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MATHEMATICAL MODELLING OF REACTION LATENCY: THE STRUCTURE OF THE MODELS AND ITS MOTIVATION

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Abstract. The basic structural assumptions concerning the dynamic models of the reaction latency are presented. The linear dynamic stochastic model of the reaction latency is considered as a special case of dynamic model. The biological motivation for using these models are outlined. These models express the reaction latency as a first access time of the random threshold of a certain stochastic process. This approach was used in modelling the reaction latency in escape and avoidance experiments (the results will be presented in subsequent papers).

THE ROLE OF MODELLING IN BIOLOGY

It is a frequently met question: is mathematical modelling truly required in biology? To answer this question one must think about the advantages of mathematical modelling which are not accesible with other methods.

The first advantage of modelling is the possibility of presenting otherwise known results in an exact, precise form. Therefore the modelled results should be capable of having the required degree of precision. However, the biological facts often have only a qualitative nature, which must be recognized at the very earliest stages of model building. But just this qualitative nature of biological description requires development of adequate mathematical tools to handle and analyze such phenomena.

The second, frequently noted advantage of mathematical models is that they make it possible to handle large sets of data and facts. This is useful in analyses of results of experiments. One cannot handle results of neuron stimulation or of behavior experiments without even simple models. The most popular models treat these results as a sample of a number of random variables. Because of this assumption, statistical analyzes may be applied. Initially a distribution function is computed, but this can be computed without using a probabilistic (modelling) framework (it is then referred to as cumulative frequency function). In such cases one cannot treat the cummulative frequency function as a distribution function and to interpret the results statistically. Thus, one cannot use the results of this analysis without adding a probabilistic framework. Even frequently used averaging of sequences of data of an experiment may, in fact, be used only when related to a mathematical model. In fact, averages as they are normally computed, do not have the interpretations usually given to them unless the averaged elements are considered as random variables with appropriate mathematical properties which permit the use of the limit theorems of probability theory. Often averaging is done without checking the assumptions about the model, but this situation becomes dangerous only when one is using the model without bearing this hazard in mind.

The third role of mathematical models is the most important, because mathematical models of composite phenomena make it possible to handle and analyze such phenomena. In consequence, models may lead to discovering new features of these phenomena which were not earlier noticed because of their complicated nature. Properly chosen models can handle the observed facts in a simpler way than one could do without them. In effect, mathematical models allow one to explain known facts or to present them in simpler form. Models may also lead to new experiments which verify these models and also uncover new facts.

The goal of modelling has a strong impact on the shape of the model. In the modelling of technical systems, many types of models can be distinguished on the basis of their purpose. For example, there are models for control applications; on the basis of these models the rules of control of a technical system are developed. Another type constitute models for prediction. These models are used to predict future behavior of the system under analysis. We also meet with "cognitive models". In these models it is required to have all behavior of the model very close to the behavior of the real system. Depending on the goal, we would choose different models of the same system. Models should describe only those features of the modelled system, which are essential from the point of view of the goal of modelling. All unessential features should be neglected. In effect, elements of the model do not necessarily have to be identical with the elements of the modelled event. If, for instance, a random variable is included in the model, then this random variable would not exist as a physical object in the modelled system. Elements of mathematical models are mathematical abstracts. They should be interpretable in the sense that the behavior of elements of the model should have the same behavior as elements of the modelled system.

In all cases there exist a number of differences between the model and the reality. These differences provide the basis of one important way for the classification of the models. Deterministic models interprete these differences in terms of numbers. Stochastic (probabilistic) models treat them as random variables or stochastic processes. There are other interesting types of models, for instance fuzzy models.

Frequently in modelling one can assume only the structure of the model and the parameters must be determined on the basis of experimental data. Therefore, an essential role is played by the theory of identification together with the connected branches of mathematics such as estimation theory.

The last stage of modelling should be verification of the model. The verification procedure has its mathematical framework: theory of hypothesis testing and other branches of statistics can be used. But one should also perform a second, no less important, stage of verification, that is client verification. In biology, only the biologist can accept or reject the model on the basis of biological behavior of the model. This phase of modelling which will be called *acceptation* is often skipped in practice but, in the author's opinion, it is the most important stage of verification and, therefore, of modelling. When either the verification or the acceptation have not been

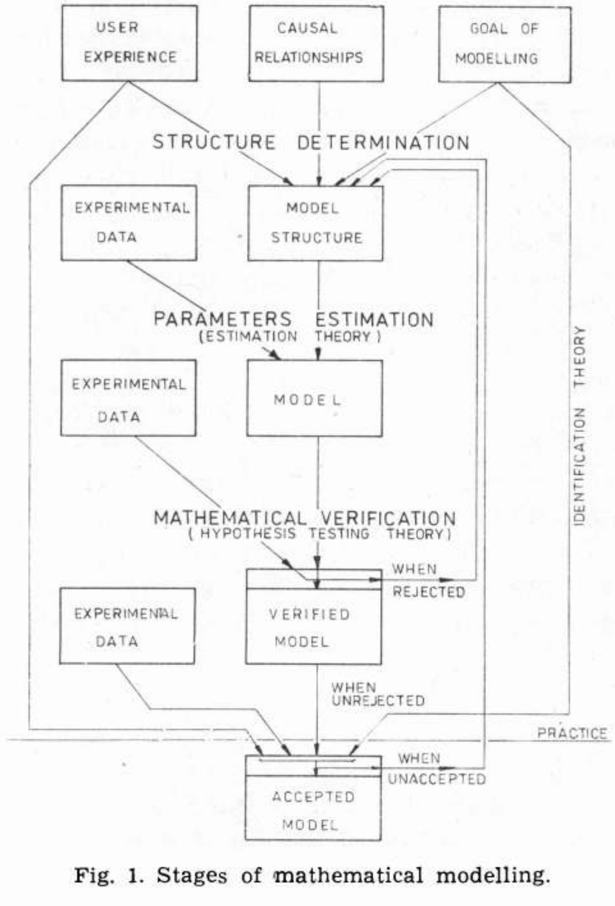

Fig. 1. Stages of mathematical modelling.

successful, one must return to the stage of structure determination (or to the stage of estimation but with the use of larger — or better — data sets). The whole procedure of model building is presented schematically in Fig. 1.

THE MODELLED PHENOMENON

The subject of modelling presented in this paper is the latency of reaction in the experiments on cats which were performed in the Nencki Institute of Experimental Biology. Each cat was placed in a cage and subjected to a sequence of stimulations. The cats were trained to press the bar placed on the wall of their cage. Two experimental procedures will be discussed. Both experiments consist of series of trials.

The first procedure called escape experiment (12) consists in applying an electric shock to the paws of the cat in each trial. In this procedure the cats were trained to perform an escape response, that is, pressing the bar, in order to terminate the painful stimulation.

The second procedure called avoidance experiment (13, 14) consits in possibility of applying two stimuli in each trial. Each trial begins with applying the conditioned stimulus (an acoustic white noise with constant applitude). If the animal performs the proper reaction during given period (that is, bar-pressing response) than the trial terminates at the moment of pressing. If it doesn't answer properly then after this given period the unconditioned stimulus is applied together with the conditioned one. The proper reaction causes termination of the trial. A lack of such reaction after sufficiently long time forces experimenter to make some extraordinary activity which is beyond the scape of the model. It is worth pointing out that it also happens that the animal performs the reaction without stimulation (so called intertrial responses).

The latency of the reaction was measured in both the experiments. The results of the experiments are — from the numerical point of view — a data series expressing latencies of reactions in consecutive trials. The models presented in the paper treat this data series as a series of random variables, that is, as a discrete-time stochastic process generated by the model. In the course of the experiment, the cats underwent a learning process, which caused changes in the model parameters. These changes were the basis of the model verification. This problem will be treated later (Pacut; Pacut and Tych, in preparation). In the following, the structure of the model will be specified and some remarks concerning the model behavior and identification problems will be made.

GENERAL STRUCTURE OF THE MODEL: DYNAMIC STOCHASTIC MODEL

The model under consideration, called the dynamic stochastic model, needed to be useful in analysis of the experimental data so it had to be relatively simple to make it possible to identify its coefficients, but at the same time complicated enough to be able to handle all the substantial features which were contained in the data. Therefore the model had to have a structure that would be consistent with the biological principles associated with the experiment.

The structure of the dynamic stochastic model can be divided into three functional parts. These are the transformation system, the decision system, and the execution system (Fig. 2). The model aims to describe the dependence of reaction latency on

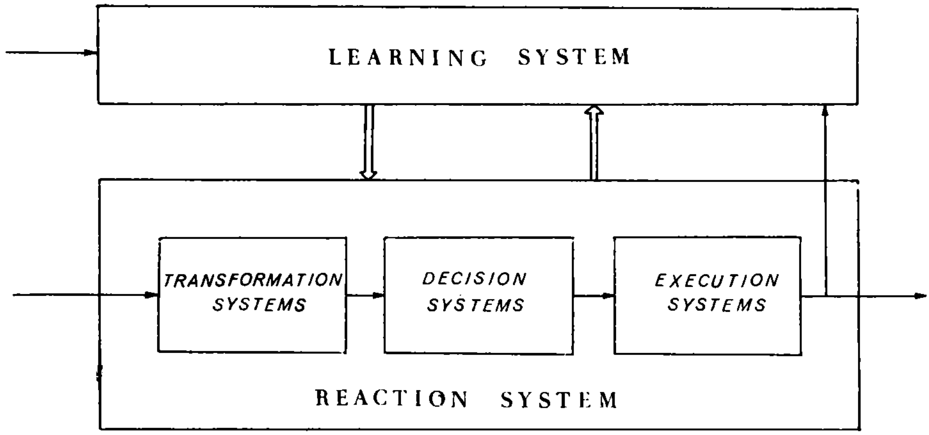

Fig. 2. General structure of the model.

the stimulus. Therefore the stimulus is the input signal to the model (it does not matter what we mean by the term "stimulus"). The activity of the transformation system is connected to the sensory systems of the animal, among other things. It generates a hypothetical time function called the excitatory potential. This function is a development of ideas of Hull (6), Spence (11) and Grice (3, 4). The transformation system represents all the transformations of the stimulus before it reaches the next link — the decision system. This decision part of the model compares the excitatory potential with a certain threshold value and may initiate execution of the reaction which, in turn, is performed by the execution system. One may imagine the composite net of transformation, decision and execution systems (Fig. 3) which connects all the sensory inputs through many decision systems with many reactions. There are pathways in this net which describe nonspecific reactions or performance of the learned reaction to nonexperimental stimuli. Nevertheless, only one small portion of this net will be considered more deeply, that is the pathway(s) which connects the experimental stimulus (or stimuli) with the reaction desired by the experimenter (called the experimental reaction). The paths that have to be used in the "active" part of the model depend on the type of experiment.

In the escape experiment (12) the animals were trained to respond to the unconditioned stimulus of electric shock by pressing the bar. The input used by the model

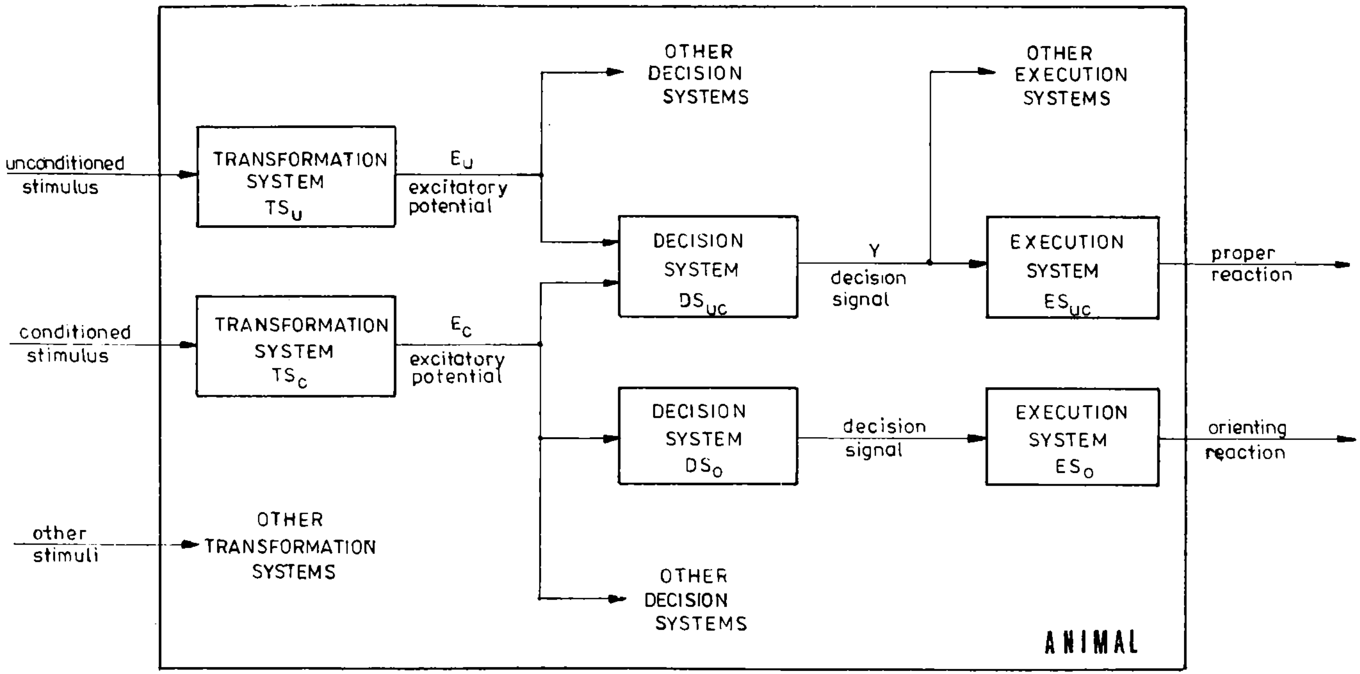

Fig. 3. Composite net of model elements.

is the intensity of the electric shock. But there are other influences, such as fear or the whole experimental setting, which affect the animals behavior, and these may be treated as other inputs in the model, which were not measured. In our models we will extract only one input, the intensity of electric shock, and the remaining influences will be treated as stochastic disturbances in the model.

In avoidance experiment (13) there are two basic stimuli: an electric shock and an accoustic white noise. Therefore at least two inputs must be considered in the model: electric noise intensity and acoustic noise intensity. The remainder of the stimuli which act on the animal will be treated as the model noise.

It is worth noting that the extraction of only these one or two inputs does not imply that the rest of the cues is beyond treatment by modelling methods. If the experimental procedure were changed even without changing these one or two controlled stimuli, the model would have to be modified because the structure of the stochastic inputs to the model would be changed.

There is a similar problem with the output from the model. The controlled reaction is (in the experiments described in (12) and (13)) pressing the bar placed on the wall of the cage. But there are of course many other reactions to the same experimental stimulation. Only a small portion of these reactions is dealt with instrumental procedure. The instrumental procedure can be treated as negative feedback — say "instrumental feedback" — which connects the desired reaction with the experimental stimulus (Fig. 4). Let us underline that the reaction which is fed back by feedback

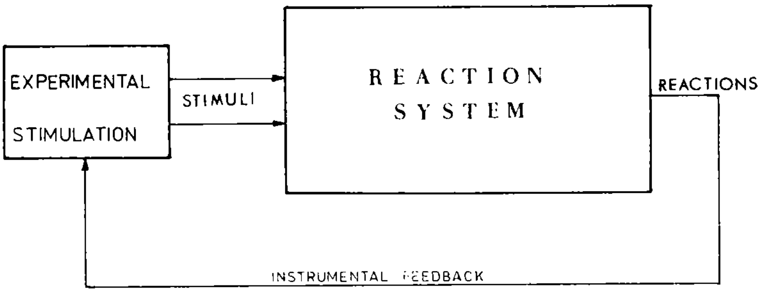

Fig. 4. Instrumental conditioning as feedback.

loop is not only pressing the bar but also all the other activity which is naturally connected with this pressing. Therefore from the point of view of identification there is no possibility of differentiating between elements of the different patterns of actions which might be performed during desired response to the stimulus. All of them will be treated together and called the output of the model.

The logic of the model is as follows. The external stimulation changes the level of the hypothetical excitatory potential. Values of this potential are compared with the threshold and decisions concerning if and how to react are then taken. Several models of reaction latency previously considered by other authors can be considered as special cases of the dynamic model discussed here. Spence (11) postulated that the overt reaction may be considered as one of unobserved reactions in which oscillations are generated. The observed reaction occurs when the oscillation attains an amplitude greater than some level. In consequence Spence's model may be included in the class described above (Fig. 5). Its transformation system transforms input

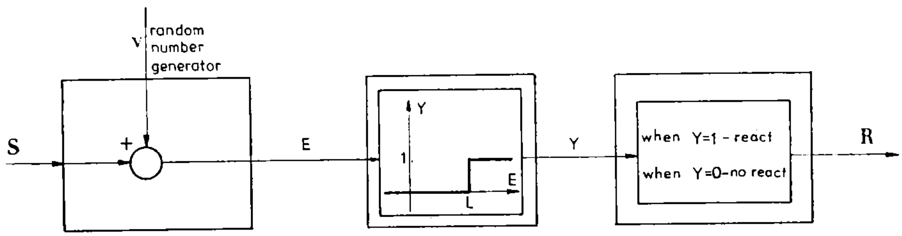

Fig. 5. Spence's model as special case of dynamic model.

signals to a white Gaussian sequence[1] and its decision system is given by a threshold element. A modification of Spence's model which leads to a better behavior of this model is given in another work (7).

A very impressive model has been proposed by Grice (3). He supposed that the stimulus consists of series of impulses which are counted by some probabilistic counter in the organism. The reaction occurs at the first moment that the cumulative

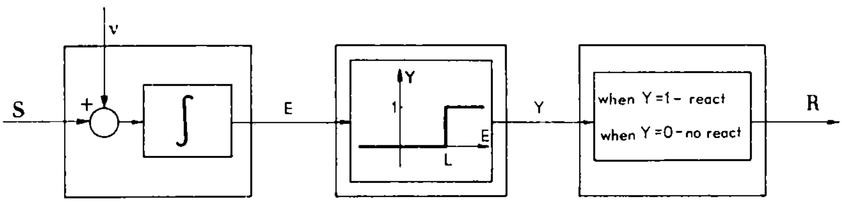

Fig. 6. Grice's model as special case of dynamic model.

count reaches some given level (random, in general). Some generalizations are given in the later work (4). Remarks on modified versions of these models are given in another work (7). The model of Grice may also be included in the class of general dynamic models (Fig. 6). Grice's transformation system is an integrating (counting) element and the decision system is a threshold element with a possibly random threshold.

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[1] i.e. the sequence of independent random variables which have Gaussian distribution.

In consequence Spence's and Grice's models have the structure of the dynamic model which has been proposed. This structure is too general to be useful without beeing specified further, and we now proceed to do this.

FURTHER STRUCTURAL ASSUMPTIONS: LINEAR DYNAMIC STOCHASTIC MODEL

The special structure which we call the linear dynamic stochastic (LDS) model, i- described as follows. Let the transformation system be described by a linear firsts order dynamic system driven by a stochastic noise. Let the decision system be based on a threshold mechanism and the execution system acts without delay. The above assumptions, which are specified below in detail for the escape and avoidance experiment, completely describe structure of the LDS model.

For the escape experiment we consider one stimulus (one input) and one reaction (one output). Therefore, one transformation system, one decision system and one execution system, coupled in series, will be considered. The execution system will be modelled by the first order stochastically disturbed differential equation. This type of equation may be considered as a local approximation of more complicated relationships and was successfuly used in various applications. Namely,

$$dE(t) = (ks(t)-aE(t))dt+dw(t), \qquad E(0) = E_0, \tag{1}$$

where:

t is time which is measured from the moment of the initiation of the stimulation,

$E(t)$ is the excitatory potential created by the stimulus,

$w(t)$ is a stochastic Wiener process with $\mathscr{E}w(t) = 0, \mathscr{V}dw(t) = \sigma_w^2 dt$, where $\mathscr{E}$ denotes expectation, $\mathscr{V}$ denotes variance and dw is a stochastic differential (see, for instance 2),

E_0 is a Gaussian random variable independent of the process $w(t)$ with $\mathscr{E}E_0 = m_0$, $\mathscr{V}E_0 = \sigma_0^2$,

$s(t)$ represents the stimulus strength for the stimuli which will be considered, $s(t) = 0$ for $t < 0$ and $s(t) = S$ for $t \geqslant 0$,

k denotes the static gain

a denotes the dynamic gain

The decision system will be modelled by a random threshold element whose output we denote by $y(t)$. This means that

$$y(t) = \begin{cases} 0 & \text{if} \quad E(t) < L, \\ Y & \text{if} \quad E(t) \geqslant L, \end{cases} \tag{2}$$

when $y(t) = Y$ the reaction occurs and there is no reaction if the output is 0. L is a Gaussian random variable representing the random threshold, independent of $w(t)$ and E_0 with parameters

$$\mathscr{E}L = m_L \text{ and } \mathscr{V}L = \sigma_L^2.$$

In other words

$$y(t) = \begin{cases} 0 & \text{if} \quad E(t) \notin R, \\ Y & \text{if} \quad E(t) \in R, \end{cases} \tag{3}$$

where

$$R = \langle L, \infty) \tag{4}$$

is a region on a line called reaction region (see Fig. 8*a*). This notion will be more useful in the modelling of avoidance reaction. The execution system will be modelled by simple nondynamic transducer. Therefore the whole model structure is as shown in Fig. 7.

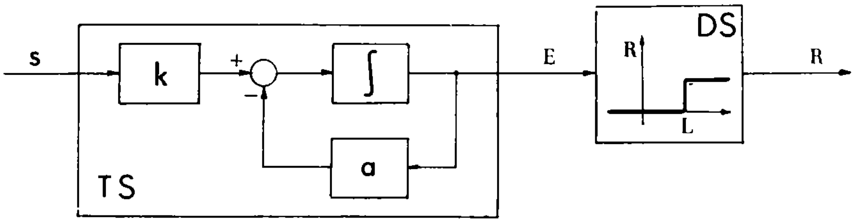

Fig. 7. Model of the escape experiment.

For the avoidance experiment we consider two stimuli (two inputs) and one reaction (one output). Therefore two transformation system will be assumed, each of them having the same form as described above for the excitatory potential. In other words,

$$dE_c(t) = (k_c s_c(t) - a_c E_c)\,dt + dw_c(t), \qquad E_c(t) = E_{c0}, \tag{5}$$

where the subscript c denotes functions and parameters connected with conditioned stimulus, and

$$dE_u(t) = (k_u s_u(t) - a_u E_u)\,dt + dw_u(t), \qquad E_u(0) = E_{u0}, \tag{6}$$

where the subscript u denotes functions and parameters connected with the unconditioned stimulus. It may be assumed that $s_u(t) = 0$ for $t < T$, where T is the moment of initiation of the unconditioned stimulus. Nevertheless it cannot be assumed that the random variables which are connected with the u-subscripted (unconditioned) part are independent of the corresponding random variables which are connected with the c-subscripted (conditioned) part.

The decision system is more complicated because it makes a decision based on a comparison two excitatory potentials (to be called conditioned and unconditioned, respectively) with some associated thresholds. It will be assumed that the decision system consists of two thresholds, each of them being a random variable, and correlated with the other. The execution signal which causes the activation of the execution system will be sent when any one of the excitatory potentials reaches its threshold value.

This means that

$$y(t) = \begin{cases} 0 & \text{if} \quad E_c(t) < L_c \quad \text{and} \quad E_u(t) < L_u, \\ Y & \text{if} \quad E_c(t) \geqslant L_c \quad \text{or} \quad E_u(t) \geqslant L_u, \end{cases} \tag{7}$$

where $L = \begin{bmatrix} L_c \\ L_u \end{bmatrix}$ is a random Gaussian vector with expectation vector $\mathscr{E}L = m_L = \begin{bmatrix} m_{Lc} \\ m_{Lu} \end{bmatrix}$ and covariance matrix

$$\mathscr{V}L = \begin{bmatrix} \sigma_{Lc}^2 & \varrho\sigma_{Lc}\sigma_{Lu} \\ \varrho\sigma_{Lc}\sigma_{Lu} & \sigma_{Lu}^2 \end{bmatrix},$$

where ϱ denotes the correlation coefficient between the two thresholds: one connected with the conditioned stimuli and the other connected with the unconditioned one. It may be more fruitfull to write relation (5) in the form

$$y(t) = \begin{cases} 0 & \text{if} \quad E(t) \notin R, \\ Y & \text{if} \quad E(t) \in R, \end{cases} \tag{8}$$

where

$$E(t) = \begin{bmatrix} E_c(t) \\ E_u(t) \end{bmatrix}$$

s called the excitatory vector and the region R, to be called the reaction region, s given by

$$R = \{(e_c, e_u): e_c > L_c \quad \text{or} \quad e_u > L_u\}. \tag{9}$$

In other words, R is a region on the plane in which at least one of the coordinates is greater than the corresponding threshold value. Because L_c and L_u are random variables, R is a random region.

In consequence, for both models (of the escape reaction and the avoidance reaction), the decision system has the common form (3) or (8). The decision regions are given in Fig. 8 for both models. The execution system will be assumed to have the same form as for the escape model. The whole structure of the avoidance model is given in Fig. 9.

Therefore the LDS models for escape and avoidance have a common structure. As we will see, the parameters and the functions of this structure have a biological interpretation.

Consider the transformation systems. There are two parameters for each of them: the static gain k and the dynamic gain a. The static gain may be interpreted as a parameter connected with unit and scale changes as well as with changes of carrier of information, for instance from the acoustic signal to the electric one. The dynamic gain is the coefficient in the negative feedback. Therefore the rate parameter (time constant) of the excitatory potential is equal to $1/a$. This means that the average speed of excitatory potential increase depends on this dynamic gain.

One of the inputs to the transformation system is the stimulus and the second is a stochastic white noise which is a convenient description of the derivative of a Wiener

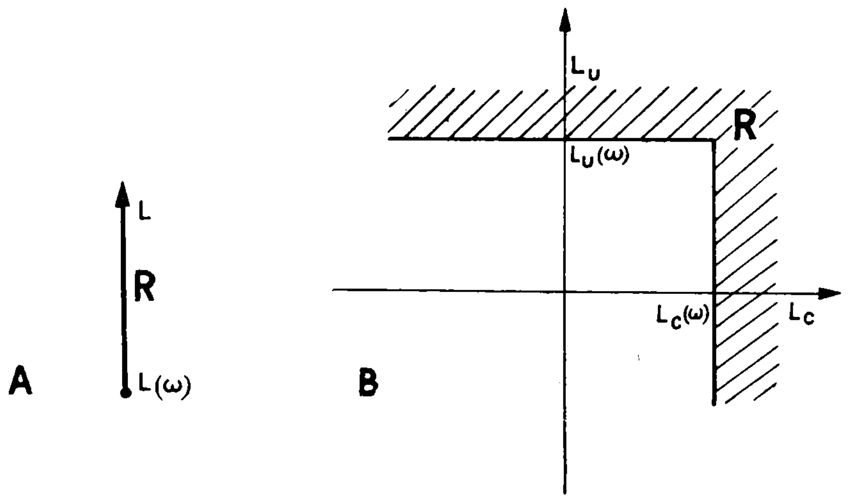

Fig. 8. Decision regions R for escape A, and avoidance B, model.

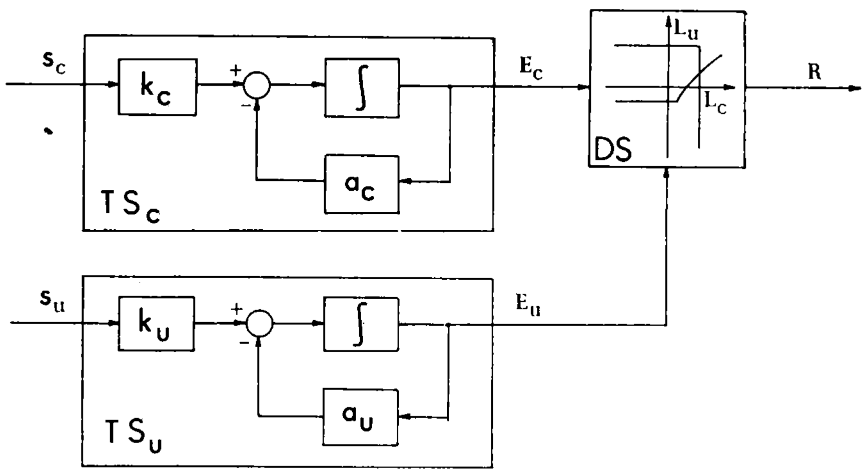

Fig. 9. Model of the avoidance experiment.

process with respect to time. This noise may be interpreted as existence of uncertainty in nervous system which causes changes of its activity even without stimulation. The integrator in the transformation system is responsible for accumulating the impressions caused by the stimulus.

Next consider the decision system. For both models the elementary actions of the decision system consist in comparing the excitatory potential with a given value. Such a comparison is easily interpreted on the basis of the threshold-like activity of neurons. The randomness of the threshold represents random variations of the threshold from trial to trial.

The situation may be compared to that in the theory of signal detection, where the noise is compared with the signal corrupted by noise. The decision what is observed: noise or signal plus noise may be taken on the base of distribution function analysis (5).

A very simple model has been chosen for the execution system. It was assumed that the delay caused by this system is small in comparison to other sources of delay. Some effects of this delay has been modelled as random disturbances. A direct inclusion of this delay into the model would make the model identification much more complicated. Special attention should be devoted to random elements in the model. There are at least two main sources of randomness. The first one is connected with fluctuations of the state of the system even without stimulation. This source is expressed by the Wiener process at the input of the model and by assuming random initial conditions. It may be noted that when there exists no stimulation and $s(t) = 0$, then the excitatory potential $E(t)$ is given by the equation $dE(t) = -aE(t)dt + dw(t)$ and therefore $E(t)$ has an asymptotically (for $t \to \infty$) Gaussian distribution with parameters $\mathscr{E}E(t) \to 0$, $\mathscr{V}E(t) \to \sigma^2_w/2a$ (for $a > 0$). Thus if one assumes that the time distance between two consecutive trials is much greater than the latency, then the parameters of the random variable expressing the initial conditions may be expressed through input noise parameters.

The second source of randommess, which is assumed to be independent of the above one is connected with the threshold. For the case of the escape experiment this is a one-dimensional Gaussian variable and for the case of the avoidance experiment this is a two-dimensional Gaussian variable.

It may be noted that the zero and the unit of excitatory potential is not subject to identification. The excitatory potential is hypothetical function and therefore the hypothetical zero and unit may be chosen.

It will be reasonable to assume that zero of this scale is connected with the asymptotic situation when no stimulation exists. In consequence, it leads to the assumption $m_0 = 0$.

The choosing of the unit of the excitatory potential will be considered when analyzing the properties of random threshold models.

It is easy to check that the models of Spence and Grice are also the special cases of LDS models of the escape-type reactions (for this problem see 7).

ANALYSIS OF LDS MODELS

It is not a simple matter to fully analyze the behavior of the LDS models. It is a simple task to know the behavior of the excitatory potential but it is a rather involved one to solve the so-called first access problem for the stochastic process $E(t)$. We consider both problems briefly.

It can be shown (8) that the excitatory potentials have an exponential shape "in the average", namely

$$E(t) = ks/a+(E_0-ks/at)\exp(-at) + \int_0^t \exp(a\vartheta)\exp(-at)dw(\vartheta) \tag{10}$$

for the escape experiment and, in a slightly modified form, for the avoidance experiment. Therefore the individual excitatory potential may be illustrated as in Fig. 10 for the escape model and in Fig. 11 for avoidance model.

For both models the latency time τ can be written as

$$\tau = \begin{cases} \inf\limits_{t \in \mathscr{S}} \{t\colon E(t) \in R\} & \text{if } \{t\colon E(t) \in R\} \neq \emptyset, \\ \infty & \text{for the opposite case,} \end{cases} \tag{11}$$

where $\mathscr{S}$ is the stimulation period and $\mathscr{S} = \langle 0, t_{max} \rangle$. Because of the randomness of $E(t)$ and R the latency τ is a random variable. The problem of determining the latency distribution is, therefore, the first access time problem[2] for the process

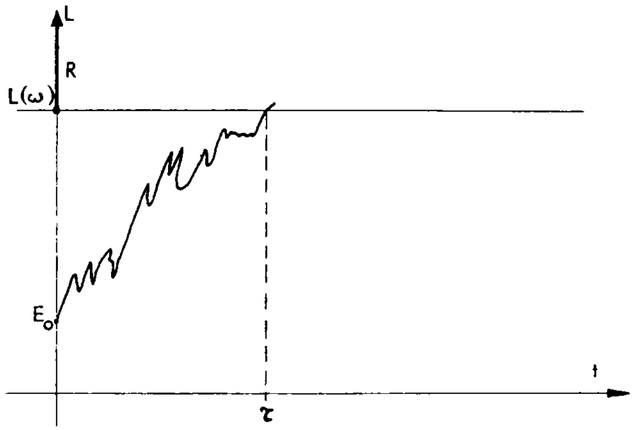

Fig. 10. Reaction evocation for escape experiment.

$E(t)$ and the region R. This problem has been effectively solved only for a small class of stochastic processes (1, 10). A very useful survey of existing techniques is given in Ricciardi (9).

[2] First access problem. For a given stochastic process and a region R find the distribution of random variable τ given by (11).

The first access problem can be resolved for both models. A method for the escape model is given in (8). A method for the avoidance model can be based on the same approach. However, only the Laplace transformation of the distribution function of

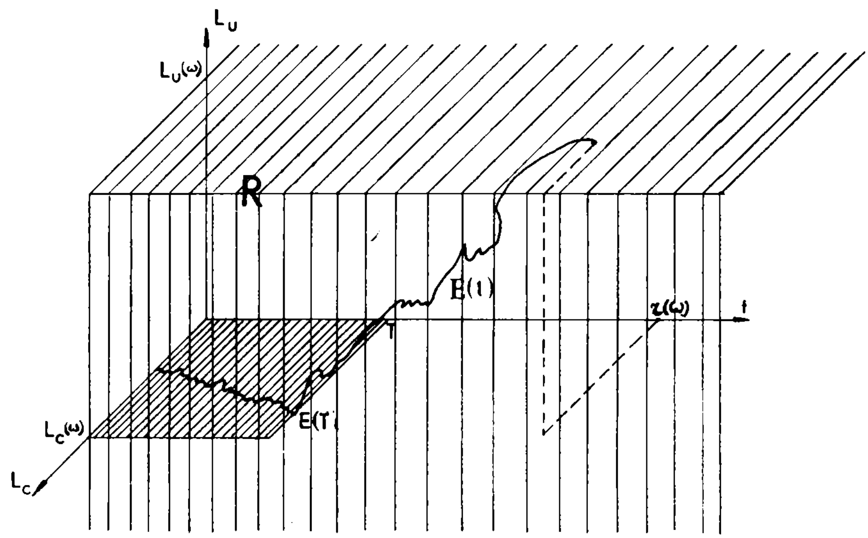

Fig. 11. Reaction evocation for avoidance experiment.

the first access time is known. This solution is not useful for solving the identification problem and a numerical method of solving the problem in terms of a time-domain analysis must be used. For a discussion of these problems the reader is referred to (8).

IDENTIFICATION PROBLEMS

The only observations which can be used for the identification of the model parameters is the first access time. However this time is a random variable and it cannot be identified on the basis of a single observation. The sample distribution of this time must be derived from experimental data.

A problem arises of how to compute the sample distribution. The problem consists of the fact that there is learning during the experiment and therefore the latency data cannot be treated as a stationary series of random variables. There are several ways to handle this problem. One good approach is to model the reason for the nonstationarity. This approach cannot be directly used. The reason is that the structure of the nonstationarity is unknown. Knowledge of this structure is equivalent to knowledge of the structure of the learning process and this in its turn may be known after examination of the described model. Therefore another approach must be taken. It is assumed that the learning process behaves like a stationary one when considering only a small number of consecutive trials. If the latencies in these trials can be treated as independent then the averaging procedures can be used and sample distributions may be computed. An analogous approach may be used in examination of the structure of learning. Therefore this approach may be also treated as the initial step in modelling the learning process.

There is a substantial constraint on the quality of the identification. This depends on the number of latency measurements which can be used in the computation of the sample distribution computation. The data taken together will be called stage of learning. For the considered experiment it may never be assumed that the stage lasts longer than 50–200 trails. Moreover, it changes from animal to animal. It seems to be appropriate to assume that the time-lenght of the stage depends on the animal and is given by dividing the total number of trials by the number of stages which was assumed to be constant. In consequence, the number of parameters which may be identified on the basis of stage data is drastically constrained.

The detailed development of the concerning identification problem for the escape and avoidance models will be presented in subsequent papers (Pacut; Pacut and Tych, in preparation).

CONCLUSIONS

In the paper the basic structural assumptions concerning the dynamic models and then the linear dynamic stochastic models of the reaction latency have been presented. The models have a uniform structure. Moreover, the same structure can be applied to other experiments, like differentiation conditioning. The biological motivation for using these models has been outlined. The models express the latency time as the first access time of the random threshold of a rather simple stochastic process, but even with such simple models identification is very complicated.

In the result the model must be identified in simpler form and then verification must be performed. In subsequent papers an analysis of the identified models will be presented as well as the results of the identification procedure.

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