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**A mathematical model for neural activity.**  
(Preliminary Draft)

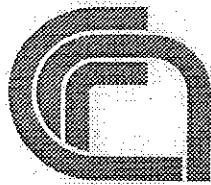
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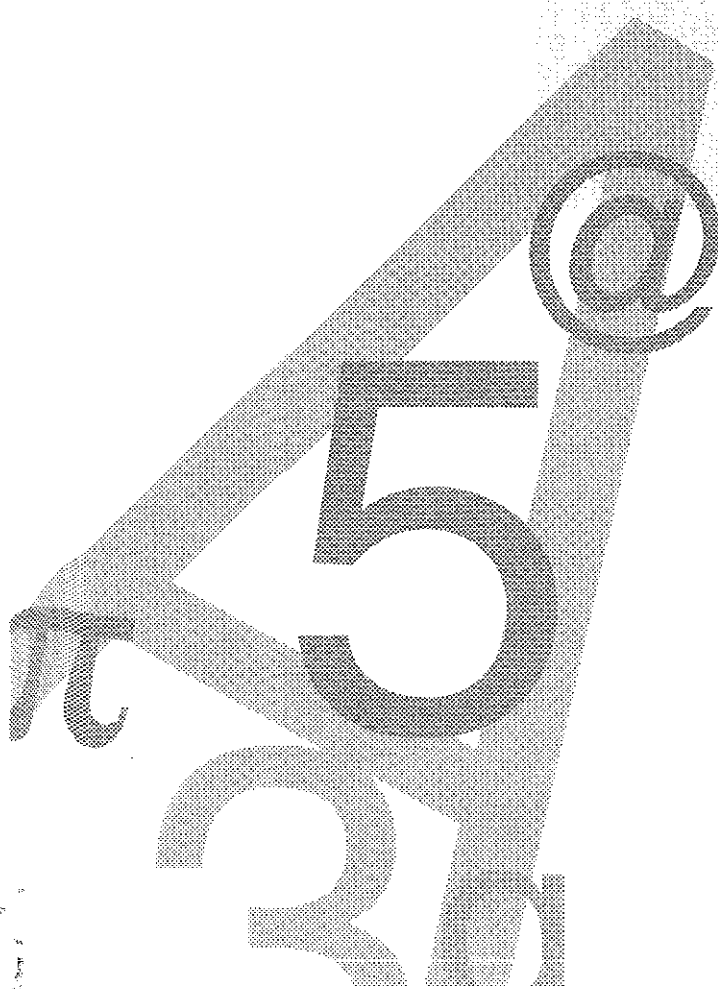
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# A MATHEMATICAL MODEL FOR NEURAL ACTIVITY (PRELIMINARY DRAFT)

RENZO BELTRAME

## 1. INTRODUCTION

In this introduction we will discuss the main features of the mathematical model that we are proposing, from an intuitive, and rather informal point of view. We also will introduce restrictive hypotheses to simplify the mathematical notation. We will follow a more general, and formal approach in the next section.

We will consider here the nervous system or its part we are concerned of, as an abstract system. As in every problem, or class of problems, we shall indicate how the elements of the system under investigation are defined, and which parameters individuate them.

Furthermore we have to assign a structure to the system; for instance, we must decide if we will treat it as a discrete or a continuum, which type of properties we require to write evolution equations, etc. Biological systems exchange matter with the environment and among their parts. Substitutions of components of the system are also usual, though the new element is not required to be identical to the substituted one, but it has to retain only certain characters.

In the next section we will discuss in detail how to give a formal description of the systems we are interested in; here we use a very crude formal trick to bypass the discussion. Let be  $\zeta$  the element of a set  $\Omega$ , which uniquely labels the elements of the system, we will individuate the system as a subset  $\Xi \subseteq \Omega$  of this set.

We will describe the values that the observables take at the elements of the system, as mappings  $x$  on the system  $\Xi$  to the space  $V$  of the values the observables can take. We will call  $X$  the space of these mappings.

For simplicity sake, in this informal discussion we will suppose that the observables values describe the spatial position, the time, and the activity, of the elements of the nervous system. To simplify the mathematical notation, a monodimensional space will represent the values of the activity; that is, we will think the activity for instance as spikes frequency only. We shall remove this limiting hypothesis in the formal presentation of the next section.

Furthermore we shall assume as safe hypothesis that the time takes finite values only, and that these values have a maximum. In this way we have data that only refer to a finite interval of time, and we satisfy the requirement that a theory only gives predictions which concern observable facts.

Nevertheless we prefer to conceive the activity in a slightly general way by assuming that the distribution of the spikes frequency, or of their inter arrival time, characterizes the activity. Many other factors can thus change the activity, in addition to the change in spikes frequency usually related to the strength of excitatory signal. We think in particular to everything that can influence the tone of the neural activity, and to the sculpturing effect of the inhibitory activity of other neurons through the various types of inhibitory synapses.

Hence we will suppose that each observable can take different values at the same element of the system according to a given probability distribution; and the theory shall thus contain relations among probability distributions. The space  $X$  must be a linear space to support these assumptions. This structure is in fact required to evaluate probabilities, average values, moments, etc. The observables values are, or can be treated as, real numbers, and probability values are real numbers, thus the properties we require for  $X$  follow in a natural way by the properties of the range of the mappings  $x \in X$ .

We will discuss the consequences of this assumption at the end of this section, and the mathematical aspects in the next section. Here we continue the informal presentation by supposing that single real values completely individuate time, place, and activity of the system elements. In the first part of this informal discussion we will assume that systems have only a finite number of degrees of

freedom; that is, only a finite number of labels (elements) characterize the system. We shall extend the discussion to fields at the end of this section.

The mappings  $x \in X$  must globally concern all the elements of the system  $\Xi$ , and we will present some examples to clarify how these mappings can be interpreted.

Let a mapping  $x \in X$  associates two different elements  $\xi_1$  and  $\xi_2$  of the system, to the two values  $x(\xi_1) = (t_1, x_1, a_1)$  and  $x(\xi_2) = (t_2, x_2, a_2)$ .

We can interpret this fact as a correlation of the activity  $a_1$  that occurs at place  $x_1$ , and time  $t_1$ , with the activity  $a_2$  that occurs at place  $x_2$ , and time  $t_2$ .

We can also interpret this correlation as the effect of an interaction among the elements  $\xi_1$  and  $\xi_2$ , which correlates the activity  $a_1$  that occurs at place  $x_1$ , and time  $t_1$ , with the activity  $a_2$  that occurs at place  $x_2$ , and time  $t_2$ .

Let be  $t_1 \leq t_2$ , we can interpret the correlation as a delayed action of the element  $\xi_1$  on the element  $\xi_2$ . In this way we can model memory phenomena that are consequence of a delay in the interaction. Dynamic memory phenomena are good candidates for this type of representation, because this representation does not require that we introduce changes in the parameters, which characterize the material that composes the system.

Situation like  $x(\xi_1) = (t_1, x_1, a_1)$ ,  $x(\xi_2) = (t_2, x_2, a_2)$  and  $x(\xi_3) = (t_2, x_3, a_3)$  give rise to a single-valued mapping. Situation like  $x(\xi_1) = (t_1, x_1, a_1)$ ,  $x(\xi_1) = (t_2, x_1, a_2)$ ,  $x(\xi_2) = (t_3, x_2, a_3)$ , and  $x(\xi_3) = (t_3, x_3, a_4)$  would instead give rise to a multivalued mapping, if we would continue to use this scheme.

Formally we should need a multivalued mapping when the interaction associates two or more different triples  $(t, x, a)$  to a same element of the system. One of the more frequent cases is the case we exemplified above, where the interaction associates to a same element different activities, at the same place, and at different instants of time.

Nevertheless we prefer to model these facts, and their effects on the system behavior, in a different way; that is, as modifications that activity locally induces in the material of which the system is made, and so in the response of the system to further actions. We will discuss this approach below, in the context of long term memory phenomena.

Hence our mappings  $x \in X$  shall be single value mappings, and the larger is the subset of events that the correlation involves, the more sophisticated is the interaction. The mappings described above can thus model physical behavior which has different degree of complexity, and which depends on subsets of events that span over space and time in very different way.

As a consequence of the assumptions we made, each mapping contains data which describe a certain interaction. The interaction is described as a correlation among activities that are associated to different places, and time, and as a field of the activity on the space of events, when we pass to a continuum approach. This field concerns, in particular, a certain interval of time, because we usually have a delayed interaction. Furthermore, we assume that each mapping describes an interaction which acts alone.

To gain more insight about this way of modelling the interaction, we can observe that very often in biological systems the properties of an isolated part may significantly differ from the properties of the whole system. It is trivial that a piece of cat does not behave like a cat, whereas a little quantity of water has the same physical and chemical properties of a greater quantity of water.

A behavior like that of the water is quite frequent in physical systems, and leads to a simple mathematical representation. In fact we can describe such a systems by means of the ordered repetition of a rather simple, small structure, often a point of a continuum; and the main interaction involves only the neighboring elements. Suitable boundary conditions of the whole system characterize the particular problem under investigation.

Systems where the parts behave like the whole system, are both the justification and a strict consequence of the mathematical model described above. Because the behavior of the biological systems significantly differs on this point, we avoid to introduce from the beginning a particular order structure in our mathematical model; and we prefer a general, formal representation of the interaction among the parts of the system. Furthermore we expect that an interaction with both neighboring and remote elements of the system shall be necessary to obtain the behavior we observe in the biological systems of our interest. Clearly we can continue to use the simple mathematical model described above, when we have subsystems where it is acceptable to assume that the parts behave like the whole subsystem.

We continue this informal discussion by assuming a point of view where all the variants of the processes can occur, and the theory has to explain how the environment actions force a particular process to occur. This approach is rather common in immunology and in many evolution theories, here we will call it *descriptive approach*.

In a descriptive approach,  $X$  is the space of all the possible mappings, we will associate an initial probability value to each mapping  $x \in X$ , and we will model the effects of the activities in the system as changes in the probabilities of the various mappings. The initial distribution of probabilities either is part of the definition of the particular system under investigation, or another part of the theory shall evaluate the initial conditions of the system by starting from a given set of conditions.

For clarity sake we will discuss separately the cases where a locality principle holds for the effects of the processes that occur in the system, and the cases where it does not hold.

In a biological system we plainly assume that activity induces changes on the material by which the system is made. Nevertheless these changes on the material must be interpreted in a broad sense, and the following situation is a good example. Let, for instance, a protein A be a gene regulatory protein that activates its own transcription; if a transient action turns on the expression of the protein A, then all the cell's descendants shall produce the protein A [Alberts et al., 1994, p. 443-4].

We can model these changes as modifications of the system parameters, and a locality principle holds for these modifications; that is, the change of the parameters which describe the material of a system element, only depends on what happened in the past to that element only, or, at most, to a small neighborhood of the element. Long term memory phenomena are of this type.

Functionals of the activity history can be used to describe the modifications; and usually they are not monotone, because we have to model fading phenomena too.

As consequence of the material parameters change, the same action of an element on another element can induce different responses, and we can interpret this fact as a different correlation among the activities that can occur in the system. In our model changes in the probability of the various mappings are the counterpart of different correlations among the activities that can occur in the system. Hence we shall introduce in the model a change in the probabilities of the various mappings  $x \in X$ , which depends on functionals of the activity history at the various elements of the system.

On the other side, when the activity that occurs at one element can induce an activity on another element of the system, and the delay between the two activities is significant, we will lower the probability of the mappings, whose described activities do not agree with the activities that occurred in the system. A locality principle clearly does not hold for these situations.

Another essential feature of the model is thus a continuous redefinition of the probabilities that we associate to the mappings  $x \in X$ . When an activity occurs on certain elements of the system, the probability of the mappings  $x \in X$  changes according to the following rules:

- (a) the probability changes only by effect of the renormalization factor, when the activity is not expected in the mapping;
- (b) the probability becomes very high, when the activity is expected in the mapping;
- (c) the probability becomes very low, when a different activity is expected in the mapping.

The dynamical redefinition of the probabilities is particularly interesting in our model, where we consider significant the delay in the interaction. Hence during a successive, suitable interval of time we continue to modify the probability of the mappings as consequence of the past activity in the system, until the effects of the delay in the interaction are exhausted.

Let be  $t_0$  the time at which the activity occurred, and  $t$  the current time. We must assign a very low probability to all the mappings where a different activity is expected at the time  $t_0 - t$  for the system elements that were active at the time  $t_0$ . Consequently we must assign a very high probability to all the mappings whose expected past activity agrees with the occurred past activity.

This dynamical change of the probabilities of the various mappings can also model changes of the interaction. The mappings shall assume an higher probability, which describe the new interaction.

The various kinds of probability changes we discussed above, generally occur together in our systems. We prefer to deal with them separately, because the physical processes are conceptually different, which underlie the various types of probability changes. Hence we expect that different mathematical relations describe them.

This criterion seems to me preferable to the time scale of memory phenomena. In fact memory phenomena, which can be modeled by means of changes in the parameters that characterize the

system's material, encompass both short-term and long-term facilitation phenomena [Kandel et al., 1991, Ch.65].

This continuous redefinitions of the mappings  $x \in X$  induces a probability decay of the mappings whose expected activities do not occur, and this consequence becomes a very important feature in modelling the behavior of intelligent systems.

In our model we need a further rule which shall describe the long time changes of the mappings probabilities, which are induced by the short time redefinition of the probabilities. These long time changes of probability have an interesting effect: they produces a long time decrease of the probability of the mappings where a poor correlation occurs among the activities, and a parallel increasing of the probability of the mappings where no correlation exists.

This feature can be used to model situations, which we describe at psychological level as situations where the subject learns to consider indifferent a fact because no other fact can be expected from its occurrence.

The congruence conditions, which describe an aspect of the dependence on the history, cause at every instant of time a strong reduction in the number of the mappings that have a probability to happen. Nevertheless the number of possibilities remains very high for at least two reasons:

- the strong dependence on the history only extend over a limited interval of time;
- the interaction involves a limited number of system elements; that is, the constraints only concern a limited number of elements in the system.

Some aspects of the model can be studied separately, and a good example of this strategy is the theory of the various type of sensory neurons.

Sensory neurons can be conceived as elements which respond to environment actions only in a narrow band, and with an high gain. Furthermore only a little number of the system elements respond to a specific action. The main problem is here the correlation of the neuron activity with the physical actions to which it can respond, and the very high specificity of the interaction allows us to study each kind of sensory neuron separately. So we can often treat the environment actions that are mediated by this kind of neurons as independent boundary conditions.

Nevertheless we have situations where we cannot treat the environment actions as independent boundary conditions; for instance, because we wish to model dependencies of the environment actions on preceding actions of the system on the environment.

The voluntary movements offer a good example of this situation. We are now interest to connect in the theory actions on the environment, which correspond to motor neurons activity, with actions of the environment on the sensory neurons, which follow from the previous environment modifications; for example, the displacement of an object.

Many other situations require to be treated in this way. Some neurons, for example, release chemical substances that have distant target organs, and we are interested in the effects of the activity of these organs on either the same or other neurons. We can think at the synaptic transmission mediated by a second messenger also as a mode of interaction, where distant organs act on the nervous system by means of chemical substances that they release in the blood circuit; and we should not need to suppose neurons with high specificity. This kind of interaction seems of theoretical interest in studying, for example, moods, emotions, and motivations.

In conclusion we need a theory where that we treat some environment actions as independent boundary conditions, and other environment actions depend on previous modifications that the system made on the external environment.

The picture we outlined above offers a conceptually simple and unified point of view. Nevertheless the experiments systematically concern very small subsets of the system elements.

Each experiment describes a connection among small subsets of the system observables, all the other observables do not vary, and it assumes that the system be in a well defined, initial state. Instead the descriptive approach conceptually concern all the elements of the system, and the system state evolves continuously. So we have to patch together the results of different experiments both to build a description of the system behavior that shall agree with the descriptive approach, and to obtain a theory suitable to predict the behavior of the system in a real environment, where the environment actions and the internal activities follow certain temporal paths.

Each experiment starts with certain values of the independent variables, and, by repeating the experiment, we can obtain either the same value of the dependent variables, or different values. In



the latter case we must repeat the experiment until we can assign a reasonable probability to find in the different intervals the values of the dependent variables that we observed.

We are thus led to assume a constructive approach; that is, we shall introduce atomic mappings, which directly represent experiments, or which are derived from the experiments; and we shall give the rules of combining atomic mappings to describe both the system, and its behavior *in vivo*, because the atomic mappings clearly do not cover all the possible situations.

A procedure is known (see Section 6.1) for constructing a topological space by patching together a family of topological spaces  $(X_\lambda)_{\lambda \in L}$  in such a way that, in the topological space  $X$  so obtained, the  $X_\lambda$  are identified with open sets of  $X$ . Unfortunately this procedure solves only one of the mathematical aspects of the problem, and we have further constraints because on the space  $X$  of the mappings we need to compute integrals over its subsets to obtain average values of the observables, moments of higher order, etc..

We can freely patch together two atomic mappings  $x_1$  and  $x_2$ , even in the cases where they concern two disjoint subsets of the system  $\Theta_1 \subset \Xi$  and  $\Theta_2 \subset \Xi$ , that is  $\Theta_1 \cap \Theta_2 = \emptyset$ , only after checking that no mutual influence exists between the variables of the two mappings; and the patch concerns the subset  $\Theta_1 \cap \Theta_2 \subseteq \Xi$  of the system.

When two atomic mappings  $x_1$  and  $x_2$  concern two subsets  $\Theta_1 \subset \Xi$  and  $\Theta_2 \subset \Xi$  that are not disjoint, that is,  $\Theta_1 \cap \Theta_2 \neq \emptyset$ , we must carefully investigate the mutual influence of the variables of the two mappings that we expect to exist in the subset  $\Theta_1 \cap \Theta_2$ . Usually this investigation requires a new series of experiments, which must concern the subset  $\Theta_1 \cap \Theta_2 \subseteq \Xi$  of the system, and all the variables that the mappings  $x_1$  and  $x_2$  involve.

We will briefly come back to the assumption that the space of the mappings  $x \in X$  be a linear space. Let be  $x_1$  and  $x_2$  two mappings. The mapping:

$$y = ax_1 + bx_2$$

can be defined as:

$$\xi \mapsto ax_1(\xi) + bx_2(\xi)$$

because the ranges of  $x_1$  and  $x_2$  are  $\mathbb{R}^n$  spaces.

When we assume the descriptive point of view,  $y \in X$ , because  $X$  is the space of all the possible mappings, and  $X$  is thus a linear space. When we assume the constructive point of view, a mapping  $y$  linear combination of two atomic mappings might not be an atomic mapping. Hence the subset  $Y \subseteq X$  of the atomic mapping may not be a linear subspace of the linear space  $X$  of the mappings.

In conclusion we must always spend a lot of work to verify whether a set of atomic mappings can be patched together; and this work is equivalent to the construction of mappings that concern all the elements of the system. Furthermore the procedure is too much dependent on the properties of the single cases, and it is rather difficult to give general rules.

For these reasons we continue our discussion by assuming that the mappings  $x \in X$  concern the whole system  $\Xi$ , and we will discuss now the leading ideas along which we will develop in the next section the formalization of the model.

The continuous redefinition of the probabilities and the related coherence conditions that we discussed above are a crucial point of this formalization; Hence the theory must allow us to evaluate the probability distribution of the values of each observable, and the time is one of these observables.

We assume that the labels, which identify the elements of our systems, belong to a closed, bounded subset of a tridimensional Euclidean space  $E^3$ . This assumption seems quite natural, because a biological organism always occupies a finite volume of a tridimensional Euclidean space. Hence the subset of this space can be used to identify the system, which the system occupies at a certain instant of time.

The idea of the mappings  $x \in X$  of the system to the space of the observables values is taken from the kinematics of continuum media, and we expect that many results of the kinematics of continuum media can be transferred into our model.

As we discussed above, the continuous redefinition of the probability of the mappings  $x \in X$ , and the related coherence conditions are a central feature of our mathematical model; and we will discuss them by relaxing the limiting hypothesis that the values of each observable be fully described by a single real number.

We will outline two formal approaches, which seem suitable to describe changes of these probabilities. The first uses directly a measure defined on the space  $X$  of the mappings, but it is rather

crude; the second tries to follow as close as possible the approach of the constructive quantum field theory.

We can realize the change in the probability of the mappings  $x \in X$  by means of changes in the measure that we use in calculating the probabilities; so we will refer to change of measures instead of to change in probabilities.

Changes of measure concern the whole space  $X$ , hence we can think at a process that describe the behavior of the system as a mapping:

$$\pi: [0, 1] \rightarrow M$$

from the real interval  $[0, 1]$  into the space  $M$  of the measures defined on the space  $X$  of mappings. In this way we obtain sequential processes.

Hence a process describes the evolution of the measure that is associated to the space  $X$  of mappings; and in this way it also describes the evolution of the probability distributions associated to the values of the system observables. The real variable that spans over the interval  $[0, 1]$  in sequential processes, must be interpreted as an ordering variable, and in particular cases it can be identified with the time. We use a finite interval because we consider only bounded processes.

We shall refer to this general method as a conceptual tool to describe changes of measure; measures, in fact, are defined on very general spaces, hence they have only general mathematical properties.

Some refinements can be introduced, we can introduce, for instance, operators that act on the space  $X$  of the mappings, to represent measure and its changes. The leading idea is to have operators, which go from the space  $X$  of the mappings into the space  $M$  of the measures. In this way we can represent a measure  $\mu$ , as an operator  $T$  applied to an elements of the space  $X$ :

$$T: X \rightarrow M$$

For example we shall have:

$$\mu = Ty$$

with  $y \in X$ .

So we can represent a sequential process as a function from the space of the order parameter into the space  $X$  of the mappings:

$$\pi: [0, 1] \rightarrow X$$

and we can obtain the required measures by applying the operator  $T$  to the range values of the process; that is by:

$$\mu_i = T\pi(i)$$

with  $i \in [0, 1]$ .

When  $X$  is a Banach space, and the measures  $\mu$  are continuous, they belong to the dual space  $X'$ . Thus we can define our operator  $T$  as:

$$T: X \rightarrow X'$$

and we can use the mathematical properties of the dual spaces.

When the space  $X$  is an Hilbert space, and the measures  $\mu$  are continuous, we can represent them as a mapping from  $x$  to real scalar products:

$$\mu: x \mapsto (y|x)$$

and we know that this representation is unique (Riesz representation theorem).

In this case we obtain nice algebraic properties by the linearity of the real scalar product, which gives:

$$\alpha\mu_1(x) + \beta\mu_2(x) = \alpha(y_1|x) + \beta(y_2|x) = (\alpha y_1 + \beta y_2|x)$$

This first approach and its variants is not suitable to write equations that describe the changes of the probabilities that we define on the space of tyhe mappings  $x \in X$ . These equations, in fact, can conceptually involve both the actual values of the probabilities, and their rate of change.

The second approach will represent probabilities and their changes by using distribution formalism, which can be conceived as a generalization of the density functions on  $X$ .

We recall that a density function is a mapping:

$$\rho: X \rightarrow \mathbb{R}_+$$

and the probability that  $x \in A$  shall be given by:

$$Z^{-1} \int_A \rho(x) d\mu(x)$$

where  $Z^{-1}$  is a normalization factor. Two density functions are equivalent when  $\rho_1(x) = \rho_2(x)$  almost everywhere in  $X$ .

Unfortunately we cannot easily find a unique density function, which describe the required measure over the whole space  $X$ , and it is not easy to describe changes of the measures over the whole space  $X$  by means of change of density functions. Furthermore density functions might not have derivatives of every order on  $X$ . So we are led to introduce distributions, which are more general, and have derivatives of every order.

For this purpose we have to introduce a space of functions  $f \in C_0^\infty$  continuous with all their derivative over a compact support: the *test functions*. We have the choice to define them either on the space  $X$  of the mappings, or on the Euclidean space  $E^4$  that describes the space time.

We present firstly the second alternative, which seems to me more intuitive; and we suppose to have to describe the activity of our system.

According to our field approach we define a density of activity by means of a real valued distribution:

$$\omega(f) = \langle \omega, f \rangle$$

and according to our past simplifying hypotheses we will think the activity  $\omega$  as a real scalar field; that is  $\omega$  is a functional that associate a real value to each test function.

A test function acts as a selector of the region of the space  $E^4$ , which we are dealing on. We remember that the test functions cannot have discontinuities; hence we shall approximate a selection of a subset with sharp boundary by means of a suitable sum of test functions.

In this picture every test function has a unique measure  $\omega(f)$ , and we need to consider them like a random variable. Hence we will introduce a measure  $d\mu(\omega)$  on the space of the  $\omega$ .

The generating functional:

$$S\{f\} = \int e^{i\langle \omega, f \rangle} d\mu(\omega)$$

is now the analogous of the characteristic function of a random variable in the probability calculus. In this picture we clearly have a generating functional for each observable, and it allows to evaluate, for instance, the various moments of the observable distribution over the subset that the test function selects.

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