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Slowly forgetting the Pavlovian adventure?

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Abstract

This paper analyses an interesting story, that of the physiologist Ivan Petrovitch Pavlov. While investigating the causes of salivary secretions in the waking, behaving dog, he discovered a class of causes that he called psychic, since they were associated with perceiving a visual, acoustic or other signal, delivered before food that normally created salivation. A temporary relationship was therefore established, between the secretory command and the cerebral site associated with an initially neutral stimulus that had become a signal. This gave rise to the "conditional reflex". Pavlov was probably not the first who had observed this kind of association, but he very skilfully exploited these data to create a coherent conceptual system. In 23 "lectures", he very precisely summarized his views and retraced the fundamental issues explaining the main features of the purely physiological cerebral command of behaviour. The Pavlovian system necessarily became, in the particular environment of the soviet regime, a kind of *credo* on physical-mental relationships based upon a generalized reflexology, not allowing any deviation, nor any dissidence, nor any concession to subjectivity. The notion of conditional reflex has indeed resisted to time, but number of subtelties of the Pavlovian thinking and many phenomena that he described now seem forgotten and to have lost much of their heuristic value. Most of the recent theories of learning have only rarely followed Pavlov's line, to concentrate on more complex learning modalities. ***To cite this article: P. Buser, C. R. Biologies 329 (2006).***

Résumé

L'aventure pavlovienne est-elle oubliée ? L'exposé qui suit retrace une curieuse aventure, celle du physiologiste Ivan Petrovich Pavlov. C'est en explorant les causes de la sécrétion glandulaire du système digestif chez le chien libre, éveillé et implanté de canules à demeure, qu'il en découvrit une classe, dite « psychique », c'est-à-dire liée à la perception d'un signal visuel, acoustique ou autre qui, par l'arrangement de l'expérience et non génétiquement, était devenu pour l'animal annonciateur de nourriture. Une liaison temporaire s'était ainsi créée entre le domaine sécrétoire et une commande cérébrale liée à ce stimulus initialement neutre, mais devenu signal d'un événement à venir. Ainsi naquit la notion de « réflexe conditionnel ». Pavlov n'était probablement pas le premier à avoir constaté la possibilité de ce type d'association, mais il a su excellemment exploiter ses observations, et bâtir tout un système conceptuel autour du conditionnement. En 23 « lectures », un des documents les plus connus résumant ses œuvres, il en retrace les traits fondamentaux, les « lois », qui, à travers ce phénomène, devaient à ses yeux expliquer l'essentiel de la commande cérébrale purement physiologique du comportement. Le système pavlovien allait ensuite inévitablement devenir, dans l'environnement très particulier du régime soviétique, un credo sur les rapports du physique et du mental basés sur une réflexologie généralisée, n'autorisant, ni écart, ni dissidence, ni concession à la subjectivité. La notion même de réflexe conditionnel a sans doute résisté au temps, mais les subtilités de la pensée pavlovienne et nombre de phénomènes qu'il a décrits semblent actuellement bien oubliés, et en tout cas désormais dépourvus de réelle valeur heuristique. Les théories plus récentes des apprentissages n'ont

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que rarement suivi la ligne tracée par Pavlov, puisqu'elles se sont concentrées sur des modalités plus complexes d'apprentissage.
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Mots-clés : Inhibition ; Analyseur cortical ; Différenciation ; Extinction ; Sécrétion psychique

1. Introduction

While Ivan Petrovitch Pavlov investigated the digestive function of dogs by externalising a salivary gland so he could collect, measure, and analyse the saliva produced in response to food under different conditions, he noticed that the dogs tended to salivate before food was actually delivered to their mouth, and set out to investigate this 'psychic secretion', as he called it. He decided that this was more interesting than the chemistry of saliva, and changed the focus of his research, carrying out a long series of experiments in which he manipulated the stimuli occurring before the presentation of food. He thereby settled down the basic laws for the establishment and extinction of what he called 'conditional reflexes' – i.e., reflex responses, like salivation, that only occurred conditional upon specific previous experiences of the animal. Perhaps unfortunately, Pavlov's terms 'conditional reflex' was mistranslated from the Russian as 'conditioned reflex', and other scientists reading his work concluded that since such reflexes were conditioned, they had to be produced by a process called conditioning.

It may be interesting to consider Ivan Petrovitch's (from now on 'I.P.') scientific trajectory before the discovery of what he termed a conditional reflex. He was born in 1849 in a small city in deep Russia; his father was a minister and his first training was at the seminar. Soon however, he became attracted by the new progressist ideas, including those of Setchenow, the founder of Russian physiology, and left religion for science. In 1870, he trained in natural sciences at St Petersburg University, graduated in 1875, and continued training in physiology. In 1879, he obtained a grant from the Academy, and became Director of the Physiological Laboratory in Pr Botkin's clinic. In 1883, he defended a Thesis on "centrifugal innervation of the heart", the main idea being about the existence of centrifugal and reflex regulations of the circulatory organs. In 1890, Pavlov was appointed organizer and then director of the Physiology Department at the Institute of experimental Medicine, where he remained for 45 years. He became Professor of Physiology and remained there until 1925.

From 1891 to 1900, Pavlov undertook studies on the digestive tract and more precisely on the control of gland secretions. These studies were performed on behaving animals bearing fistulae, in conditions that would nowadays be called 'chronic', allowing him to follow the flow of secretion in quasi-normal conditions, contrasting with the then mostly used studies on anaesthetized animals. Thereby Pavlov was a pioneer, highly aware of the need to explore regulations and controls, humoral and/or nervous on behaving animals. As a result of these early studies, he insisted on the dominant role played by the nervous centres in controlling the digestive tract. He lectured from 1895 on regulations of the main digestive glands.

It is this interest in digestive tract physiology in dogs that put Pavlov on the way of the discovery that made him so well known. Investigating the various factors that regulate the digestive glands activity, Pavlov noticed that alimentary secretion was often triggered by 'inappropriate' stimuli, that is to say, by stimuli acting in other than their proper or normal manner, as when the sight and sound of an attendant approaching the dog sets off salivation. Pavlov elaborated a series of experiments that lasted for more than three decades and that were concerned with the way in which stimuli other than the adequate ('absolute' or unconditional US stimulus) acquired the power to elicit reflex responses when they just preceded the US, thus becoming conditional stimuli (CS).

The polemical aspect came up very soon, though, about the interpretation. The debate was opened about the meaning of the conditional reflex. "*No*", claimed Pavlov, the conditional secretion is not 'psychic' in the usual meaning of the word, but is a 'reflex' due to a temporary connection established within the brain and, more precisely according to him within the cortex. A long story was thereby beginning, that would amply go beyond the digestive control and would invade all features of mental activity and cut down any option to subjectivity. This kind of fights nowadays sounds rather obsolete and naive, but was very alive at the turn of nineteenth century. The Pavlov period became fully open to the kind of new way of debate: materialistic views were at that time considered the highlight of modern

thinking. In 1903, Pavlov delivered a lecture at the 14th International Physiological Congress in Madrid ("*The Experimental Psychology and Psychopathology of Animals*"), claiming that conditional reflexes should indeed be considered as an elementary psychic phenomenon while being at the same time of physiological nature, and thereby, to be a key to understand and interpret the most complex features of animal and human behaviours and their cerebral determinism. Pavlov was transforming the theoretical Setchenow's views on reflexology into a theoretical and general view on the conditional reflexes and even more generally on the functioning of the brain.

Pavlov was highly recognized in the world. Corresponding member of the Russian Academy of Sciences in 1901, he was awarded the Nobel Price in 1904 (for his studies on the digestive mechanisms!) and became a member of the Russian Academy of Sciences in 1907. After the October Revolution, a special government decree, signed by Lenin on January 24, 1921, noted "*the outstanding scientific services of Academician I.P. Pavlov, which are of enormous significance to the working class of the whole world*". Pavlov and his collaborators were given unlimited scope for scientific research. The Soviet Union became a prominent centre for the study of physiology, and the fact that the 15th International Physiological Congress of 9–17 August 1935, was held in Leningrad and Moscow clearly shows that it was acknowledged as such. As Pavlov's work became known in the West, particularly through the writings of John B. Watson (see below), the idea of 'conditioning' as an automatic form of learning became a key concept in the developing field of comparative psychology, and the general approach to psychology that underlay it, behaviorism. However, the precise origin of Pavlov's thinking is much more Setchenow than Watson, the vigorous promoter of behaviorism. Setchenow's psychology was more physiological than Watson's. This because it contained the notions of inhibition, facilitation and integration, concepts that were later (1906) developed experimentally by Charles Sherrington, whereas Watson was more concerned with characterizing the conventional psychophysiological functions in behavioural terms. Bertrand Russell also became an enthusiastic advocate of the importance of Pavlov's work for the philosophy of mind. Pavlov died in 1936, but the Pavlovian school remained very active, and the tradition of investigating the conditional reflexes was maintained by a large number of his collaborators in USSR and elsewhere in the Eastern countries almost until the 1970s. At that time began what can be perceived as a decrease of interest for the theoretical and experimental aspects of this mode of exploration of brain mechanisms. In the west, Pavlov's ideas and theories were not forgotten, although, since even nowadays, a Pavlovian Society still exists in the USA.

2. The Pavlovian system

It is now time to consider some of the main features of the Pavlovian system. These experiments were carried out in the 1890s and 1900s, and were known to western scientists through translations of individual accounts, but first became fully available in English in a book published in 1927. This book contains 23 'lectures' which well describe the salient features of Pavlov's thinking [1,2]. Noteworthy, however, in the address he gave on receiving his 1904 Nobel prize, he already announced that he had undertaken a program of research on conditional reflexes, his term for a behaviour that is learnt, not inborn. While being in the Russian tradition of Setchenow (1829–1905), the father of Russian reflexology, his theory closely resembled the classical principle of association by contiguity, despite his explicit championing of objectivism and vigorous opposition to the mentalism of classical associationism. In this line Pavlov can be situated in another closely related tradition, that of Thorndike (1874–1949), with his well known law of effects enouncing that the responses to a situation which is followed by a rewarding state of affairs will be strengthened and become habitual responses to that situation [3].

Firstly, Pavlov distinguishes the positive alimentary conditional reflex (CR), with food being delivered after a conditional signal (CS), from the avoidance CR, where a drop of diluted acid was introduced into the animal's mouth and was followed by a variety of mouth and head movements of refusal and rejection. He concludes, after a thorough analysis, that the connection takes place in the higher brain centres, in fact the cerebral cortex.

Very importantly, a considerable importance was attributed by Pavlov and his co-workers to a variety of cases of inhibition of the conditional reflexes. In fact two classes of inhibition of a given CR were distinguished. Firstly, what he considered as 'external inhibition'. In experiments where external distracting or disturbing signals or stimuli existed or occurred, the reflex would not take place, the temporary connection between the conditional stimulus and the motor response command being temporarily interrupted. This class of observation was taken very seriously by Pavlov who managed to arrange a special laboratory space as best as possible protected against any kind of external perturbation (au-

ditory, visual or else). This became known as the 'tower of silence' in Petrograd.

The second class of inhibition was termed 'internal'. With a variety of distinct patterns corresponding to several different paradigms. In all cases, it was the conditional stimulus itself that, due to its particular modality, elicited an inhibition of a previously established conditional reflex. A first case was observed when the CS was not reinforced for several successive trials. The reflex progressively weakened (progressive reduction of salivation, increase in latency of salivary response), a phenomenon that Pavlov termed 'extinction'. The important point noticed by the Pavlov team was that extinction was not simply a disappearance of the reflex, a disconnection of the temporary link, but rather an active inhibitory process taking place somewhere in the central operator, this because the CR could suddenly reappear after a period of non responsiveness, either spontaneously, or upon a facilitation elicited through a new pairing of the stimuli (desinhibitory process). This statement was a strong one, since it introduced a really new phenomenon in the central mechanisms of the sensory-motor automatic machinery (as expressed in modern terms).

Another type of internal inhibition was that called 'conditional or differential inhibition'. It concerned the case when the positive CS was suddenly coupled with a joint stimulus (JS). "*It might have been considered as a case of external inhibition, but in fact it is not*", Pavlov writes. The timing of succession of the JS with respect to the CS as well as its intensity plays a major role. For instance, when sounding an automobile horn 10 s before the CS, the CR is reduced or even suppressed.

The third type of internal inhibition was termed by Pavlov 'delay inhibition'. This occurred when the latency between CS and absolute stimuli was increased beyond the usual values efficient for a positive conditioning. As this delay was increased, the animal ceased to respond, and this was accompanied by a state of quasi somnolence. That this phenomenon was a true inhibitory state was again revealed by the 'arousing' effect of an extra stimulus, which at the same time elicited a sudden restoration of the reflex.

A fourth and very important class of internal inhibition occurs during differentiation. Some stimuli may incidentally at first act as CSs, if they have some similarities with the stimulus that has become a CS for the animal. This process of generalization is, however, in most cases discontinued by another important feature, namely differentiation between the active CS and other, even similar stimuli that are not reinforced. This differentiation is also accompanied by an episode of internal inhibition. Differentiation was thoroughly analysed in a great variety of conditions, including stimuli that were exciting the same class of analysers (e.g., the eye) but differed either in shape or luminance. All sorts of combinations of excitatory CS and negative (not reinforced) stimuli were delivered and the important conclusion was drawn that inhibition can even act upon the excitatory reflex just following. This was especially clear when using for instance four distinct local mechanical stimuli on a dog's leg. One of the stimuli was not reinforced, while the others were. After several deliveries of the negative stimulus, the efficiency of the positive ones became reduced, the more so that the positive stimulus was closer to the negative. This was interpreted as demonstrating that the inhibitory action progressively spreads over the somatic cortex from the 'negative' cortical site to the other 'positive' sites. This complex interplay between excitations and inhibitions was thus situated by Pavlov at the cortical sites, the cortex thus becoming the final stage "where integration of excitatory and inhibitory takes place". This issue, that the cortex is the major or even sole site for conditional reflexes became a kind of absolute *credo* in the Pavlovian orthodoxy, even in the post-Pavlovian era up to the seventies. It was only much later, when western data on the functional importance of the midbrain and thalamus became popular and crossed the iron curtain, that some followers of Pavlov began to criticize the exclusion of subcortical structures as possible sites for CR control or elaboration.

A next step was taken when Pavlov showed how internal inhibitory processes could propagate and extend over a large part of the cortical mantle, involving representations of other sensory domains (e.g., with auditory negative conditioning, inhibition may invade the visual as well as the cutaneous mechanoceptive sensory areas). The opposite may also occur, i.e. a spread and intensification of the excitatory process, for instance, when a foreign visitor, unknown to the dog, suddenly attends the session.

To sum up at this stage, the overall picture that is brought to us by Pavlov is that conditioning is accompanied by excitatory and inhibitory processes extending over the hemispheres according to a variety of laws. Pavlov never really went beyond this broad view of the larger hemisphere mantle. To him, the cortex was a conceptual object with very little allusion to precise localisation (except perhaps when he discussed the spread of excitation and inhibition in the somatic 'analyzer'). However, investigating further into the precise sites responsible for this or that did not really retain I.P.'s interest at that time. It is true that lesion experiments were

run in his Institute, but they did not seem to play a decisive role in his own conceptual thinking.

Another important notion concerns what I.P. termed reciprocal induction. Conditioning induces not only excitation and inhibition but also after-effects, so that excitation may secondarily reinforce the inhibitory reflex and vice versa. This interplay with a new factor, time or better, successive action, ended up on a complex dialectic view on brain mechanisms and processes. On this occasion, Pavlov referred to Sherrington's findings on excitatory and inhibitory processes in the spinal cord. He also stressed at length how his experiments on the CRs, through illustrating the subtle interplay of simultaneous and successive interactions, provided an objective way to analyse brain processes which were at that time considered as only accessible through subjective analysis. In his further lectures, I.P. honestly also stressed some of the major difficulties that he and his teams had encountered during these CR studies. In one of his lecture, he precisely describes the variability of some of the obtained results on interactions between inhibitory and excitatory processes, partially due to individual characteristics of the animal.

The view that he develops on the structure of the cortex is also interesting. It is a complex mosaic, he writes, of small neuronal groups, that largely goes beyond the distribution of sensory or motor representations (already roughly known at that time). Our data are only one first step, he adds, the laws of spread of excitation and inhibition are at their dawn only. The fact that both processes, excitation as well as inhibition, can spread over distinct cortical sites, reinforcing or inhibiting a given CR, may influence the contours of the cortical mosaic. To sum up a long story, it is as if Pavlov had introduced a factor that appeared rather new at this period, in words the flexibility in cortical functional integration, with complex combinations of excitations and inhibitions of variable extension over the cortical command zones. This view ended on two issues: (*i*) the existence of 'conceptual' cortical units which integrate altogether the sensory-motor operation from a given CS to a given CR, a view that appears, in the modern thinking, as an astonishing simplification about cortical mechanisms; (*ii*) the continuous interaction between these units, with possibilities of mutual excitations and inhibitions, which is an original but even so, a highly simplified explanation of these mechanisms. All in all then, Pavlov's concept of cortical mechanisms was highly synthetic and imaginative. Speculative also, since it rests on a limited number of observations. No one would probably nowadays accept to publish data based on so few animals, with so many parameters in play and no real statistical analysis, to end up on reliable and credible results. Was it because Pavlov was a kind of genius, or because he was exploring a new field, where each fact, each pattern of the dog's reaction represented a new discovery? Hard to conclude!

In his fifteenth lesson, Pavlov finally approached the question of sleep. After showing that repetitive excitatory CSs end up on a state of internal inhibition, "*to protect the cells against destruction*", the next step in his thinking was to hypothesize that internal inhibition leads to sleep, the two phenomena being pretty close to each other and finally perhaps belonging to the same class. The animal passing from a state of internal inhibition during one of the negative signals progressively falls into sleep. In his view, internal inhibition during waking represents a partial, local "*falling asleep of a group of cerebral units*". Real sleep would in this view be due to irradiation of this state of internal inhibition into the whole cortex. Finally, concluding this simplified hypothesis on sleep and its mechanisms, at the same time both holistic and reductionist, Pavlov rightly expresses his regrets that no graphic representation or illustration were at hand to support his statements!

The next lecture (the 16th) deals with partial sleep, that which may occur when the animal displays, under monotonic stimulations, a bizarre state which is not complete sleep; it may remain aroused, but motionless, no more reacting to an excitatory CS. According to Pavlov, this state was a case where the greater hemispheres "*only exerted their inhibitory effect on cortical structures without reaching the lower centres of posture and static*". This is, of course, a highly simplified but very skilful view on some of least known phenomena occurring in animals and also in humans, those which roughly correspond to hypnosis. Those are difficult to characterise and are often completely overlooked.

Pavlov then considered pathology. Firstly, he described what he called 'the extreme cases', with two animals with opposite behaviours and different ways of reacting to the CR situation, especially to inhibitory CSs. He considered these states as two distinct types of neuroses. One dog was hyperexcitable and the other one was, on the contrary, very quiet and rather prone to internal inhibition. Other dogs were also considered and diagnosed as pathological subjects. Further cases were described in many details, with dogs trained both to a positive, excitatory conditioning and to a negative one. Closely associating the two stimuli in succession led some of these animals into a state of non responsiveness to the positive CS. During several weeks they would not respond at all to both stimuli, which was indicative, Pavlov thought, of a pathological invasion of the

excitatory process by the inhibitory one. One can only admire I.P's intuitive way of explaining the observed changes, only based on inductive–deductive mode of combining and arranging the various stimuli, with no invasive experimental intervention. As we shall see below, this class of observations led Pavlov to some hypotheses regarding human 'neurotic states'.

Three chapters in his book deal with lesioned animals. Pavlov is very careful and looks sometimes rather sceptical regarding interventions on the brain (this is my personal judgement). However, he nonetheless describes at large the various observations made in his groups, on animals after a variety of lesions. He speaks at length about the convulsive stage often reached by the animals, probably due to the operative procedure used in these early days of neurosurgical approach. He describes the case of a dog with complete decortication (as previously performed by Goltz). The animal had been trained to a special type of CR, that called 'water CR', consisting in salivation elicited through introducing as a CS some drops of water in the mouth. The result after decortication was the reappearance of some type of reflex, but which Pavlov did definitely not consider as a true CR. His (careful) conclusion ("*without pretending to an absolute rightness*", he writes) is that the hemispheres are the main site for CR: their synthetic function reaches a higher degree of perfection than any other brain centres.

Further studies were performed with more restricted cortical lesions. Firstly, the 'auditory analyzer' was considered, meaning a bilateral ablation of the temporal structures known at that time, thanks to Munk's data. Pavlov's description is rather complex: while other conditionings, via other 'analyzers' such as the visual or the somatic one were left intact, the auditory CRs disappeared. Not quite completely though, since some conditioning recovered, but no complex auditory recognition. This partial recovery was interpreted by Pavlov as indicative "*that in addition to the special domain of the auditory analyser, some auditory elements might spread all over the hemispheres*." Pavlov's view was essential for future studies and issues on cortical mechanisms. He really predicted thereby three phenomena that nowadays dominate thinking about the cortex. Two new ones: (*i*) cortical plasticity, allowing structures to change structurally and functionally in time, even in the adult; (*ii*) the possibility that other cortical sites, outside the primary projection area(s), could replace the missing zone; (*iii*) finally, a third, older one, namely that processing of complex perceptive patterns, that others would have called 'psychic' (in this case auditory, but the statement is more general) is not necessarily located at the same cortical site as elementary auditory 'hearing of a sound'.

Numerous other observations were performed in this line, with one or other class of lesion. The 'visual analyzer' was investigated, first after complete Goltz type hemispherectomy and also in animals with posterior 'occipital' lobectomies. In all cases, fine visual CSs became ineffective, while very elementary signals not requiring subtle analysis (such as simple changes in luminosity or some simple shapes) could act as CSs. Here again, Pavlov considered that this residual sight discrimination was due to an 'anterior visual analyzer', a conclusion that is in a way predictive of more modern findings. Other studies were performed on the 'cutaneo-mechanical analyzer', and still others on the olfactory system.

The book ends, firstly with other lesion experiments in dog; I.P. describes a variety of cortical ablations, unfortunately with no pictural data. His conclusions are in fact very cautious: "*my goal in this chapter was only to ask questions to the physiology of the hemisphere and to show how difficult or even impossible it seems by now to solve them*." Pavlov was heavily impressed by the complexity and variability in some experiments, which were far from being always controllable. He describes at length what he considers as 'errors' made by him and his collaborators in the first years of his experimental work on conditional reflexes.

Finally, he hypothetically tried to extend his observations and conclusions to human pathology, to neuroses and psychoses. Analogy is of course difficult to establish and he remained very careful when trying to compare some mental illnesses to 'neurosis' in a dog which would be facing some difficult conditioning situations, with excitations and inhibitions. Another interesting analogy or similarity between animal behaviour and human pathology is what we designate as hypnotic states. Pavlov draws some close analogy between some of the postures and behaviours of the animal in extreme states of inhibition and some of the human hypnotic states. However, he also recognizes that we are far from understanding the real nature of human hypnosis and far also from being able to interpret it in terms of the animal's behaviour under conditioning. These latter chapters are certainly not the best part of his contribution, as compared to other careful analyses of the interplay between excitation and inhibition in the cortical mantle.

To sum up, Pavlov was a very skilful scientist. The bulk of his theory was based upon carefully observing the animal placed in a particular stimulus-response situation. Reasoning in terms of 'brain hemispheres' as the site of integration of these reflexes appeared as a real

challenge, but it was taken very seriously and – in the politico-philosophical context of the USSR in its early days – was very well adapted to a dialectic approach. Pavlov quite naturally included as a major part of the reflex operation the cortical mantle, a view that later on, after his death, was considered as a major principle, a kind of absolute law, excluding any other explanation and, most importantly, forbidding speaking and writing about the possible role of sub-cortical structures. But one of his major merits is that of introducing a subtle interplay of cortical excitation and inhibition, thereby allowing an extremely efficient way of explaining brain operations without considering brain lesions as an essential tool.

3. What has happened after Pavlov? Konorski, Miller and the operant conditioning; discussions with Skinner; Pavlov continued?

Pavlov passed away in 1936, but as I mentioned before, Russian groups remained very active on the problem of CRs for quite a long period after him (say, until the 1970s). However, as early as 1928, Jerzy Konorski in Warsaw, and his collaborator Stephan Miller published a paper in which they described a new type of CR, that they called instrumental or operant [4]. This new type of learning profoundly differed from the Pavlovian paradigm, by its sequences and the issues it raised. As is well underlined by numerous authors (see, for instance, Hall [5]), while in Pavlovian conditioning, the unconditioned stimulus US occurs shortly after the presentation of the CS, in instrumental/operant conditioning, an outcome providing a reward or a punishment is forthcoming after the animal has emitted a specified pattern of behaviour, possibly in connection with the occurrence of a stimulus, in this case becoming a response to a first stimulus. Long discussions took place throughout the history of behaviour analysis, regarding the distinction between Pavlovian and 'operant' conditions. The earliest debate as to whether they differed occurred between Konorski and Skinner [6,7]. According to Skinner's views, a prior stimulus was unnecessary for the emission of an operant; yet he acknowledged that a stimulus may often elicit a response through its temporal correlation with reinforcement. These exchanges between Konorski and Miller, and Skinner thus set the occasion for the evolution of behaviour analysis formulated on three assumptions: first, no prior stimulus is required in operant conditioning but is a necessary condition in Pavlovian conditioning; second, operant and Pavlovian behaviour involve different muscle systems, somatic in the first type, autonomic in the second one; and third, in operant conditioning relations between responses and stimuli are established while in Pavlovian conditioning relations between stimuli are established. In fact, the second statement turned later on to be incorrect when it was established that cardiac rhythms can be instrumentally conditioned and, conversely, that one of the mostly used paradigm, leg retraction to an electric shock as US, with a sound as CS, has been and still is considered as typically Pavlovian.

A large number of theoretical discussions took place after 1930, some of them still persisting, meaning that the interest for Pavlovian conditioning remains a major milestone in the studies of learning in general and is far from neglected in western countries. Conditional reflexes were first brought to the attention of American scholars in a paper by Yerkes and Morgulis (1909) [8] and Lashley [9] himself was deeply influenced by Pavlov's data. One should not forget that conditioned reflexes formed the basis for Watson's behaviorism (as early as 1916, followed by his 1919 book, *Psychology from the standpoint of a Behaviorist*) [10]. W. Horsley Gantt [11], on his side, after spending a long time with Pavlov in Leningrad, went back to the US, kept working on conditioned reflexes and founded the Pavlovian Society in 1955. Theoretical analyses of learning, despite their complexity and the fact that their problems went amply beyond the pure Pavlovian tradition, still kept Pavlovian conditioning as a fundamental reference. Despite the fact that some new data had appeared that learning theorists had to take into account, namely Garcia et al.'s data [12] on conditioned taste aversion and its building up after one single association, in other words in a single conditional trial and thus being independent of ordinary learning association procedures. In a fairly recent article, Jaylan Shella Turkkan [13] developed the view that some learning procedures that are currently now considered dependant upon operant conditioning or cognitive processes, could in fact be interpreted as representing aspects of a classical conditioning, such as relapse to drug abuse by postaddicts, the placebo effect, the immune responses, etc. She surprisingly adds that "*classical conditioning has* [even] *been found to occur in brain slices and in utero!*" In recent years, some theorists were still discussing hypotheses, such as Robert Rescola for instance [14], with some attempts at theorizing (see, e.g., the 'Rescorla–Wagner' model with even a single equation that "*allows one to model Pavlovian conditioning and explains conditioning itself, extinction, blocking, the effects of contingency and other effects*") [15].

The issue regarding the role of internal inhibition, unfortunately often overlooked nowadays, should de-

serve, we think, regained interest. Very few attempts have been made yet, to relate this behavioural, global phenomenon to some underlying nervous processes. The relation of this phenomenon to nervous inhibition as defined by the neurobiological explorations remains so far rather ambiguous. The use of a common word to designate two phenomena occurring at quite different scales is highly confusing. To our knowledge, only a few studies were achieved that tried to make the link. It is therefore interesting to quote Daniel Kimble who, based on lesion studies in rats, suggested that the hippocampus plays a major role in the control of internal inhibition [16]. Some rare other contemporary studies exist, at more analytical levels. One of them is an electrocortical analysis in cats and monkeys, showing how, in an operant conditioning, a negative stimulus would be systematically accompanied by slow neocortical rhythms at 4 to 6 Hz, concomitant with a curious behaviour of absence of movement, disinterest in the surrounding, drowsiness but no sleep [17]. Other, even more reductionist studies, were concerned with identifying neurotransmission and/or neuromodulation mechanisms during internal inhibition. Some authors [18] thus suggested the intervention of GABA-ergic mechanisms (which is no surprise). Time has arrived when other neurophysiological (or else, neurobiological) investigations should try to bridge more precisely the gap between the two domains, that of the behavioural mechanisms and the ones of the neuronal circuitry. Several other modern questions on theories of learning, memory and behaviour in general as well as cognition have at least partially, their roots in Pavlovism. One may be the importance of prediction of probability of a stimulus, another one the importance of conscious versus unconscious brain operations, still another the degree of reduction that the 'associative' operations may allow, in terms of connectivity and synatic mechanisms.

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