73. On Some Impulse Responses of Cat Brain

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It is well known that the dynamic characteristics of the time
patterns of a linear input-output system may be given by the impulse
response. In the previous paper, some examples of the impulse
responses of the blood glucose and insulin levels in the glucoregulatory
system of dog were obtained by multivariate autoregressive
(AR) analysis of the sways in blood glucose and insulin following
random impulse-like rapid injections of glucose. In this paper, some
examples of the various impulse responses of the lateral geniculate
body and of the lateral and suprasylvian gyri of cat were obtained by
applying the same method of analysis to spontaneous EEGs of these
brain sites.

A cat weighing about 3–4 Kg was immobilized by Flaxedil and
mounted on a Johnson type stereotaxic instrument under artificial
respiration with oxygen mixed with moistened air. Silver-ball tipped
surface electrodes, 0.5 mm in diameter, were placed on the dura over
the middle lateral (L3) and middle suprasylvian gyri (SS3), while a
depth bipolar stainless steel wire electrode, insulated except at the
tip, was inserted into a lateral geniculate body (GL), and a reference
silver wire electrode was inserted into the neck muscle of the animal.
The approximate stereotaxic coordinates of these brain sites were L3
(A: 6.0, L: 2.0), SS3 (A: 6.0, L: 9.0) and GL (A: 6.0, L: 10.0, H: 3.0)
on the right side, respectively.

EEG potentials led from these surface and depth electrodes were
recorded simultaneously on magnetic tape (MT) through an 8-channel
polygraph and data recorder. As the visually evoked potential
(VEP) due to binocular flashing light stimulus exhibited the maximal
size at L3, this area presumably is the locus which gives rise to
the high amplitude VEP demonstrated by Doty, Berkley et al. An
example of EEGs from GL, L3 and SS3 is demonstrated in the upper
panel of Fig. 1.

AD transform of the MT recording of each EEG in Fig. 1 was
made at 20 msec intervals over 10 sec through a mini-computer
(ATAC 501, Nihon Khoden, Tokyo) to obtain three dimensional
discrete digital time series. These were subjected to three dimensional
AR analysis through a computer (FACOM, 230-30/20, Computer Room, Nagasaki Univ.) and the impulse responses obtained were traced by an X-Y plotter, as shown in Figs 1 and 2. In the lower panel in Fig. 1 are shown the impulse responses of L3, GL and SS3 elicited by a unit impulse initiated at time origin in one of the other structures. At the top left is displayed a corticopetal impulse response (GL→L3) of L3 due to an afferent unit impulse initiated in GL. This response is the largest in size and displayed damped oscillatory deflections of about 3 Hz frequency lasting for about 2 sec. Though this oscillation started from a surface positive deflection, a small but relatively sharp negative deflection was superimposed on the positive deflection. As demonstrated at the top right, a corticofugal impulse response (L3→GL) was also observed in GL due to a unit impulse initiated at time origin in L3. This response displayed repetitive deflections with lower amplitude, greater irregularity, higher frequency of 10–12 per
The existence of a cortico-geniculate projection pathway has been demonstrated in cats by anatomical studies. Physiological studies not only have revealed presynaptic inhibitory and/or occlusive corticofugal influences of the lateral gyrus upon the lateral geniculate body, but also have demonstrated facilitory cortico-geniculate effects so that manifold neuronal network systems may be organized by geniculo-cortical and cortico-geniculate connections. The corticopetal and corticofugal impulse responses of L3 (GL→L3), and GL (L3→GL) in Fig. 1 probably respectively indicate some of the dynamic activities of this system.

The corticopetal impulse responses of SS3 (GL→SS3) and the corticofugal one of GL (SS3→GL) elicited by a unit impulse initiated at time origin in GL and SS3, respectively, are shown in the middle tracings on the left and right respectively, in the lower panel of Fig. 1. The former response is composed of a surface positive deflection followed by a negative one, both of which are relatively large in size lasting for about 0.5 sec, and between them is intercalated positive deflection. The positive-negative deflections seem to be a damped oscillatory response of about 2.5 Hz with such an intensive decay that the subsequent oscillatory deflections are almost all deteriorated. The intercalated positive deflection also seems to be followed by a negative deflection as suggested by the pointed enhancement superimposed on the negative deflection, so that at least another one damped oscillatory response with a frequency higher than 2.5 Hz is suggested as the component response.

Evoked responses caused by a photic stimulus to the eyes and/or a electric shock to the optic nerve have also been demonstrated in the suprasylvian gyrus which suggest direct or indirect geniculo-cortical projections to the suprasylvian gyrus. In addition, the evidences which indicate corticofugal fascilitory and occlusive effects of the suprasylvian gyrus upon GL have also been demonstrated. Consequently, manifold neuronal network systems may be organized between GL and SS3 to exhibit the above noted impulse responses.

The bottom tracings on the left and right in the lower panel in Fig. 1 show the cortico-cortical impulse responses of L3 and SS3 (SS3→L3 and L3→SS3) elicited by a unit impulse initiated at time origin in SS3 and L3, respectively. Cortico-cortical connections through association fibers and/or via sub-cortical structures, e.g. thalamic nuclei and reticular formation, may also be capable of organizing manifold neuronal network systems to exhibit these multiple impulses responses.
Generally, the impulse response of a physiological system obtained from an autoregressive phenomenon exhibited by the system gives the time pattern of its higher-order activity.\textsuperscript{17,19} This higher-order activity is composed of some first- and second-order component activities,\textsuperscript{20} each of which may be given by expanding it in partial fractions. As an example, the corticopetal impulse response of L3 (GL→L3), elicited by the centripetal unit impulse initiated in GL in Fig. 1, was given by the seventh-order activity, which was composed of three second- and one first-order component impulse responses, as shown in Fig. 2 and Table I.

The first- and second-order component impulse responses display
a damped exponential and a damped oscillation in their time-pattern, respectively. Each of the three second-order component impulse responses of L3 oscillated with about 3, 7, and 10 Hz damped frequencies ($f_D$ in Table I) lasting for about 2, 0.6 and 0.5 sec, respectively. The response of 3 Hz is the most predominant and forms the main pattern of the seventh-order impulse response GL→L3 and is initiated by a positive phase, while the remaining two responses are far less in size and duration, and were initiated by a negative phase, so that they are both buried in the predominant response except for the initial negative sharp deflection in the seventh-order response. The first-order component response was a negative small damped exponential lasting for about 1 sec, which was invisible in the seventh-order response.

Though each of other impulse responses, L3→GL, SS3→GL, SS3→L3, GL→SS3 and L3→SS3, displays far more complex pattern than that of GL→L3, all of them were also seventh-order ones having different values of autoregressive coefficients from those of GL→L3, so that each of them is also composed of some first- and second-order component impulse responses.

Freeman\textsuperscript{7)} classified various neural sets in the brain into three levels, which were termed KO, KI and KII sets. A KO set is the lowest level of hierarchy having a common source, a common sign of excitatory or inhibitory output without any functional interactions between neurons. A KI set is composed of two KO subsets having functional interconnection by a single excitatory or inhibitory feedback loop between them. A KII set is composed of two KI subsets having various functional feedback interactions between them. The impulse response of a KO and KI set exhibit a monotonous decay preceded by a faster rise and a very slow monotonous decay preceded by a still faster rise, respectively. Both coincide therefore with the first-order impulse response with shorter and longer time constant for the decay, respectively. The impulse response of a KII set displays a damped sine
wave, so that this agrees with a second-order impulse response.\textsuperscript{20}

Usually, an impulse response of a physiological system, e.g. an evoked potential of a brain site, etc., will be produced by delivering an impulse stimulus, e.g. an electric shock, flash, click, etc., to the system. However, such an experimental stimulus is not necessary if mono- or multivariate autoregressive analysis were applied to appropriate swaying phenomena exhibited by the physiological systems, as demonstrated here. Autoregressive and the component analyses are therefore promising for obtaining some fruitful results in physiological studies.

References