depend essentially upon the differences in the amount of imbibition-water, which is shown by the refractive index varying in direct proportion to the amount of cohesion. These differences in cohesive power are also artificially produced along with corresponding changes of volume and refracting power by means which cause swelling or shrinking. In mobile granular protoplasm a separation of the fluid in the form of small droplets frequently takes place—vacuole-formation. The protoplasm may in consequence acquire a frothy appearance.

In resting protoplasm the form of the vacuoles is for the most part perfectly globular. During movement they may be much drawn out, but always return to their globular form.

This also holds good for the form of the gas-bubbles ³ which have been observed in some instances in protoplasm.

¹ Max Schultze, 'Das Protoplasma der Rhizopoden und der Pflanzenzellen,' p. 25, 1863.
For our knowledge of the chemical composition of pure protoplasm we are really dependent upon its micro-chemical reactions. On this account our existing knowledge in this respect is extremely scanty. It must be specially noted that there is no chemical mark by which contractile can be separated from non-contractile protoplasm.

In life the reaction of protoplasm is generally weakly alkaline or neutral; in *Æthalium septicum* it is always distinctly alkaline. Now and then I have seen blue litmus particles change within a few minutes after being taken into the contractile endoplasm of *Stylonychia mytilus* and *S. pustulata*, *Paramécium aurelia*, and *Améba diffluens*, to a red colour and remain so.

Among the solid substances which often make up together 10—20 per cent. of the total weight, albuminous granules make up by far the greater mass, as is usual in protoplasm. And, indeed, albuminous granules are always observable, at any rate at a lower temperature than that at which they coagulate (generally under 50°). In addition to these, carbohydrates (in the plasmodium of *Æthalium* there is a quantity of glycogenous substance), fat, inorganic substances, especially potash compounds, are seldom absent. Lecithin is also frequently present. In the plasmodium of *Æthalium septicum* a peptic enzym is found.

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3 This is possibly due to an acid secreted in an attempt to digest the particles. I have observed *Vorticella* in a watery solution of aniline blue taking it in rapidly and becoming filled with blue vacuoles, the contents of which are gradually absorbed, the blue colouring matter reappearing of a different tint in the contractile (excretory) vacuole.—TRANSL.
4 'Briefl. Mittheil.,' von W. Kuhne.
5 Krukenberg and others.
III. The Spontaneous Movements of Protoplasm.

In accordance with the peculiarities mentioned in the introduction, protoplasmic movements in general present a great variety and change in the manner of their appearance, and this is the case to such an extent that it is impossible to give a short description applicable to all cases. Certain definite types may, however, be distinguished, and we may almost limit ourselves to describing these and referring to the fact that they are connected with each other by numerous transitional forms.

1. Movements of Naked Protoplasm.

Three chief types may be distinguished, and may be called respectively—Amoeboid movement, Streaming movement, and Gliding movement.

The amoeboid movement shows itself in the protrusion and retraction of smooth, round, conical, or flattened, at first generally hyaline processes, into which the granular mass from the interior streams in and out. The processes may remain separate from one another, or they may ramify and even form networks. In the simplest cases of this kind of movement only slow unimportant changes of the external form of the mass occur, which do not cause a change of position. This is the case with the egg cells of many Vertebrata before fertilization. The phenomena soon become more complicated, as shown in the movements of Amœbæ, Myxœbæ, Arceæ, Difflugiaæ, many Monads, numerous egg cells (Hydra, Sponges), the white blood-corpuscles of most animals, pus-corpuscles, wandering cells in connective tissue, and many epithelia (frog's cornea), &c.

We now come to those extensive and often very active streamings which occur in very granular central masses, and those considerable changes of shape which come about

1 First, and very well described by O. Fr. Müller, ‘Animalcula infusoria, &c.,’ p. 10, 1786.
in consequence of the appearance and disappearance of processes which, although taking on very various forms, almost always remain unfused with one another. As these processes fasten themselves to fixed bodies, they can, by shortening themselves, draw the remaining protoplasm after them, and produce a movement of translation. The rapidity with which they can do this varies with the particular body and its surroundings, but always remains microscopic. A velocity of 0.5 mm. a minute which is sometimes attained by an Amoeba may be considered as exceptionally rapid. The force with which amœboid movement takes place may be regarded as of a quite important value. The wandering cells of the frog’s cornea, for instance, move between the fibrillæ and lamellæ and between the other epithelium cells, which in doing so they must push apart from one another.

Fig. 1 shows the different forms (a—p) which the same

Fig. 1.—A colourless blood-corpuscle of a frog under the influence of (a—m) a gradually increasing temperature, which (n—p) subsequently diminishes.
colourless blood-corpuscle of a frog assumed at intervals of one minute.

The plasmodium of Myxomycetes is very good for the study of amoeboid movement, on account of the great size of the protoplasmic masses and the extreme rapidity of the movements, which are visible even to the naked eye. The processes here run together in networks, which may cover more than four square centimetres.

A. De Bary describes the movements thus:—"There are two varieties. In the first place, in every mass of transparent plasmodium a large number of granules are to be seen in active streaming. In all the thread-shaped branches there is always one current only along the axis of the branch; where branching takes place the current divides, following the branches, or if the movement is taking place in the other direction the currents in the branches flow together into the main stream; not unfrequently, however, the streaming proceeds in one lateral branch only, while in the other no movement, or one in the opposite direction, prevails.

"In smooth, skin-like expanses numerous branching streams generally run either in the same or in different directions, and often streams going in directly opposite directions run side by side.

"The peripheral substance, within which the granulated protoplasm streams, exhibits a movement which appears for the most part unconnected with this, and which consists in a slow flowing or undulating change of the margin, small processes being continually extruded and withdrawn again. The granules are often quite unaffected by these movements, but sometimes are carried in smaller or larger numbers into the small tentacle-like branches. The activity of the peripheral movements varies much, under continued observation. Very trifling changes in the margin are to be seen, and the flat expanses in particular often look like a perfectly still surface sprinkled with motionless granules while the streams flow through it.

"Especially in the latter case the plasmodium has often the appearance of being composed of two quite different substances—a streaming fluid filled with granules, and a viscous, slowly-moving portion, the former appearing to move within the latter in special canals with firm walls. But new streams may be often seen to arise in the transparent portion of the plasmodium, and the granules in a resting portion suddenly fall into a main stream; others, on the contrary, cease moving, and completely take on all the properties of portions which are at rest. The resting granules on the margin of a strong stream can suddenly fall into movement, following the stream, and all sharp line between streaming and resting portions vanish.

"If one observes streams coming from the extremities of branches one of two different phenomena may be seen. On the one hand, the extremities, very much drawn inwards, pass into a condition of energetic contraction, and the streaming is most active near the extremities and diminishes in rapidity in a centrifugal direction (towards the periphery). On the other hand, the extremities from which the stream comes may sink slowly together, and the rapidity of the stream increase steadily in a centrifugal direction.

"Where an active stream runs into the ends of branches, and these rapidly swell up and new branches are given off, it looks as though the granular mass were forcibly pressed into the ends. At the same time, it is generally very obvious that the stream going towards the ends of the branches increases in velocity in a centrifugal direction" (pp. 47—48).

According to Hofmeister,¹ the granular stream of Myxomycetes commences at the periphery and extends backwards spreading as it does so; this may be also stated for numerous cases of amoeboid movement and is of theoretical value.

The streaming movement occurs in almost all Rhizopods, in Heliozoa and Radiolaria, and in some Monads. Out of the protoplasmic body spring long thin threads of protoplasm—pseudopodia (root-feet). And as a rule upon the surface there are a great number of fine granules in most active streaming

¹ W. Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 17, Leipzig, 1807.
movement. The threads themselves often at times show no movement, and at other times only slow changes of form which consist in lengthenings and shortenings, in the formation of nodules, also of curved or irregular bends and branchings. They may be quite withdrawn into the protoplasmic mass. When they touch each other they fuse together, very easily forming sheets.

The characteristic phenomenon of the movements of granules is described by Max Schultze in the following way:—“It is a gliding, a flowing of the embedded granules in the substance of the threads. With greater or less rapidity these granules move in the threads either towards the periphery or in the opposite direction, and often, even in the thinnest fibres, in both directions at once. They may either simply pass one another or may move round one another, and after a short pause move on in the original direction, or the one granule may carry the other along with it. Like pedestrians in a broad street, the granules may swarm together in a broad fibre, many of them stopping from time to time and shaking or trembling merely, always, however, following a direction corresponding with the long axis of the threads. Often they stand still in the midst of their course and reverse their direction, the most (? Engelmann), however, succeed in reaching the extremity of their threads and here first change their direction.

“All the granules in a thread do not move with the same rapidity, so that one often overtakes another, the more rapidly moving granules pushing the others on, or, the latter stopping the former in their course. Where threads join one another, granules often pass over from one into the other, and at such places there are often broad expanses which have been formed out of agglomerations of thread substance out of which then, as independent processes, further threads are formed, or into which, already existing ones are, as it were, absorbed. Many granules quite evidently run in the most superficial layers of the threads from which they may be seen projecting. Possibly they all have a superficial position. Besides the small granules

1 Max Schultze, 'Das Protoplasma,' &c., p. 11.
there are often larger lumps of substance like spindle-shaped swellings, or lateral prominences of a thread moving in the same way as the granules. Foreign bodies, which have got stuck to the thread substance and taken in, partake also of the movement.

"The greatest rapidity of single granules hitherto observed (Schultze in Miliola) attains 0.02 mm. in a second. Generally it is considerably less. It is extremely sluggish for instance in sun animalcules."

Gliding movement.⁠¹—The peculiarity of this case is that on the outside of a firm cell integument, extremely thin layers of protoplasm devoid of granules move along, and by means of their movement the whole body progresses upon a firm basis in a gliding or creeping manner; relatively solid bodies which remain sticking to this layer can be moved onwards along its upper surface. The direction of the movement is generally straight forward (Diatoms) or spiral (Oscillatoria), sometimes backwards sometimes forwards. The rapidity seldom exceeds 0.04 mm. in a second. It is almost continually changing in the same individual. The force with which the movement takes place may attain a considerable amount. This type of movement is exhibited by most Bacillaria (rocking movement of Diatoms) and Oscillatoria as well as by young stages of Nostocaceæ and Rivulariaæ.

The superficial protoplasm of these organisms is during life it appears, never visible, on account of its extreme thinness and low refractive power. Its presence was formerly inferred only, on account of the movement produced.⁠² In many cases it is only rendered visible by means which produce coagulation.⁠³

¹ Many botanists, following Nägeli's example, use this term to express the streaming of granules on the surface of threads of protoplasm.


2. Movements of Protoplasm bounded by firm Integuments.

This case is chiefly realised in vegetable cells. We can with the botanists distinguish two chief varieties:—Circulation and Rotation.

Circulation. — Here contractile protoplasmic threads stretch inwards from the cell wall, traversing the cell space, which is filled with fluid; they vary in number and are continually changing their position, form, and size. The direction and rapidity of their movement are generally inconstant, being

![Diagram of cells from the staminal hairs of Tradescantia (after Kühne).](image)

A. Fresh, in water. B. The same cell after slight local electrical stimulation. a—b. The region stimulated. c. Clumps and mops of contracted protoplasm.
often quite different in immediately neighbouring spots. The threads can divide, fuse, and form sheets, and generally exhibit streaming granules, and behave on the whole like the pseudopodia of Rhizopods (see above). This type occurs in numerous vegetable cells, in hairs from plants (Cucurbita, staminal hairs from Tradescantia, fig. 2, &c.). It also occurs in Noctiluca, Dicyema (Entoderm cells), in the cartilaginoid cells of the tentacles in Medusae and in the gill-fibres of Branchiomma, in enchondroma-cells, &c.

Rotation.—The protoplasm lining the walls of a cell (the outermost pellicle excepted) rotates as a connected mass around the interior of the cell, generally following constant tracks and with an even velocity. The direction of the movement is always one almost parallel to the long axis of the cell. Any protoplasmic contents which may exist—nuclei, chlorophyll granules, crystals—rotate along with it, generally without changing to any considerable extent their relative position.

The best known instances of this movement are the cells of the Characeae, the leaf-cells of Vallisneria spiralis and Ceratophyllum submersum, and the root hairs of Hydrocharis morsus-ranae.

Here must also be classed the rotation of the endoplasm of Paramaecium bursaria and P. aurelia and some other Infusoria (e.g. Vorticellæ).

IV. GENERAL CONDITIONS OF SPONTANEOUS PROTOPLASMIC MOVEMENT.1

1. Temperature.

For every contractile protoplasm there is a lower and a higher temperature at which its spontaneous movements stop, directly and under all circumstances. The minimum generally lies at about 0° and the maximum about 40° C. Within these two temperatures is the province of manifest contractility; and the

1 Most important literature:—Dutrochet, 'Compt. rend.,' ii, pp. 775—784, 1837 (Chara); Max Schultze, 'Das Protoplasma der Rhizopoden, &c.,' 1883; W. Kühne, 'Unters. über das Protoplasma, &c.,' 1864.
velocity of the movement increases, as a rule, with the temperature, and, indeed, in all special cases a definite constant velocity corresponds to a definite degree of temperature. This, however, is no longer the case if shortly before, a rapid and extensive fluctuation of temperature has taken place. Such fluctuation acts like a mechanical or electrical excitation, and will be spoken of later. For similar increments of temperature, the increase of velocity appears in many cases to be greater, the higher the absolute temperature.

Naegeli, in the terminal cell of Nitella syncarpa, which was slowly warmed under the microscope, observed that a distance of 0.1 mm. was traversed by the rotating layer in 60 sec. at 1° C., in 24 sec. at 5° C., in 8 sec. at 10° C., in 3.6 sec. at 20° C., in 1.5 sec. at 31° C., in 0.6 sec. at 37° C. Schultze has shown, on the contrary, that the granular streaming in Miliola, which at ordinary temperatures is already very rapid—0.2 mm. in a second—cannot be accelerated by further warming. There is apparently in every case a certain higher limit of temperature at which the movement attains its highest velocity. This optimum temperature generally lies several degrees below the maximum temperature compatible with movement. If the temperature rises above the optimum the movement indeed becomes just at first even more active, but dies out after some time. There is generally some delay before this occurs, but this is the less the nearer the prevailing temperature to the maximum. If the temperature attains the maximum, all movement stops in a moment. The protoplasm then enters upon a condition of apparent death or rigor—temporary heat rigor, heat tetanus—in which it remains, as though under continued artificial stimulation. It is drawn together so as to expose the smallest surface, and is only relaxed when cooling occurs, when, and in which case only, the movements are able to start once more. The optical properties of the protoplasm are not necessarily altered in this condition.

2 Max Schultze, 'Das Protoplasma, &c.,' p. 47.
Naked masses of protoplasm of microscopic size, such as Amœbeæ, colourless blood-corpuscles, when gradually warmed up to the maximum, become spherical. Protoplasmic threads of Rhizopods, vegetable cells, &c., generally become at first varicose, and finally withdrawn into the main mass of the protoplasm. Fig. 3 shows the different shapes assumed by a

![Diagrams of different shapes](image)

Fig. 3.—A colourless blood-corpuscle of a frog under the influence of 
(a—m) a gradually increasing temperature, which (n—p) subsequently diminishes.

colourless blood-corpuscle of a frog, under the influence of gradually warming and subsequent cooling, at intervals of five minutes.

From a to c the temperature was 12° C., the shape is only slightly changed. At c the microscope, with the preparation in a moist chamber, was placed in a Sach’s warm box filled with water at 50° C. After a few minutes the movements had become visibly more active, and the cell crept forwards with, up to l, an ever-increasing rapidity. At m it commenced, and at n had completely entered into heat-rigor. The preparation
was then removed from the warm chamber and cooled gradually to the temperature of the room, 12° C. At 0 changes of shape commenced again, and at p were already quite active.

When the temperature exceeds the maximum the protoplasm dies at a certain degree, which may be called the ultramaximum, and exhibits suddenly a shrinking and loss of clearness, on account of the coagulation of the albumens, and, as a rule, the vacuoles are extruded. This heat-death or lasting heat-rigor may also come about even at a lower temperature when the warming has been very long continued. Subsequent cooling then naturally produces no further change.

Freshwater Amoebae which, after warming for one minute at 35°, showed only passing rigor, Kühne found would, after fifteen minutes’ warming at the same temperature, become completely globular and lose all power of movement. After shorter warming of Amoebae at 40° they appeared like “globular, sharp, and doubly-contoured vesicles, which contained a brownish-looking and, by transmitted light, very opaque lump, which was generally attached firmly to one side of the periphery, and filled up some three parts of the spherical space. The remaining space was filled with a transparent clear fluid, in which small granules in active molecular movement swarmed about.” Kühne subsequently treated such individuals with water at 45°; the molecular movement in the previously clear portion of the vesicle stopped, and formed here also a firm coagulum.¹

When the protoplasm enters suddenly into heat-rigor it has no time to change its form. Max Schultze ² saw, for instance, the protoplasmic threads of Miliola, when warmed quickly, at any rate up to 45°, enter at once into rigor: similarly with Tradescantia.

Concerning the value of the maximum and ultramaximum for different species of contractile protoplasm, the following table gives some idea:

¹ W. Kühne, ‘Untersuchungen über das Protoplasma,’ pp. 43—45.
² M. Schultze, ‘Das Protoplasma, &c.,’ p. 22.
Maximum about Ultramaximum about

Didymium serpula .... 30° C. .... 35° C. Kühne.
Aethalium septicum .... 39° C. .... 40° C. "
Actinosphærium Eichornii 38° C. .... 42° C. M. Schultze.
Miliola .............. 38° C. .... 43°—45° C. "
Urtica urens .......... 44° C. .... 47°—48° C. "
Tradescantia virginica . 46° C. .... 47°—48° C. "
Vallisneria spiralis .... 40° C. .... 47°—48° C. 1
Nitella syncarpa .... 37° C. .... — 2
Chara flexilis ........ — .... 45° C. 8

If the temperature sinks gradually to the minimum, the spontaneous movements stop after they have first become slower and slower. Simplifications of the shape generally occur, and existing processes and branchings are gradually absorbed and new ones are no longer developed. But the complex form may remain, under certain circumstances, as observed by Kühne in Amoeba diffluens (l. c., p. 46) and Actinosphærium (l. c., p. 68). Optical changes do not generally accompany the entrance into this cold rigor. But Hofmeister 4 saw the walls of a protoplasmic mass in Cucurbita, after standing for a long time at 0° C., become filled with vacuoles and quite frothy. Artificial excitation remains potent, and raising the temperature above the minimum causes a resumption of the movements.

It appears that contractile protoplasm may be kept at the minimum temperature, and even much below it, for an almost unlimited time without sustaining permanent injury. No lower temperature limit, ultraminimum, at which death inevitably ensues, has been described. Even after actual freezing the protoplasm when thawed will, under certain circumstances, resume its spontaneous contractions. And in this case it does not even appear necessary that the thawing should take place very slowly, a condition which otherwise is very essential for the revivification of organic structures rich in water.

3 Dutrochet, 'Compt. rend.,' 1837, ii, p. 775.
4 W. Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 55.
Kühne\textsuperscript{1} allowed Tradescantia hairs to freeze to the walls of a platinum vessel without adding water. It was quickly lowered to a temperature of $-14^\circ$ C., and allowed to remain for more than five minutes at this temperature without death of the protoplasm ensuing. Taken out and quickly examined in water, no trace of protoplasmic network was present, but the violet interspaces in the cells presented near the naked nucleus a great number of separated round droplets and little lumps. A few seconds later these began to exhibit exceptionally active amoeboid movement. After some minutes they began to run together into single larger droplets, and these, again, united with other groups, and in about ten minutes the original protoplasmic network was there again; and even after twenty-four hours the threads were found in active streaming. Hofmeister\textsuperscript{2} has corroborated these observations.

2. Imbibition Water.

The amount of imbibition-water acts like the degree of temperature. For every protoplasm there is a maximum and minimum for the amount of contained imbibition water at which spontaneous movements stop. Exact determinations have not been made, but the minimum may be stated as on the average below 60 per cent. and the maximum over 90 per cent. Within these limits the activity of the protoplasm generally varies, with a corresponding increase of volume and decrease of refractive index, with amount of the contained imbibition water. Rapid changes in the extent of concentration of the medium, which induce rapid swelling or more especially shrinking, may act like an excitation (see below). There is always an optimum for the amount of imbibition water.

When the maximum is gradually approached the protoplasm takes on its simplest form (globules, varicosities, &c.). Removal of the excess of water with indifferent substances (weak sugar solutions, salt solutions, &c.) often reinduce the move-

\textsuperscript{1} W. Kühne, 'Unters. über das Protoplasma,' U. S. W., p. 100, et seq.
\textsuperscript{2} W. Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 54.
ments after even some minutes of water-rigor. When treated for any long period with distilled water the protoplasm dies. The phenomena attending this are not always the same. The protoplasm may form vacuoles and deliquesce, or it coagulates at once, in which case the form corresponding to the non-contracted condition may remain preserved for a considerable time longer.

The withdrawing of water by indifferent or diluted solutions leads eventually to a temporary or lasting rigor (dry-rigor). In vegetable cells, moreover, as discovered by Al. Braun in Chara, the protoplasm generally withdraws itself from the cell-wall as a continuous sac, the movements continuing for a considerable time. Naked protoplasm (Amoebae, Myxomycetes) which has been shrunk up by the action of 1—2 per cent. salt solution often becomes covered with a large number of fine, pointed, hyaline, cilia-like processes. After dilution with water the protoplasm returns to its original condition. Protoplasm which has been completely dried in the air at ordinary temperatures and entered in consequence into rigor, can under certain circumstances after mixture with water become active again, and this even after several years. This is certainly the case for instance with encysted Amoebae and Infusoria. It may, however, be also observed in naked plasmodia and in many other even quite highly organised bodies.

It is important to note that when the concentration is exceptionally slowly increased, protoplasm can in many cases (all?) accommodate itself to the solutions, while if the action is more

2 Kühne, 'Untersuchungen, &c.,' pp. 48, 82; cf. De Bary, 'Die Mycetozoen,' 2 Aufl., p. 46, pl. ii, fig. 16; iii, figs. 11 and 12; Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 24, fig. 28; V. Czerny, 'Einige Beob. über Amoeben,' 'Arch. f. mikr. Anat.,' v, p. 159, 1869; Strasburger, 'Studien über das Protoplasma,' 'Jen. Zeitschr. f. Naturwissensch.,' x, p. 407, Jena, 1876. The cilia-like processes are produced, according to most of these observers, without any noteworthy change in the concentration of the surrounding medium, in connection with a shrinking in of a process; this I can also corroborate.
RAPID it would be at once destroyed. It appears that in such a case no corresponding strong contraction takes place.

In sea-water which I had preserved for more than a year, and which by gradual evaporation had become so concentrated that there was 10 per cent. of saline matter, numerous Protozoa, even Worms, Arthropods, Diatoms, Green Algae, &c., still lived and apparently quite comfortably. I was also able to repeat Czerny's experiment with fresh-water Amoebae, and accustom them in the course of several weeks to 4 per cent. solutions of common salt. With the action of 10 per cent. solution of common salt, according to Kühne, fresh-water Amoebae immediately pass into spherical bodies which quickly break up and throw out a network of fine mucous-like threads, while the rest passes into the form of coarser and finer particles which move about with active molecular movement. Salt-water Amoebae behave in a similar manner.

3. Oxygen.

In media quite free from oxygen spontaneous movement can without the least doubt only go on for a short time—at most for some hours. The gradually advancing cessation can always in its early stages be stayed by the admission of oxygen, and indeed in this way only. With regard to the connection between the energy of the movement and the amount of the absorption of oxygen in the surrounding media, only so much can be said with certainty, that the movement in many (all?) cases is a permanently maximal one at very slight pressures, far under the normal. At great pressures of oxygen (3—6 atmospheres) it diminishes, but is accelerated when the pressure is lowered again.

Evidently the living protoplasm enters into chemical union with the surrounding media, and the oxygen thus firmly com-

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1 Cf. also Dutrochet, 'Compt. rend.,' 1837, ii, pp. 781, 782.
3 Kühne, 'Unters. über das Protoplasma, &c.,' p. 48; cf. also Czerny and others.
bined, of which under normal circumstances a certain amount must be taken into each protoplasmic body, is constantly used up during the movements, probably by the giving off of CO₂.

Corti observed the streaming cease in the cells of Chara, when the air was removed by olive oil, as well as after long standing under the best vacuum obtainable under the receiver of an air-pump. Hofmeister¹ observed a cessation in Nitella after five minutes in olive oil, and after thirteen minutes in very rarified air. In the first case the movement started again after the restoration of the air in thirty minutes, and in the second case after twenty-two minutes.

Kühne removed the atmospheric air by means of pure hydrogen. After the gas had been passed for more than twenty-four minutes, fresh-water Amoebæ fell motionless to the bottom of the drop (they responded in this condition to induction shocks, but a markedly stronger excitation was necessary in this case). Spontaneous movements recommenced seventy-five minutes after the entrance of air. Plasmodia of Myxomycetes and also the protoplasm of Tradescantia hairs showed no further movement, after some hours of contact with hydrogen, and were in active movement again a few minutes after the readmission of air. And even after standing twenty-four hours in hydrogen readmission of air reinduced the movements. I found that contractile cells from the lymph sac of a frog required two hours' transmission of the purest hydrogen through a hermetically sealed moist chamber to stop the movements; most of the cells became spherical. The same happened with fresh-water Amoebæ. A drop of haemoglobin solution after being under similar conditions for ten minutes, no longer showed in a microspectroscope the two absorption bands of oxy-hæmoglobin, which were previously very distinct. Under very long treatment with pure hydrogen protoplasm dies completely, generally first becoming cloudy and forming vacuoles and finally falling to pieces.

Tarchanoff,² following in the steps of Paul Bert's discovery

¹ W. Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 49.
² Tarchanoff, 'Arbeiten der St. Petersburger Gesellschaft der Naturf.,' vii,
of the injurious action towards life of oxygen at high pressures, experimented with this agent. He observed that the colourless blood-corpuscles of the frog become round and motionless at 3—6 atmospheres of oxygen pressure, and resume their movements at ordinary pressures.

4. Other Chemical Conditions—Poisons.

Like all the vital phenomena of elementary organisms the spontaneous movements of the protoplasm can only continue for any time when the reaction of the imbibition fluid is neutral or almost neutral. A trifling excess of alkali or even more surely of acid causes a cessation which for a time may be counteracted by neutralization of the excess.

Dutrochet saw the movement in Chara stop completely in potash solution of 0.005 per cent. in thirty-five minutes, in potash or soda of 0.1 per cent. in two or three minutes, in tartaric acid of 10 per cent. in ten minutes, of 0.1 per cent. in an hour.

Max Schultze confirmed the injurious action of diluted acids (hydrochloric, acetic, and osmic) and alkalis on Miliola, Actinosphærium, Tradescantia, Myxomycetes. And Kühne also on Amœba, Actinosphærium, Myxomycetes, Tradescantia.

In diluted caustic alkali the protoplasm swells up strongly, deliquesces and completely breaks up. Before the cessation

p. 122, 1876 (Russian). I am acquainted only with Hoyer and Mayzel's abstract in Hofmann and Schwalbe's 'Jahresber.,' v, 1876, p. 22.

1 Dutrochet, 'Compt. rend.,' 1837, ii, p. 781.

2 Max Schultze, 'Das Protoplasma, &c.,' pp. 22 and 37.

3 Ibid., p. 32.

4 Ibid., p. 49.

5 W. Kühne, 'Untersuch. über das Protoplasma und die Contractilität., p. 49 (HCE 0.1 per cent., KHO 0.1 per cent., and 1 per cent.).

6 Ibid., p. 64 (HCE 0.1 per cent., KHO 0.1 per cent., Ammonia Vapour); p. 67 (CO₂).

7 Ibid., p. 85 (Ammonia Vapour); p. 89 (CO₂).

8 Ibid., p. 100 (HCE, KHO).
the normal movement is often observed to be accelerated.\(^1\) In
diluted acids death generally sets in with opacity and shrink-
ing (coagulation of the albumen).\(^2\) Carbonic acid has also
this result, if passed over the preparations in a concentrated
stream for some time.\(^3\) Movements, which have stopped in
consequence of the action of weak CO\(_2\) can by its replacement
by air, generally also by hydrogen, be reinduced, in conse-
quence of which any existing opacity is removed.

Ether or chloroform act in the same way as CO\(_2\) causing a
temporary or permanent coagulation. They need only be
mixed in small quantities with the air to effect their destruc-
tive action, which is also at first easily stayed by the introd-
uction of pure air.\(^4\)

It is interesting to note, as they specially agree in this respect
with the contractile substance of muscle fibres, that many kinds
of protoplasm are acted on in a poisonous way by veratin.\(^5\)
Kühne observed that freshwater Amœba,\(^6\) Actinosphæ-
rium,\(^7\) and Myxomycetes,\(^8\) in exceptionally diluted, barely
alkaline, even neutral solutions of this poison, become quickly
coagulated, becoming opaque and completely breaking up. Tra-
descantia cells, however, still showed the normal movements
after seventeen hours' immersion in a watery veratrin solution.

Binz\(^9\) and others have observed that quinine exercises a
strongly destructive action on many kinds of protoplasm and
on colourless blood-corpuscles. On the other hand, I have
given frogs such large doses of quinine sulphate by subcuta-

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1 By Dutrochet (l. c., p. 781), in Chara; By Kühne (l. c., p. 49), in
Amœba.
2 Kühne, l. c., pp. 49, 64.
3 Ibid., p. 51 (Amœba); p. 67 (Actinosphærium); p. 90 (Myx-
omyces); p. 106 (Tradescantia).
4 Ibid., p. 66 (Actinosphærium); p. 100 (Tradescantia).
5 Kühne, l. c., p. 47, et seq.
6 Kühne, l. c., p. 47.
7 Ibid., p. 65.
8 Ibid., p. 86, et seq.
9 C. Binz, "Ueber die Einwirkung des Chinin auf Protoplasma-bewegung,"
neous injection as to kill them, and have observed the lymph-corpuscles after some hours in active movement.

V. Behaviour of Protoplasm Towards Artificial Stimulation.

Protoplasmic contractions may, like the movements of muscles and other excitable organs, be called forth, not only by the normal physiological stimulus, but by numerous external influences, so-called artificial stimuli, or, as is more frequently the case, existing movements can be thus influenced. These stimuli are in reality the same as those for other excitable structures; as a general rule, any disturbance of the electrical equilibrium acts as a stimulus when it takes place with a certain rapidity or exceeds a certain amount, also, all electrical impulse, change of temperature, mechanical or chemical influence.

The amount of irritability, as measured by the weakest stimulus which calls forth an effect, varies with the kind of the protoplasm, the kind of stimulus, and the special conditions.

The protoplasm of fresh-water Amœbæ, Diatoms, Valisneria, &c., behaves to very weak induction currents in the same manner as do blood-corpuscles.¹

The protoplasm of Pelomyxa, which otherwise is not specially sensitive, is violently affected by suddenly admitted strong light, which has not necessarily any stimulating effect upon other kinds of protoplasm.²

The general conditions which affect artificial stimulation, with which it increases or diminishes, are the same as those which affect the power of spontaneous movement. They have, however, rather wider limits, as is shown, amongst other things, by the fact that artificial stimuli are potent even after spontaneous movements have ceased to exist (e.g. as a result of cooling, warming, withdrawal of oxygen, excess of CO₂).³

¹ Author’s observations.
The visible phenomena resulting from artificial stimulation may vary to a very great extent. We must here consider especially whether the protoplasm was in movement at the time of the excitation or not, and in the former case the kind and energy of the movement; further, whether the protoplasm was excited at the same time all over and to the same extent, more especially whether the stimulation was stronger at some spots than at others; further, whether it was free to move or was shut in a firm cell-wall, &c. The following special observations give some idea of the manifold character of the phenomena.

Generally, the effect of artificial stimulation shows itself in the directly excited portion of the protoplasm receding without visible change of volume, drawing itself together so as to expose the least possible external surface, and taking on a spherical form, just like a stimulated muscle. The rapidity and power with which it does this generally range within the same limits which exist for the spontaneous movements of the same object.

1. Electrical Stimuli.

Electrical currents only cause a movement in protoplasm when they flow directly through it, never from a distance only. Moreover, it is especially sudden changes in the intensity of a current which are followed by movements. The change in the current, as in the case of muscles, is not nearly so important as is the occurrence itself of the current, but after the breaking of a constant current, responsive movement takes place, as a rule, only in those cases where the current, after attaining its full force, has continued to flow for some time.

This time may amount, as in the case of Amoeba, to more than a second. Kühne observed in Actinosphærium that

1 Becquerel ("Compt. rend.," 1837, ii, p. 786) found strong galvanic streams (10—30 elements) quite inactive when passed through a wire bound round Chara, whatever the direction of the current.


the effect remained at the side of the animal which was in contact with the positive pole so long as the circuit remained closed. As a rule, however, the protoplasm soon regains its original condition so long as the current continues to flow with a constant intensity. Becquerel has observed this in Chara.

Making a constant current is a specifically stronger stimulus than breaking it, but the latter requires a longer duration of the current, or that the current should be more intense. Often, more especially when the object is very sensitive to the making shock, breaking a very strong current is quite inactive.2

The effect called forth increases very markedly within certain limits with the suddenness and the extent of the variation of the intensity of the current. Induction shocks are therefore as a rule more effective than making constant currents.

The effect of stimuli following one another at short intervals may be cumulative, and in this way singly ineffective stimuli may together produce a visible and powerful effect. The intervals between the stimuli, in order that the summation of effects may take place, must be as a rule of considerable amount (e.g. with many Amoeba and vegetable cells four seconds and more), and it appears that the more sluggish the spontaneous movements of an object the longer are the intervals necessary.3

After powerful excitations exhaustion sets in, stronger excitations are then necessary to produce the same effect, or, the excitations remaining the same, longer intervals of time for recovery. Very strong excitations will kill protoplasm; it becomes opaque, enters into rigor, and shrinks up or breaks to pieces: or they call forth secondary effects which completely upset the course of physiological events.

Behaviour of various types of protoplasm towards electrical stimulus.—The action of single induction shocks

1 Becquerel, 'Compt. rend.,' 1837, ii, p. 787.
2 'Arch. f. d. ges. Physiol.,' iii, p. 311, 1870.
3 Author's observations.
upon frogs' blood-corpuscles in active amöboid movement, according to Golubew, is that after some time (generally $\frac{1}{2}$—1 min.) the processes at first pointed become blunted, and gradually draw themselves into the cell-body. "If the stimulus acts more strongly a very rapid and complete drawing together of the cell so as to form a rounded lump may be observed. In this condition the cell remains for some time, and then resumes its ordinary movements." With still stronger excitation the cell almost always becomes suddenly spherical. In a few minutes a small droplet suddenly extrudes from some spot, increases in size for a time, more body substance flowing into it; it then decreases in size again, while at one or more spots new droplets are extruded. In this manner changes of form may occur which are at first very rapid and striking, but soon become slower; the droplets are drawn in, and the ordinary irregularly pointed processes are reformed. Fresh-water Amœbæ behave in a similar manner, only much more quickly. It must be noted that after a latent period, which with weak excitation amounts to some seconds but with stronger excitation may become imperceptibly short, there follows a slowing, or more probably a stopping altogether of the granular streaming movements, and of the shifting of position. After this follows—it is apparently simultaneous only when the excitation is very strong—a withdrawal, a shortening and thickening of the processes, which may amount within a few seconds to an assumption of a spherical shape. Soon after this are thrown out, generally by jerks, one or more hyaline protuberances into which the granules proceed forthwith to stream. The latter fasten themselves often to the surface of the outer pellicle. One of the processes enlarges more and more, stretches itself lengthwise, and finally takes the whole of the mass of the protoplasm.


PROTOPLASMIC MOVEMENT.

into itself. After as much as ten seconds' stimulation Amœbe will recover their original appearance and movement. Myxomycetes appears to behave in essentially the same way. The phenomena are, however, somewhat altered here, as the size of the object admits, as a rule, of partial excitation only.¹

Rhizopods (Miliola, Actinosphærium) draw their pseudopodia in when electrically excited, and these as a rule shortly become varicose.²

A stronger excitation is required to excite the pseudopodia which lie at right angles to the direction of the current than for those which lie parallel to it. The protoplasmic threads of vegetable cells which exhibit circulation behave in a similar manner (Tradescantia type).³

So long as the excitation is weak, as with amœbid protoplasm, slowing and stopping of the movements generally occurs at first, then varicosities, lumps, &c. are formed. Especially instructive are the phenomena in the case of partial excitation. Kühne⁴ observed (cp. fig. 2, p. 402) with Tradescantia, "that at one portion of the cell the stronger threads drew together, forming lumps and spheres, in which, after a resting period, movement of the granules commenced, which might have been mistaken for molecular movement if it had not been evident that the granules obeyed another impulse, owing to the very altered condition of the ground substance. As soon as the lumps and spheres became flattened again they moved onwards one by one with the streams in the neighbourhood which had

¹ Kühne, 'Unters. üb. d. Protoplasma, &c.,' p. 75, et seq.
² M. Schultze, 'Das Protoplasma, &c.,' p. 38; Kühne, 'Unters., &c.,' p. 56.
⁴ Kühne, 'Unters. üb. das Protoplasma, &c.,' p. 99 (Tradescantia). W. Velten, "Einwirkung strömender Elektricität auf die Bewegung des Protoplasma, &c.," 'Sitzber. d. Wiener-Mathem. Naturw.,' Cl. lxxiii, p. 351, et seq., 1876. The phenomena of swelling described by Velten have not been observed by other observers, nor by myself. I must state that, at any rate, when the current is not over maximal, they do not take place in any marked manner.
continued to flow, and finally came to completely resemble them. Where the lumps are formed the finer threads become broken through, and in such places the thickenings are quickly drawn out again into threads either from one or both sides."

![Cell image](image)

**Fig. 4.—Cells from the staminal hairs of Tradescantia (after Kühne.)**

A. Fresh, in water. B. The same cell after slight local electrical stimulation. a—b. The region stimulated. c. Clumps and nobs of contracted protoplasm.

The rotating protoplasm of Chara and Vallisneria cells, when excited simultaneously at all points, shows a slowing or stopping of the movement.¹

After this, if the excitation is sufficient, it draws itself up

together, as appears to be almost universally the case with vegetable cells containing moving protoplasm, at the short transverse walls (ends of the cells), and the whole mass contracts, so as to expose the least superficies, the process thus corresponding with the formation of spherical bodies by naked protoplasm when subjected to excitation. Brücke observed upon the stinging hairs of Urtica that after short powerful excitements threads of protoplasm with pointed ends and swellings in the middle, or knob-like, club-shaped processes stood out from the primordial utricle, being afterwards withdrawn again.

2. Thermal Stimuli.

Both positive and negative alterations of temperature may act as stimuli, and produce results similar or identical with those produced by electrical stimuli. This, of course, only when the alterations fall within the temperature range of contractility. In this case also the effect is the more pronounced and lasting the more rapid and extensive the change of temperature. Negative changes (always?) appear to act to a specifically greater extent than positive.

If after a change the temperature remains constant, the movements gradually assume the condition which they would have assumed by quite gradual warming or cooling, as the case might be, to a corresponding degree.

In Chara, which exhibited a moderately rapid rotation in water at 7°, Dutrochet observed that the movements completely ceased in four to five minutes when plunged into water at 32°. After some hours in water at 32°, the movements commenced again, and in two more hours had become quite active once more. Replaced in water at 7° the movements were again destroyed in four minutes, but recommenced quite slowly after half an hour at this temperature. After somewhat slower


2 Dutrochet, "Compt. rend.," ii, p. 777, 1837.
warming, from 18° to 27°; from 27° to 34°, and from 34° to 40°, the rotation stopped for a time, varying from some minutes to an hour.

Hofmeister\(^1\) observed a temporary cessation of the rotation in a preparation of Nitella which was taken from a room at a temperature of 18°-5° C. into one at 5° C. and left there for two minutes. The same thing\(^2\) happened after six to eight minutes with hairs of Ecballium agrestes, which exhibiting active streaming at 16—17° C., were taken into a temperature of 40° C., the protoplasmic network becoming much simpler and quite motionless. The streaming commenced again at the latter temperature only after a pause of from half an hour to two hours, and, once started, attained in a few minutes the activity normal to such a temperature. Rapid cooling from 40° to 17° C. rendered the protoplasm of the same object motionless. Again, "at numerous spots it had formed knotty varicosities." The movements recommenced only after seven minutes, and became once more normal (temperature constant at 16° C.) only after eighteen minutes.\(^3\) On rapidly warming the stinging hairs of Urtica up to 40° C. and higher, Schultze\(^4\) often observed the same curious changes of form of the protoplasm which Brücke has described as occurring after strong shocks with the magneto-electro-motor. (See above.) Kühne's and Hofmeister's observations upon the effect of rapidly freezing Tradescantia cells have already been described.

3. Light Stimuli.

The greater number of kinds of contractile protoplasm appear insensible to light or changes of light. This is the case, for instance, in the protoplasm of the colourless blood-

\(^1\) W. Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 53; cp. also Hugo de Vries, in 'Flora,' 1873, p. 25 (Hydrocharis morsus ranæ).
\(^2\) Ibid., p. 55.
\(^3\) Ibid., p. 54.
\(^4\) M. Schultze, 'Das Protoplasma, &c.,' p. 48.
corpuscles and other amœboid cells of Vertebrata and Invertebrata, the common Amœbæ, many Rhizopods, Infusoria, and vegetable cells. In green cells from which light is shut off, the movement stops, but only with the whole vegetation of the plant; in Chara, for instance, as shown by Dutrochet, only after twenty-four to twenty-six days.

In special cases the intimate structure of the protoplasm obviously alters with long exposure to light or the reverse. The plasmodium of Æthalium creeping upon the surface of tan while in the dark will withdraw itself again into the deeper layers upon exposure to bright light, and while in the light it puts forth only short much crowded processes, in the dark long, narrow, thin branches are developed. Here then illumination appears to act similarly to artificial stimuli. It is also well known that changes in the illumination cause changes in the contractile pigment cells which occur in the skin of many Fishes, Amphibia, and Reptiles—changes which bring about a change in the colour of the whole animal. The black pigment cells, for instance, in the frog's cutis, which in the dark are much branched, contract gradually upon exposure to a bright light to small spheres, in consequence of which the skin appears lighter in colour. But it appears that in this case the action of the light upon the contractile elements is indirect, and is transmitted

1 Author's and other observations.
3 Dutrochet, 'Compt. rend.,' ii, p. 779, 1837.
4 Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 21, 1867; Baranetsky, "Influence de la lumière sur les plasmodia des Myxomycetes," 'Mém. Soc. des Sciences Nat. Cherbourg,' xix, p. 321, 1875 (finds the blue rays specially active, the yellow not).
by the nerves, as Lister and Pouchet have specially shown with respect to the reflex of the eye.

Differing, however, from the above-cited cases, we have the behaviour of the protoplasm of Pelomyxa palustris.

This large fresh-water Amœba creeps about very actively in the dark, but when suddenly exposed to the light (diffused daylight is sufficient) the streaming of the granules ceases, and in a few seconds it draws itself together into a sphere. If it continues exposed to the light, movements recommence, but of a weak sluggish nature only. If the darkness is changed quite gradually to light (the change extending over about a quarter of an hour), there is no excitation-effect. There is also no excitation-effect when, after long illumination, the light is suddenly shut off.

It should here be noted that when portions of green leaves of Phanerogams, Mosses, or Fern prothalli are put into strong shade and kept there for some time, they assume a darker colouring in consequence of the gradual change of position of the chlorophyll grains which are contained in the protoplasm. These heap themselves together under the influence of light—especially of short-wave rays—at the sides of the cells which are turned towards the surface of the leaf, while in the dark they accumulate at the walls of the cells perpendicular to the surface. Although these changes certainly depend upon the movement of the protoplasm, it must remain uncertain how far they express a direct influence of light on protoplasm, or an indirect influence in consequence of the primary changes which the light exerts upon the chlorophyll bodies.*

2 G. Pouchet, "Sur les rapides changements de coloration provoqués experimentalement chez les poissons," 'Compt. rend.,' lxxxii, p. 866, 1871. Cp. also G. Seidlitz, 'Beiträge zur Descendenztheorie,' Leipzig, 1876, who has collected the instances of colour changes among animals.
4. Mechanical Stimuli.

All sudden mechanical disturbances of any importance act as mechanical stimuli—pressing, pulling, bruising, and tearing to pieces. The phenomena are really the same as those called forth by electrical excitation.

More than one hundred years ago Rösel observed that when touched Amoebae draw themselves together. Colourless blood corpuscles, Rhizopods, &c., after violent pressure draw in their processes and often become varicose. The streaming of the plasmodia of Myxomycetes is easily slowed or brought to a standstill for some time by any disturbance whatsoever. The protoplasmic threads in the staminal hairs of Tradescantia will, after strong sudden bruising, tear apart, "draw themselves together into short clubs or balls, and fuse partly with the protoplasm, which is heaped up around the nucleus, and partly with the protoplasm lining the cell-wall"—the primordial utricle. After ten to fifteen minutes the normal arrangement and movement commences again. The rotation in Chara cells, as was observed by Gozzi, and afterwards by Dutrochet, and others, stops after the tying of a ligature round the cell or sharply bending. But rotation soon commences again in the two halves. Dutrochet observed a stoppage of some minutes after cutting or tearing the cell. It is without doubt due to mechanical excitation that freshly-made preparations of Chara, Vallisneria, &c., only exhibit motionless protoplasm. The movement recommences.
after the preparation has been left quiet for a time. This also holds good according to some observations, for Diatoms and Oscillatoria.

5. Chemical Stimuli.

Sudden chemical reactions produce the same effects as are observed after electrical excitations, but complicated and interrupting accessory phenomena are often present (shrinking, swelling, coagulation, &c.). So only in very few cases is it possible to observe the special effects of the excitation as evinced by the form and temporary structure.

Sudden changes in the amount of the contained water may act as stimuli.

Dutrochet placed Chara in salt solution of more than 1 per cent. After four minutes the movements stopped, and after eight minutes more recommenced again. Gradually this became very rapid, and continued for ten days. A similar preparation in which the movement had been stopped, and after ten hours' immersion had become quite active again, was plunged into pure water at the same temperature, and this caused a cessation of the movement in four minutes which lasted for five minutes. Hofmeister says, after observations on Chara, Vallisneria, Hydrocharis, and Tradescantia:—"The treatment of a cell which contains streaming protoplasm with a watery solution of a substance not directly injurious to the vital activity of the plant when of a concentration sufficient to cause the sudden drawing together of the protoplasmic contents of the cell, stops all flowing movement of the protoplasm for a short time during the contraction of the protoplasmic contents, but a rapid streaming of the undivided peripheral layer soon commences again."

After the sudden dilution of a solution in which a cell with easily permeable walls (e.g. leaf-cell of Vallisneria, root

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1 Hofmeister, l. c., p. 50.
2 Dutrochet, 'Compt. rend.,' ii, pp. 781, 782, 1837.
3 Hofmeister, loc. cit., p. 52; cp. also ibid., p. 27, for corresponding observations on Didimene serpula.
hairs of Hydrocharis), is showing the normal movement, a temporary cessation only, takes place.¹

Fresh-water Amœbæ which I accustomed to salt water of 2·5 per cent. drew themselves rapidly together on the addition of ½ per cent. salt solution, but recommenced, however, to move in the original manner after a few minutes. Cærny ² has made similar observations.

Similar observations have also been made concerning the influence of acids and alkalies.

In Dutrochet's ³ experiments on Chara an immersion for five minutes in potash or soda of 0.05 per cent., or tartaric acid of 0·1 per cent., caused an acceleration of the movement.

Kühne ⁴ found that after very short and weak applications of ammonia vapour to Actinosphærium the processes became very small, short, and strongly varicose, but after a long pause resumed their original condition.

VI. Theoretical Conclusions.

No theory of protoplasmic movements, leading back to their elementary physical and chemical processes, can be deduced from the hitherto collected facts. As it is, in fact, possible only to directly perceive the mechanical portion of the process, any theoretical conclusion must be limited to what relates to the mechanism of the movements, and an investigation into the nature and connection which the visible phenomena have with the invisible molecular action which underlies them must be left to futurity.

Every attempt at an explanation of the mechanism of protoplasmic movements must not only take into account all the known modifications of such movements, as Hofmeister ⁶ has

¹ Hofmeister, loc. cit., p. 53.
³ Dutrochet, 'Compt. rend.,' ii, p. 78, 1837.
⁴ Kühne, l. c., pp. 64 and 65; pp. 48 and 49 (Amœba); p. 82 (Myxomycetes); also Schultze, l. c., p. 82 (Actinosphærium); and p. 37 (Miliola).
⁵ Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 59.
already rightly insisted, but must be applicable in its principle to all other phenomena of contractility. The essential agreement which exists between them all in the mode of appearance and conditions of occurrence, and especially the gradual transition between them, show that we have here in all cases to do with expressions of the same principle, with the same elementary mechanism of movement. As a starting-point for the closer analysis of protoplasmic movement, we may take the acknowledged fact that each smallest microscopically distinguishable particle of every contractile protoplasmic mass is capable of independent movements. Ample proof of this is furnished by the changes of form and position which may take place, spontaneously or in consequence of artificial excitation, at every point in any otherwise quiescent protoplasmic mass, as also in the smallest artificially isolated protoplasmic particles.

It follows as a very close and, I believe, most natural consequence, that we may regard protoplasm as an aggregate of most minute contractile, excitable form-elements, and that the movement as a whole is the result of changes of form of these very small elements. The nature and cause of the changes of form of the latter remain provisionally undetermined.

We have, as yet, no reason for considering that the most minute particles of protoplasm which are to be distinguished with the microscope are the contractile elements themselves; we must think of the latter as still smaller—as of molecular dimensions. With regard to their form, we may take it for granted that when in a condition of maximal excitation they are almost spherical, or as nearly spherical as possible, and when not excited are generally elongated, with a fibre-like shape. The reason for the first of these assumptions lies in the observation that even the smallest particle of protoplasm which can be experimented upon assumes a spherical shape as a result of artificial excitation, that is to say, if it be not already spherical. Supporting the second assumption we have, firstly, the fact that the smallest protoplasmic particles which have contracted to spherical shape in consequence of excitation,
when that excitation is removed generally take on an elongated, even exceptionally slender, form, fibres, pseudopodia, &c.; secondly; resting hyaline protoplasm, as already described, not unfrequently split up completely into exceptionally fine fibrillæ; thirdly, the smallest distinguishable form-elements of other contractile structures (ciliated organs, myophanes, muscle-fibres) have in a resting stage an elongated form.

The mechanical behaviour of naked protoplasm especially teaches us that the changes of form, particularly the shortening of its contractile elements, must take place with a force which, as a rule, exceeds at any rate the force which the elements, if they were fluid, would put forth in order to assume a spherical form.

For shortness the hypothetical contractile elements will be called in the sequel “Inotagmata.” In connection with this it must be pointed out that in them the power is generated which causes the contraction, and which has been described as molecular combination (Tagmata, Pfeffer\(^1\)). Very probably all inotagmata are positive uniaxial doubly-refracting, hence contractility in general appears to be bound up with the existence of positively uniaxial particles.\(^2\)

The active as well as the passive phenomena of protoplasmic movements compel us further to the assumption that the inotagmata of the protoplasm are not, like those of muscles and ciliary processes, arranged together in a relatively firm manner, with the axes all in one definite direction, but are, as a rule, fastened together very loosely, and are capable of moving one against the other in all directions, as a natural consequence of which the possibility of the temporary or permanent grouping of a lesser or greater number of inotagmata into definitely-shaped larger masses (fibres, membranes, &c.) is not excluded.

As a reason for the possibility of alteration of arrangement of the protoplasmic particles, and in connection with the prevailing views concerning the molecular structure of organised masses, we must assume the existence of a capability for the

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\(^1\) W. Pfeffer, ‘Osmotische Untersuchungen,’ p. 32, Leipzig, 1877.

\(^2\) ‘Contractilität und Doppelbrechung,’ ‘Arch. f. d. ges. Physiol.,’ xi, 1875.
imbibition of important quantities of water between inotagmata and inotagma groups. The motility, as already shown, increases or diminishes with the quantity of this water.

The preceding observations afford a first step only towards explaining protoplasmic movement, in so far as they allow the many different forms under which it appears and the changes which it undergoes as a result of all kinds of influences, to be referred to a single process, which itself requires further explanation—the changes of form of inotagmata.

Let us detail at least some of the most important cases in this connection.

1. Formation of Spheres by Naked Protoplasm on Excitation.

This clearly must follow from the simultaneous assumption of a spherical form by inotagmata, in so far as therewith the surface attraction which they exert over one another, and thus the cohesion of the entire mass, must be equally observable everywhere and in all directions.

A good proof of the correctness of the latter conclusion exists in the sudden assumption of a spherical form by the air-bubbles in the protoplasm of Arcella upon electrical excitation. As in so doing the volume of the air-bubbles undergoes hardly any diminution, it is evident that the assumption of the spherical form cannot be a consequence merely of a contraction of the peripheral layer of the protoplasm, as is often thought. The force with which this approximation to the spherical form is brought about depends essentially upon the force with which the inotagmata change their form, and upon the average amount of the cohesion of the protoplasm; and as the latter decreases as the amount of imbibition water increases, the force must, as a general rule, decrease as the amount of the water increases. As a matter of fact, in very thin fluid protoplasm, e.g. many plasmodia, the force of gravity is sufficient to prevent the drawing together to form a sphere.

The formation of varicosities, the retraction or fusion with one another of fibre-like or flattened processes (pseudopodia
and such like), is easily explained from the above-stated principles.¹


If in a protoplasmic mass which through excitation has become spherical, or, to speak more generally, has become so reduced as to expose the least possible external surface, all the inotagmata become simultaneously relaxed, after the removal of the excitation, a visible change in the form of the whole mass will not necessarily take place. As a general rule such change will only take place when large groups of inotagmata parallel to one another become partially relaxed only, or still more if they do not relax simultaneously or do so with unequal force. The spherical condition of a naked protoplasmic body can thus correspond as well with complete repose (relaxation) as with maximal excitation (contraction of inotagmata). In addition to the lengthening (relaxation) of definitely arranged inotagmata-groups which may very easily lead to the formation of fine pseudopodia, processes may be produced in various other ways. One of the most common is the case described by O. F. Müller in Amoebae and Amœboid masses, viz. the very

¹ A word must here be devoted to Kühne's experiments upon so-called artificial muscles ('Unters. ü. d. Protoplasma, &c.,' p. 81), as it claims an importance from a zoophysiological point of view which it would most highly deserve, if the explanation given to it by its discoverer were correct. Before we can concur with this, however, we must have proof, which we have not yet had, 1, that the protoplasmic powder mixed with water and placed in a beetle's intestine develops again to a living excitable protoplasm—a revivification which, according to the best authors, more often fails than not; and 2, that if this first condition be assumed to be fulfilled, all the little lumps of protoplasm fuse into a single organically united mass, for without this the "artificial muscle" is nothing more than an aggregate of independent Amœbæ lying against one another, which would not perceptibly change its form on the simultaneous contraction of all these elements. But the experiments showed that the fulfilment of this condition also was an exceedingly improbable event. As, in addition to this, the contents of the "muscle" when emptied out consisted partly of single rounded masses, partly of pale vesicles and free granules, out of which no further movements were to be produced, it appears to be fully proved that neither the first nor the second of these conditions was fulfilled.
frequent formation of at first distinctly hyaline spherical prominences into which the granular mass of the interior subsequently streams. Here a general contraction of all the inotagmata of the protruding portion of the hyaline exoplasm may be taken as the cause. As the subsequent unhindered streaming of the granules shows, the cohesion within the hyaline process is very slight and does not sensibly differ from that of a fluid. According to the account first given by Ecker for Amœba, which is the one most widely spread among zoophysiologists, the processes are pushed forward by the contraction of the protoplasm lying behind them, especially in the superficial layer. Dujardin supposed and De Bary proved, that the cause of the advance of the mass must necessarily be produced in this case at the periphery of the stream. De Bary found the cause in a there (at the periphery) existing "relaxation or expansion by means of which the granular stream is pulled onwards, either sucked up, just as water is sucked up by a porous body, or simply streaming thither, it being the place of least resistance." Hofmeister also opposed the prevailing view most vigorously, especially upon this ground, that the granular streaming spreads backwards from the periphery where the movement, the extrusion of the process, takes place, i.e. the granules nearest the periphery are the first to move towards it, those farther away commence moving subsequently. It has been correctly remarked that no contraction of those portions of the periphery lying on the other side, the side away from which the body is moving, can be observed, contraction which must necessarily express itself in a smooth stretched superficies which is thus diminished in extent. On the contrary, as may be seen in every amœboid mass which is quickly advancing, the superficial portion of the hinder region of the body, while its volume is constantly diminishing, is not smooth, but wrinkled, folded, if not actually drawn out into fibres.

There is, however, at least according to De Bary, a forma-

1 Ecker, 'Ztschr. f. w. Zool.,' i, p. 235, 1849.
tion of processes in a manner corresponding to the older conceptions, in Myxomycetes. But here, according to De Bary, the protoplasm becomes contracted behind the streaming region quite irregularly, the rapidity of the streaming diminishes towards the periphery. In a similar manner local, and especially progressive, contractions of inotagma groups, local differences of pressure, may be produced in the interior of the protoplasm, and following thereupon occur streamings and changes of relative position of those masses which are easily moved.

The theory put forward by Brücke for Urtica, that the progressive movement of the protoplasmic contents (granules, nuclei, vacuoles, &c.) always, or at all events generally, takes place in a way analogous to that in which a fluid is moved forward by the contractions of the enclosing pipe walls, is untenable after what we have said.

Note.—It is moreover clear that the formation of processes and streamings may be brought about without physiological contractions, by mere shrinking of the superficial layer (as in partial drying, which for instance occurs not unfrequently in very large plasmodia, or by the coagulation of the albumen, e.g. after ultramaximal electrical excitations). Of course all kinds of combinations of the different means of formation of processes and streamings which have been described may occur especially in experiments with artificial excitations.

3. Rotation of the Protoplasrn within firm Cell-Walls.

This must take place when the inotagmata of the moving layers are distributed with their long axes parallel to the direction of the movement and a forward movement of the spontaneous stimulus takes place in this direction. The moving

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protoplasm creeps in this manner over the motionless cortical layer just as a snail's foot over the surface upon which it is crawling.

4. **Stoppage of Spontaneous Movements by Artificial Stimulation.**

As described above, the first result of artificial stimulation is, as a rule, a standstill or slowing of the already existing spontaneous movements in the spots directly excited. Superficially considered it might appear as if in all these cases no excitation but rather a paralysis had taken place; a view which has been specially urged by vegetable physiologists. The opposite must, however, according to our theory, take place, and it can easily be shown that according to it the result observed and no other would take place. Inasmuch as all not previously contracted inotagmata fall into contraction as a result of the excitation, the impulses to movement at all points of the protoplasmic mass become essentially equal, the entire mass thus immediately assuming a position of equilibrium. It is just the same as if all the muscles of an animal were simultaneously stimulated to the maximum; the external appearance in this case being a standstill, a stoppage of the normal movements.

Hitherto, in referring the movements of protoplasmic masses to active changes of form of the smallest component particles, we have merely postponed the solution of the real difficulty, which consists rather in an explanation of the mechanism of these changes of form. Here we must limit ourselves for the present to a few notes, which must be regarded as hints for further investigations rather than as any solution of the problem.¹

For reasons already assigned the mechanism concerned can be no other than that mechanism which lies at the basis of active changes of form of muscles and ciliary organs. With regard

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to muscles, we can now no longer doubt that changes of form of their contractile particles go hand in hand with changes in the amount of their water-contents, i.e. with the extent to which they are swollen by imbibition. As can be proved, the contractile, doubly-refracting bands of transversely striated muscular fibres swell up during vital shortening by the imbibition of fluid from the isotropic, non-contractile bands lying between them, and on relaxation this fluid is given up again to the latter. Vice versa, the characteristic shortening can be produced by artificially caused swelling of the doubly-refracting discs of muscles, even when they are no longer excitable. The same is the case with cilia. It is now a generally accepted rule that anisodiametric, doubly-refracting organised animal and vegetable structures, whether living or dead, tend to shorten on the imbibition of water (swelling—Quellung)—often with very great force and always in the direction of the optical axis. We may assume that the proximate cause of the change of form of instagmata of the protoplasm (as of those of other contractile substances) is a change of their water-contents, and thus look upon the cause of contraction as a peculiar process of swelling (Quellungs­vorgang).

Hofmeister has already, starting from the changeability of the imbibition condition of the protoplasm, looked for the cause of its movement in periodical changes of the water-contents of the smallest protoplasmic particles, and carried this theory out thoroughly in an original manner. He assumed, however, only volume- and not form-changes of the smallest particles, which does not suffice to explain the great amount of the shortening or lengthening observable in many cases. He was not then acquainted with the process of “swelling” which takes place in the contraction of muscles.

In so far as the process of contraction has been hitherto referred to a process observable in undoubtedly lifeless bodies (e.g. connective-tissue fibres dried or hardened in absolute alcohol) the further analysis of the mechanism must be left to

1 W. Hofmeister, 'Die Lehre von der Pflanzenzelle,' p. 63, et seq., 1869.
the physicist. From a physiological point of view the further question would arise, how the changes in the water-contents of inotagmata which are accompanied by the physiological phenomenon of contraction are occasioned. This is probably the point at which the chemist must take up the question. It is, however, in the present state of our knowledge, idle to express any further opinions upon the subject.