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TSWETT'S LETTER TO CLAPARÈDE ON TROPISMS AND TAXES

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SUMMARY

Part of a letter of March 30th, 1909, in which M. S. Tswett tried to give his opinion requested by his closest friend, Edouard Claparède, on the role of tropisms and taxes in metazoa, is presented and discussed. An attempt is made to provide the background to the problems discussed in the letter.

INTRODUCTION

Since it became known[1] that Tswett's letters to his most intimate friend, E. Claparède, are kept in the Public and University Library of the City of Geneva, it occurred to me[2] that in the letters addressed to a psychologist, Tswett might have revealed his motivation and his approach to science. From this point of view the letters, although interesting in many other ways, were a disappointment. Tswett's letters to the botanist John Briquet[3,4] say more about his scientific ambitions and plans than those to Claparède. Among the letters to the latter there is only the one of March 30th, 1909, which deals predominantly with scientific problems — not concerning Tswett's profession, but animal psychology, which interested his addressee. As the subject was rather complex, it was not included in the recent paper devoted to the remaining letters[5], and is dealt with here.

At the University of Geneva, Tswett attended lectures by Th. Flournoy on psychology and, in a letter from St. Petersburg to Briquet dated August 27th, 1898, he mentions an *Introduction à la Médecine de l'Esprit* by de Fleury (ref. 3, p. 21).

The letter by Claparède which Tswett answers (as all of Claparède's letters to Tswett) is not available. One would expect, however, that Claparède's views were expressed in an article entitled "Les tropismes devant la psychologie"[6]. This may be one of the "long printed letters" mentioned here by Tswett. Unfortunately, the journal of this name is not catalogued in the Prague University library and it has been impossible to obtain it elsewhere. The same applies to further relevant papers by Claparède[9].

It has therefore been necesssary to draw on secondary or tertiary sources, the most important of which were the autobiography of Claparède[7,8] (followed by an article by Piaget[11] on Claparède's psychology), a book by Georges Bohn[12] and a textbook by Piéron[13].

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Before reproducing the letter, we should outline the background, *i.e.*, the opinions and arguments dealing with the role of tropisms and taxes in animal psychology. In 1886–1888 Jacques Loeb[14–19] studied in Würzburg and was influenced by the ideas of the phytophysiologist Julius Sachs[30], who tried to extend the notion of tropisms (heliotropism in the first place) from plants, for which the term had been coined by Darwin, to animals (bacterial chemotaxis was discovered subsequently[31]).

Tropism is now mostly understood as an orientated growth reaction of plants and fixed or sedentary animals to a spatially (directionally) defined physical stimulus or to a gradient of concentration. Changes in position or movements relative to the direction of the stimulus are usually called taxes (in French tactismes), but the terminology had not been standardized in 1909 and the word tropism was mostly used to include both tropisms and taxes, especially in animals.

Loeb's ideas on tropisms enjoyed great interest and popularity, and he was acclaimed as the Galileo of his science[32–34]. However, his attempts to reduce life phenomena to the simplest physico-chemical processes were also heavily attacked, mainly from two quarters: (a) vitalists objected to Loeb's mechanistic approach and (b) some authors, leaving aside the philosophical issues, reported observations that were at variance with Loeb's theories and sometimes even with his observations.

Let us concentrate on two authors mentioned in Tswett's letters, namely Claparède himself and Georges Bohn. Both claimed the notion of tropisms in metazoa to be limited. Claparède excluded active phenomena governed by his favourite "Law of Momentary Interest"[35] from the class of tropisms. By "interest" he does not mean a "psychological interest" (curiosity), but a "biological interest". This, in common with the "interest" of Jennings[34], has been criticized as finalism, teleology, in spite of Jennings' and Claparède's protests. Speaking about Claparède's functionalism in general, Piaget stressed that causal explanations were arrived at when functional introduction to the problem was followed by structural study.

G. Bohn defined two criteria to be fulfilled if a phenomenon had to be called tropism[36].

A PASSAGE FROM TSWETT'S M.Sc. DISSERTATION OF 1901

As a basis for Tswett's views on the physical and chemical explication of life phenomena in general, let us first quote a passage from his dissertation for the degree of Master of Sciences at the University of Kazan, "Physico-chemical structure of the chlorophyll grain" (1901) (ref. 4, pp. 43–44). In addition, in one of the eight "Propositions" (Theses), Tswett had to express his opinion on the vitalist and mechanistic doctrine in biology (ref. 5, p. 78). These propositions were not available to us.

Every objective life process eventually consists of a series of elementary material and energetic phenomena which follow each other subject to similar laws to those which are studied by science disciplines concerned with the unorganized Nature.

This postulate lies at the basis of all physiological investigations. To prove its general validity is the ideal goal of the life sciences and their history is nothing else but the history of asymptotic approximation towards this goal.

The distinctive mysterious process which takes place in the chloroplast under the surge of light waves appears to be a process most easily accessible to analysis, one of

the processes least connected with those categories of plant life phenomena in whose study the concepts of instinct and reflexes persistently impose themselves, together with the notion of the extraordinary complexity of the structural properties of the life mechanism.

The solution of a question of such an importance for both the theoretical and practical worker cannot be left to the uncertain happy chance of ingenious discovery; it must be sought by a painstaking, laborious, but faithful route including the investigation of all necessary conditions of the process.

Methodological conditions must be investigated in the first line. The haphazard, insufficiently thought-out methods may have been responsible for nearly all failures that slowed down the normal development of chlorophyll chemistry.

The biochemist must employ purely physical methods for the isolation of substances...

If we understand it correctly, then it would seem that Tswett expressed here his belief in the possibility of explaining life phenomena in physical and chemical terms; however, in the case of excitatory processes that lead to the study of the neural and mental phenomena, he considered the problem to be so complex that he avoided tackling it. He might have also been aware of the controversies which were prompted by the opinions of Academician Famintsyn on these questions[39]; see also below[51–53].

PARTS OF THE LETTER OF MARCH 30TH, 1909

As part of this letter has already been published recently[5], we shall limit ourselves to the remaining part and the postscript. Taking into account the fact that Loeb's ideas[14,24,32] on tropisms and their physico-chemical basis originated from Sachs'[30] research on heliotropism in plants, it is not surprising that Claparède took advantage of his close friendship with Tswett, plant physiologist and biochemist in addition to physical chemist, to ask for his opinion on Loeb's ideas.

Warsaw, 30th March 1909

Dear old chap,

For a long time I have been reproaching myself for not yet answering your brief written missives and long printed letters[40] on the tropisms. I wonder how it has happened that the "law of momentary interest" (of biological interest, of course)[35,41] has always thwarted my intentions of replying, thus inhibiting any demonstration of positive "philotropism"[42] uniting two such old friends as ourselves.

Once again, on reading your letters, I have found that our natural-philosophical tropisms[42] are orientated in very similar directions, although the parallelism[43] with which you have armoured yourself seems to me a very precarious refuge, simply because to be exact, as you say, it is not metaphysics.

If the abstract, slightly schopenhauerite[44] notion of tropism at which you have arrived were accepted, this would considerably disturb phytophysiological terminology. For under the name of tropisms and taxes we understand simply categories of well defined objective phenomena. For my part, after having reconsidered this subject, I would define[45] tropisms and taxes as follows: phenomena of orientation or locomotion

with respect to light, gravity or other polarized systems of energy, in which the movement is produced or at least triggered by the organism. Plants are endowed with a limited number of tropisms governed by simple laws[46]*. The protophytes and protozoa (as also the zoospores or spermatozoids of metaphytes) are equipped with various taxes, which are also limited in number and subject to not very complicated rules. If one ascends the scale of metazoa, one sees the number of tropic reactions increasing and their manifestations —due to interferences— becoming gradually more variable, more dependent on the physiological state, so that a physiology based on taxes and tropisms becomes in practice cumbersome and is transformed to the physiology of movements and the physiology of the nervous system controlling these movements, and it is here that objective study becomes insufficient and powerless and where psychology must necessarily intervene. All the active ("organically permitted") oriented movements are thus, ultimately, tropisms and taxes*[47]*. And as this notion of tropism does not involve any particular conception of mechanism, the term "tropism" could by no means help to introduce surreptitiously into animal biology the negation of Mind ("the psychic") or the affirmation of a simplistic physico-chemical mechanism. This applies all the less, since the prototypes of tropisms, that is plant tropisms, are —as you have correctly understood— just simple phenomena, explicable in physico-chemical terms and participating more or less in the way of the metazoal reflexes. Thus I do not see what on earth the animal physiologists had to gain by ascribing positive heliotropism to the unfortunate caterpillars of* Porthesia[48]*. Heliotropism —well, and so what? Does Loeb believe that he has simplified or resolved the problem of movement of these caterpillars by this terminology? To explain the movements of animals by tropisms is just putting the thing off with fine words, thus opening the door from one blind alley to another.*

In the definition of tropisms outlined above I have introduced the notion of at least partial *(not necessarily total) activity of the organism in order to include the case where the organism, directing itself —by a permitted, voluntary act— utilises an external source of energy in its movement. For example, the movement of a fish that contracts its swimming bladder and thus increases its weight due to gravity, or that of a bird that is going to land. Another limitation, difficult to express in strictly physiological language, should exclude for example the case of a tourist who leans over a precipice in order to see better, loses his balance and is thereby forced to make a movement to which he has by no means consented.*

I would very much like to attend the Geneva Congress and the discussion where Loeb's report will undoubtedly be the focal point[49]*. I do not yet know whether I shall be able to.*

...If our resort is not far from Geneva I could take time off during the Congress.

...

Yours

M. Tswett

Concerning comparative psychology extended to plants, are you acquainted with the work of one of my compatriots, Warwara Polowzew: Untersuchungen über Reizerscheinungen bei den Pflanzen *(Jena 1909)?*[39,50–53]

A PASSAGE FROM THE LETTER OF MAY 16TH, 1911

In Tswett's later letter[5] is a passage worth repeating in the present context:

I am now reading the short treatise by Bohn[54] on animal psychology. This "application of physical chemistry to psychology" struck me as being a bit naive. Isn't it an abuse of the name of physical chemistry?

CONCLUSIONS

The letter under discussion is interesting for the chromatographer as it shows that the originator of the method was deeply interested in one of the cardinal problems of biology on which Claparède sought his advice. In his experimental work, however, Tswett avoided even phenomena of excitability in plants which would have led to those of nervous and mental processes in amimals and man.

According to Piéron[32], the phenomenon of tropism (taxis) as a fact presents no particular problem, but its interpretation made it one of the most hotly debated issues at the end of the 19th and the beginning of the 20th century. This is illustrated by the extent of a rather concise overview of the problem[13].

Claparède, applying his "Law of Momentary Interest"[35], and Bohn[36], stressing "differential sensitivity" (temporal sensing of differences), cellular memory and his two criteria, limited Loeb's broad conception of tropisms as simple physico-chemically explicable phenomena underlying the behaviour of metazoa. Tswett goes even further in his scepticism. He does not acknowledge the usefulness of this concept at all, at least with respect to the mechanisms underlying mental and behavioural phenomena in multicellular animals. In 1909 he comes near to Piéron[13] who, in 1941, after a thorough analysis, arrived at the conclusion that Loeb's conception of tropisms (in metazoa) is at best of historical interest.

Does this mean that Tswett identified himself with the "old" animal psychology, against which the German physiologists[55], who contested the justification of animal psychology in general, had lanced and attack? In view of his materialistic beliefs reflected in the preface of his M.Sc. Dissertation, this is unlikely.

The controversy of which this letter gives evidence stems from a stage in which animal psychology, in common with other disciplines that had formed a part of philosophy, was starting its development as a (natural, biological) science. Some mechanists were trying to corroborate their views by physico-chemical interpretations of particular processes, which, with the state of biological and other knowledge in those days, were premature. No wonder that Tswett, as a plant physiologist (the concept of tropisms having originated in plant physiology) as well as a physical chemist, was critical of the generalizations put forward in this context by partisans of the "new animal psychology".

In recent years, David Edward Koshland, Jr., and Julius Adler have significantly contributed to the elucidation of the mechanism of chemotaxis in flagellar bacteria[38,56–63]. A letter by Koshland[64] may serve as a contribution to the dialogue bridging the span of about 70 years.

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APPENDIX: PART OF TSWETT'S LETTER IN FRENCH

Varsovie 30 III 09

Bien cher vieux!

Voici bien longtemps que je me reproche de n'avoir pas encore répondu à tes courtes missives écrites et à tes longues lettres imprimées sur les tropismes. Je ne sais comment, toujours la "loi de l'intérêt momentané" (de l'intérêt biologique s'entend) s'est venue mettre en travers de mes projects de répondre, inhibant toute manifestation du "philotropisme" positif unissant deux vieux amis tels que nous.

Une fois de plus, en te lisant, j'ai constaté que nos tropismes naturphilosophiques sont orientés vers des points très voisins, encore que le parallélisme dont tu t'es cuirassé me paraisse un abri très précaire, puisque tout justement, comme tu le dis, il n'est pas une métaphysique.

La notion abstraite, quelque peu schopenhauerienne du tropisme à laquelle tu arrives, étant admise bouleverserait considérablement la nomenclature physiologique botanique. Car sous le nom de tropismes et des tactismes nous entendons simplement des catégories de phénomènes objectifs bien définies. Pour ma part, après avoir remédité ce sujet, je définirais les tropismes et tactismes ainsi: phénomènes d'orientation ou de locomotion par rapport à la lumière, la pesanteur ou autres systèmes d'énergie polarisés, dans lesquels le mouvement est produit ou au moins déclenché par l'organisme. Les plantes sont douées de tropismes en nombre restreint, gouvernés par des lois simples. Les protophytes et les protozoaires (ainsi que les zoospores ou les spermatozoïdes des métaphytes) sont doués de tactismes divers, également peu nombreux et assujettis à des règles (lois) peu compliquées. En montant l'échelle des métazoaires on voit le nombre des réactions tropiques augmenter et leurs manifestations, par suite d'interférences, devenir de plus en plus variables, de plus en plus dépendantes de l'état physiologique, de sorte qu'une physiologie des tactismes et tropismes devient en pratique encombrante et se transforme en physiologie du mouvement et physiologie du système nerveux régissant les mouvements, et c'est ici que l'étude objective devenant insuffisante, inpuissante, la psychologie doit nécessairement intervenir. Tous les mouvements orientés actifs ("consentis organiquement") des organismes sont donc, en fin de compte, des tropismes ou tactismes. Et comme dans cette notion du tropisme il n'entre aucune conception particulière du mécanisme, le terme de tropisme ne saurait nullement servir à introduire clandestinement en biologie animale la négation du psychique ou l'affirmation d'un mécanisme physico-chimique simpliste. Cela d'autant moins que les tropismes prototypes, les tropismes végétaux, ne sont, comme tu l'as bien saisi, rien moins que des phénomènes simples, physico-chimiquement expliqués, et participant bien plutôt de la nature des réflexes métazoaires. Ainsi bien je ne vois pas du tout ce que les zoophysiologistes auraient à gagner en dotant d'héliotropisme positif les infortunées chenilles du *Porthesia*. Héliotropisme —soit! Et puis après Loeb croit-il avoir par cette dénomination simplifié ou résolu le problème des mouvements des dites chenilles? Expliquer les mouvements des animaux par des tropismes c'est se payer des mots, c'est d'une impasse s'ouvrir une issue dans une autre impasse.

Dans la définition ébauchée plus haut des tropismes j'ai fait entrer la notion d'activité *au moins partielle* (pas nécessairement totale) de l'organisme afin d'embrasser les cas où l'organisme se dirigeant (par acte consenti, voulu) utilise dans le mouvement une énergie extérieure, par ex. le mouvement d'un poisson qui contractant sa véssie natatoire gagne le poids par l'effet de la pesanteur, ou bien celui de l'oiseau qui vient se reposer à terre. Une autre restriction, difficile à apporter en langage strictement physiologique devrait exclure par ex. le cas d'un touriste qui se penchant sur l'abîme pour mieux voir, perdrait l'équilibre et serait précipité dans un mouvement nullement consenti.

J'aimerais beaucoup assister au Congrès de Genève et à la discussion dont le rapport de Loeb sera sans doute le centre. Je ne sais encore si je le pourrais.

...Dans le cas où notre lieu de cure ne serait pas très éloigné de Genève, je pourrais faire une absence à l'époque du Congrès.

...

Ton M. Tswett

A propos de psychologie comparée, étendue sur végétaux, as-tu connaissance du travail d'une de mes compatriotes: Warwara Polowzew: *Untersuchungen über Reizerscheinungen bei den Pflanzen* (Jena 1909)?

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10 Charles Bonnet, b. 1720 in Geneva, d. 1793 in Genthod or Geneva, one of the fathers of modern biology. He discovered parthenogenesis in aphids, studied regeneration in various species and respiration in insects and plants. His "palingenesis" was a modified theory of preformation. *Essai de Psychologie*, Leiden, 1754, and *Essai Analytique sur les Facultés de l'Ame*, Copenhagen, 1760, deal with animal psychology. Cf., P. E. Pilet, "Bonnet, Charles", in C. C. Gillespie (Editor), *Dictionary of Scientific Biography*, Vol. 2, C. Scribner & Sons, New York, 1970, pp. 286–287.
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14 Jacques[15] Loeb[16–19], b. 1859 in Mayen, near Koblenz, d. 1924 in Hamilton, Bermuda. He studied in Berlin, Munich and Strasbourg, where he graduated in 1884. He was impressed by Goltz' studies of the physiology of the brain. In 1886–88, as an "Assistent" at the Institute of Animal Physiology in Würzburg, he started to study tropisms[20] and physiological morphology[21]. In 1889–91 he worked in the Biological Station at Naples. In 1891 he came to the U.S.A. He worked at Bryn Mawr College, the University of Chicago and Berkeley. In 1909 he was given honorary doctorates in Cambridge (England) (D.Sc.), Geneva (M.D.) and Leipzig (Ph.D.). From 1910 he was Head of the Division of General Physiology at the Rockefeller Institute of Medical Research in New York, where he started the *Journal of General Physiology*. He tried to demonstrate that life phenomena can be reduced to physico-chemical laws. Tropisms (including taxes) remained his favourite subject throughout his life[20,23–25]. He studied regeneration (chemical theory)[26] and became famous by inducing, in 1899, parthenogenesis by an artificial stimulus ($MgCl_2$)[27]. He described heterogenous cross-breeding elicited by an increase in alkalinity. By studying the antagonistic influence of salts on the cell (*e.g.*, developing egg) he laid the foundations for the ion theory of excitation. He is credited for having placed the issue of proteins (zwitterions, isoelectric point, etc.) on a stoichiometric footing[28] and systematized the interactions of inorganic ions with proteins. Moses Kunitz was his research assistant in 1913–24[29].
15 In different sources the spelling of the first name varies between Jaques and Jacques.
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29 S. S. Cohen, "Finally, the beginnings of molecular biology", *Trends Biochem. Sci.*, 11 (1986) 92–94.
30 Julius Sachs, b. 1832 in Breslau (Wroclaw), d. 1897 in Würzburg; Prof. in Poppelsdorf, Freiburg, from 1868 in Würzburg, plant physiologist (*cf.*, *Der Grosse Brockhaus*, Bd. 16, F. A. Brockhaus, Leipzig, 1933, p. 282). Studied, among other problems, the influence of temperature and light on the growth of plants.
31 T. W. Engelmann, *Pflügers Arch. Ges. Physiol.*, 57 (1902) 375–390; W. Pfeffer, *Untersuch. Bot. Inst. Tübingen*, 2 (1888) 582–589[57–59].
32 Unfortunately, Loeb's classical publications[24] on this topic were not available to me. However, the field was reviewed in retrospect in a chapter[13] from which the following is quoted (p. 137): "The existence of static or dynamic orientation reaction controlled by localized stimulation does not, by itself, pose special problems. But Loeb's formulation of certain theory of tropisms which puts forward a very simple mechanical interpretation of the orientation reactions, has aroused a very lively interest, a lot of research and often passionate controversies." The theory is exemplified by the case of phototropism (heliotropism): "Light energy which reaches unequally the two sides of the symmetrical body of the organism and which is transformed on each side to the tonus of tissues and muscles, causes a tonic dissymmetry which is manifested by a change in position that orientates the organism against the light source (or the other way, respectively). If the position adopted exposes both sides equally to the influx of the light energy, the tonic equalization maintains this orientation.., If the animal approaches the light (or retires from it), this is the result of the initial tonic dissymmetry which has brought about a directed position which is then preserved during the movement... Loeb insisted on the perfect similarity of the animal and plant tropisms, trying to prove the same laws in the effect of light... In aspiring to explain mechanically all the acts of animals or possibly even Man, Loeb has presented the tropisms as the components of instinctive and voluntary actions." In animals which have a nervous system, Loeb admitted neural links between the receptor and effector. Eventually, he identified tropisms with reflexes and other "forced movements"[24,25].
33 "At the beginning of the century, he (J. Loeb) thought that he had found here the elementary unit of behaviour, which for the ethologists would be equivalent to the living cell of the biologists. Presently, the theory of tropisms is invoked only for some orientation reactions of animals and plants." C. Viaud, *Le Phototropisme Animal*, Faculté des Lettres de Strasbourg, 1938; *Les Tropismes*, PUF, Paris, 1951, quoted by R.-J. Darchen, "Les tropismes", in R. Chauvin (Director), A. Quillot and R. Ropartz (Editors), *La Biologie. Les Etres Vivants. Les Dictionnaires Marabout Université*, Vol. 8, Gérard et Cie, (Paris ?), 1973, pp. 82–90.
34 Piéron[13] quotes Herbert Spencer Jennings (1868–1947, botanist, microbiologist, geneticist, ethologist) as one of the earliest and most important opponents of Loeb. Jennings experimented especially on the simplest animals, including protozoa. He gave many examples of external and internal sources of variation (different "physiological states") and of behaviour modifications incompatible with the con-

ception of "irreversibility" of tropisms; these modifications often amounted to a true regulation. According to him, the "law of interest" decides the selection of favourable acts in different reactions available to lower animals. As "trials and errors" he designated primary reactions which are subject to progressive selection during the true learning process.

35 Claparède's Law of Momentary Interest was defined by him as follows: "At any given moment, that instinct which is of greatest importance takes precedence over the others", or "At any given moment, an organism acts according to its strongest interest" (ref. 7, p. 76; ref. 8, p. 17). "Biological interest is what is useful for the individual from the point of view of its maintenance and development of its personality", E. Claparède, *Psychology of the Child and Experimental Pedagogy* (Czech translation from the 8th edition of 1920), Vol. 2, Ústř. spolek jednot učitelů nas Moravě and Dědictví Komenského, Brno and Prague, 1928, p. 123. The "interest" is not identical with the need, but corresponds to its anticipation. The law is part of the generalizations which Claparède advocates in describing mental phenomena and derives from his basic biological, functional point of view expounded in Piaget's analysis of Claparède's psychology; ref. 11, pp. 52–66.

36 For Georges Bohn (1868–1948) (ref. 12, p. 17) tropisms are produced by the different rates of chemical reactions on the right and the left sides of the plane of symmetry. This led him to postulate two objective criteria (explained here in the case of phototropism). (a) If light of equal intensity from two sources reaches an animal attracted by light and the animal "chooses" one of these lights and moves towards it, this is no tropism. If the animal orientates itself so as to be equally illuminated on both sides, this is tropism. (b) If one receptor (*e.g.*, one eye) is eliminated while the contralateral one is active, manege movements ensue. Both of these criteria were criticized by other authors who observed fluctuations between true tropisms, as defined in this way, and other patterns of behaviour in the same animals[13]. Bohn emphasized another class of phenomena which, in agreement with Loeb[20,24], he called "differential sensitivity" (Unterschiedsempfindlichkeit). This term is not happily chosen. It denotes reactions to the temporal change in the intensity of the stimulus[37]. As the third class of simple phenomena, Loeb mentioned cellular memory. Going up the evolutionary scale, Bohn sees fewer and fewer true tropisms and other simple phenomena to occur (already in arthropods they may be superimposed by associative memory), whereas Loeb tries to extend the notion of tropisms to very complex reactions, including vertebrates and man.

37 Interestingly, the simplest of taxes, bacterial chemotaxis, has been shown to be based on temporal sensing of the difference in concentration[38], thus in Loeb's and Bohn's terminology it would be "differential sensitivity".

38 R. M. Macnab and D. E. Koshland, Jr., *Proc. Natl. Acad. Sci. USA*, 69 (1972) 2509–2512.

39 Incidentally, Vladislav Adolfovich Rotert, of Polish descent, who is reported to have been engaged in the study of heliotropism in Famintsyn's Cabinet of Anatomy and Physiology of Plants of the Academy of Sciences in St. Petersburg, was a Privat-Docent of botany at the Kazan' University in 1889–97 (ref. 4, pp. 51 and 80).

40 It is probable that journal articles rather than typed letters are meant. One likely candidate is ref. 6.

41 By "biological interest" Tswett may be jokingly referring to "psychological" interest in biology.

42 By calling "philotropism" mutual sympathies of the two friends and "naturphilosophical tropisms" their interest in the philosophy of Nature, Tswett probably makes fun of the extension of the term tropism to higher mental functions.

43 Here again, the term "parallelism" oscillates between two meanings: the parallel ways of thinking of the two friends, and the psycho-physical parallelism which Claparède describes (ref. 7, pp. 73–74; ref. 8, p. 14), in the context of the heated discussions between the opponents and defenders of animal psychology in 1890–1910 and repetition of these discussions a quarter of a century later (behaviorism): "For my part, in these discussions I adopted Flournoy's point of view of parallelism, not as a metaphysical principle —he declared that parallelistic dualism had never been asserted in philisophy [see T. Flournoy, "Sur le panpsychisme", *Arch. Psychol.*, 4 (1905) 137–138]— but as a methodological principle [see T. Flournoy, *Metaphysique et Psychologie*, Geneva, 1890, new edition 1919, and E. Claparède, "Th. Flournoy", *Arch. Psychol.*, 8 (1921) 2]. While it is a scientific expression of the close union which exists between processes of conscience and cerebral processes, this principle also has the great advantage of removing all sterile discussion as to the nature of this union. It enables psychology and physiology to remain in close harmony with one another".

44 It is likely that by "schopenhauerite" Tswett hints at the spontaneity, the activity which, according to Claparède's "Law of Momentary Interest", should disqualify a phenomenon, as "tropism".

45 Both Tswett and Claparède emphasized definitions as a way to prevent misunderstanding. Tswett

chose the following quotation of the mathematician Henri Poincaré as the motto of the introductory part of his *Chromophylls of the Plant and Animal World, Doctor's Dissertation* (in Russian), University of Warsaw, 1910: "La rigueur ne pourrait pas s'introduire dans les raisonnements si on ne la faisait entrer d'abord dans les définitions". Claparède says (ref. 7, p. 92; ref. 8, p. 34): "This same desire for clearness of thought led me to study terminology, and I would have liked our Congresses to be a means of attaining unity in this respect, as is the case with those of chemists and botanists (*e.g.*, "Rapport sur la terminologie psychologique", *C.R. Congr. Int. Psychol.*, Geneva, 1909). This is the reason which made Binet say I had a taste for doing the police work of psychology [A. Binet, *Année Psychol.*, 17 (1911) 490]. A taste, no, but I considered it a necessity, and I must admit, it satisfies at the same time my systematizing demon and, perhaps, the sublimated remnants of my infantile desire for domination."

46 Simplicity of the prototype tropisms may be more apparent than real: now that considerable progress has been achieved in the elucidation of one of the simplest taxes, the chemotaxis of bacteria, we may consider the complicated physiology of the sensory detection, transmission and processing of the signal, memory function, motor performance, adaptation at several levels and genetic control of these functions. The mechanism of the effect of auxins in plants is no less complicated.

47 By saying that, in a sense, all tropisms are active, Tswett contradicts Claparède who excluded "actions" from tropisms. *Cf.*, Claparède's autobiography (ref. 7, p. 79; ref. 8, p. 21) where he mentions his paper[6]. "The conception of interest has also been my criterion to distinguish an *action*, a *conduct* from any other kind of movement of an organism, such as, for instance, the tropisms in the sense in which Loeb uses the word. An action, a spontaneous reaction (as opposed to tropism or the simple, mechanical reflex, such as the patellar reflex) is any reaction governed by the Law of Momentary Interest, which law adapts itself to the varying needs of the organism (the stimulation remaining the same)." As we have said in the Introduction, Claparède did not accept the degree to which Jacques Loeb extended the notion of "tropism" to cover mental phenomena, but even Claparède's compromising views did not appeal to Tswett. He saw no advantage in Claparède's differentiation: all positions or movements orientated with respect to some directional external energy could be called "tropisms" or "taxes", but none of them was passive and no useful purpose was served by attaching a label without demonstrating mechanism.

48 The larvae of *Porthesia chrysorrhoea* hibernate in a nest and then climb up the branches towards sunlight (positive heliotropism). After they have fed on leaves, this heliotropism ceases. According to Loeb, if they are left to ascend in a cul-de-sac (an inverted test-tube illuminated near its end) where there is no food, they starve to death. (This is probably why Tswett calls them "unfortunate".) "The animal is placed in a field of forces of which he is a toy, sometimes even leading to death" (Loeb[24]). Piéron (ref. 13, p. 148), on the other hand, quotes Deegener and Manquat, who observed that, if these caterpillars do not find any leaves at the end of the branches which they explore, they descend and do not hesitate to search in shaded areas.

49 J. Loeb and G. Bohn were among the "rapporteurs" whose reviews on topical themes were printed in advance for the 1909 Sixth International Congress of Psychology in Geneva, presided by Th. Flournoy, of which Claparède was General Secretary. Loeb's and Bohn's rapports enjoyed great popularity. The year 1909 brought a general recognition of Loeb's work. As already mentioned, honorary doctorates were conferred on him in Cambridge, Geneva and Leipzig.

50 Unfortunately, we were unable to find the book in the catalogue of the Prague University library. One suspects that the work of Varvara Polovtseva was connected with the research carried out by Academician A. S. Famintsyn (in whose laboratory Tswett had worked in St. Petersburg) on excitation phenomena in plants[51–53]. It would be interesting to know whether there was any connection between Varvara Polovtseva and her namesake V. V. Polovtsev, who in 1895 (ref. 4, pp. 51, 57, 61 and 62) founded the botanical section of P. F. Lesgaft's "St. Petersburg Laboratory of Biology" and directed it until 1897, when he left for Famintsyn's Cabinet and Tswett succeeded him in Lesgaft's Laboratory. Polovtsev worked on bacteria and the effect of X-rays on plants in Lesgaft's laboratory and on respiration in plants in Famintsyn's Cabinet. The spelling of V. V. Polovtsev's name is controversial. Senchenkova consistently spells it Polovtsov whereas the Bol'shaya Sovetskaya Entsiklopediya gives Polovtsev wherever the name is mentioned. (Heliotropism was studied in Famintsyn's Cabinet by V. A. Rotert[39], geotropism by F. F. Zelinskii; ref. 4, p. 51).

51 These studies were severely criticized by K. A. Timiryazev. While defending A. S. Famintsyn (1835–1918) in other respects, Senchenkova[52] admits that K. A. Timiryazev was justified in criticizing some of Famintsyn's theses on the excitability in plants; yet she does not agree with those who, mainly for his ideas on excitability, labelled Famintsyn as a partisan of phytopsychology, superficial evolutionist,

anti-darwinist, boaster, reactionary clerical, pseudoscientist singing from the parts of German obscurants.

52 E. M. Senchenkova: "The discovery of chromatography and the Academy of Sciences" (in Russian), *Priroda*, No. 5 (1975) 92–101.

53 G. V. Platonov, *The Weltanschauung of K. A. Timiryazev* (in Russian), Moscow, 1952[52].

54 This book was not available to us. It is possible, however, that the book of 1912[12,36], which I studied, is a translation of the book referred to by Tswett in 1911. Its first chapter is entitled "Anwendung der physikalischen Chemie auf die Psychologie". Some examples may illustrate the reasons for Tswett's disinclination to this book. Page 8: "According to Jacques Loeb animals are chemical machines and scientific analysis of mental phenomena has the sole task to find out the physico-chemical laws which underlie them. Loeb himself brought the proof that this claim can be met, and I should like to mention here at least the most important results which have been obtained by the application of physico-chemical methods to psychology. [*Cf.*, J. Loeb's lecture on the Congress of Geneva (1909) and *Die Bedeutung der Tropismen für die Tierpsychologie*, Leipzig 1909]...".

As one of results which are brought forward as an argument in favour of the physico-chemical interpretation of life phenomena, Bohn quotes (p. 12) the case of a weakly heliotropic animal made strongly heliotropic by treatment with a chemical substance. Loeb describes fresh-water Copepoda (crustaceans) which show no phototropism in an aquarium illuminated on one side. When water rich in carbonic acid is added, they become strongly positively heliotropic. Loeb assumes that the surplus in the overall mass of substances, which are produced photochemically on one side of the body, is normally insufficient to produce a noticeable increase in the muscle tonus on one half of the body in these animals in comparison with the other half. The acid could act as a catalyst, as in the catalysis of esters, where, according to Stieglitz, the acid increases the active mass of the material which undergoes reaction. "Tentatively, we can assume that the acid acts by increasing the active mass of the photochemical products and hence the difference in their amount." Another example of "physico-chemical" reasoning is the concept of an excess of energy in the sexually excited dog as opposed to a deficiency of energy manifested by the enonomy of Pavlovian conditioned reflexes (p. 153).

55 Th. Beer, A. Bethe and J. von Uexküll, "Vorschläge zur einer objektivierenden Nomenklatur in der Physiologie des Nervensystems", *Biol. Centralbl.*, 19 (1899) 517; ref. 12, p. 1.

56 J. Adler, *Science*, 160 (1969) 1588–1597.

57 D. E. Koshland, Jr., "The chemotactic response in bacteria", in L. Jaenicke (Editor), *Biochemistry of Sensory Functions*, 25. Mosbacher Coll. der Ges. für Biol. Chem., 25–27.4.1974, Springer, Berlin, 1974, pp. 134–160.

58 J. Adler, "Chemotaxis in Bacteria", *Annu. Rev. Biochem.*, 44 (1975) 342–356. He quotes here Alfred Binet (1857–1911), *The Psychic Life of Micro-organisms*, Open Court, Chicago, 1889, pp. iv–v: "If the existence of psychological phenomena in lower organisms is denied, it will be necessary to assume that these phenomena can be superadded in the course of evolution, in proportion as an organism grows more perfect and complex. Nothing could be more in consistent with the teachings of general physiology, which shows us that all vital phenomena are previously present in non-differentiated cells."

59 J. Adler, "The sensing of chemicals by bacteria", *Sci. Am.*, 234, No. 4 (1976) 40–47: "The basic elements that make behavior possible in a higher organism are thus present in a single bacterial cell; they are sensory receptors, a system that transmits and processes sensory information and effectors to produce movement. Whether the mechanisms of any of these elements in the bacterium are similar to those in more complex organisms remains to be established. Obviously there must be major differences; for example, since bacteria are independent cells, the cell-to-cell synaptic action that is so important in determining behavior in more complex organisms cannot possibly exist in bacteria, at least not at a cellular level. Still, it appears that the bacterial system may be a good model for the study of behavior."[63]

60 D. E. Koshland, Jr., "Special topic: Chemotaxis and motility", *Annu. Rev. Physiol.*, 44 (1982) 499–500. A. Boyd and M. Simon, "Bacterial chemotaxis", *Annu. Rev. Physiol.*, 44 (1982) 501–519.

61 J. M. Lackie and P. C. Wilkinson (Editors), *The Biology of the Chemotactic Response*, Society for Experimental Biology Seminar Series, No. 12, Cambridge University Press, 1982, pp. xiii + 177. The meeting confined itself to unicellular chemotaxis.

62 J. Stock and A. Stock, "What is the role of receptor methylation in bacterial chemotaxis", *Trends Biochem. Sci.*, 12 (1987) 371.

63 For the investigation of chemoreception in bacteria, J. Adler won the R. H. Wright Award in Olfactory Research 1987; B. P. Clayman, *Trends Biochem. Sci.*, 13 (1988) 9.

64 University of California, Berkeley
Department of Biochemistry

July 31, 1975

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I am pleased to send some reprints on our work on chemotaxis and I was very interested to learn of the historical connections with Michael Tswett.

I am not sure I would find a conflict with Tswett's conclusion, although I might invert it and say that I believe the higher neural functions must be "physical, chemical, well understood physical phenomena subject to simple laws." The important feature is the complexity of the system. In my opinion the relationship of bacteria to the human brain is that of a small, hand calculator to the giant computers. Our studies have shown that bacteria do not do something very simple, such as slow down as the concentration of sugar increases. That could be explained by very simple physical laws. At least twenty different gene products affect their behaviour and probably many more which we have not discovered yet. However, each of these products by itself follows simple physical laws. Hence the difference between bacteria and higher species is that there are just a great many more gene products involved in the human brain than in the small microorganism.

There is a danger of making shortcuts, but there is a danger of being blind to relationships. The genetic code and the metabolism of carbohydrates were both worked out in microorganisms and turn out to be essentially the same in man. It would be surprising if sensory processes did not have a similar biochemistry in all species.

Sincerely yours,
Daniel E. Koshland, Jr.