tional power of parameter selection and rapid resolution of sequential experimental questions. The operant controlled neural event, however, provides no more and possibly less information regarding the behaviors being coded than do correlative methods. The same problems of multiple determination and multiple representation of behaviors by brain events exist in the present system, with the exception that there is greater assurance that the relevant behaviors are in a steady state. The elucidation of specific behaviors or classes of behaviors related to specific neural events must await measurement of behaviors and brain events on the same time base with the same zero time and with the same resolution.

At present, it is difficult to think of behaviors which may be measured continuously with millisecond resolution in such an analog fashion. The major problem of brain-behavior relationship may now be in the measurement of behavior.

Finally, the operant controlled neural event has been demonstrated as being capable of experimentally separating functional implications of parameters and components of waves in brain. To the extent that electrophysiologists have developed hypotheses regarding microanatomical correlates of bioelectrogenesis in brain, in terms of cortical morphology or synaptic configuration or connectivity (*7*), such hypotheses should serve as a rational guide in the selection of parameters to be investigated as operant controlled neural events. To the extent that such microanatomical substrates are already understood in terms of parameters of electrical events or the reverse, the operant controlled neural event allows the determination of the relative independence of these as well as the separate and conjoint functional role of such anatomical systems in brain.

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Midbrain Single Units Correlating with Pupil Response to Light

Abstract. *The consensual response of the pupil in the cat was driven by means of a light flux impinging on the contralateral retina. Spike trains recorded extracellularly from single units in the midbrain show correlation with the concurrently recorded pupil area. The temporal dynamics found confirm two earlier studies of single-unit responses and quantitative nerve stimulation. Both of these indicate that most of the 200-millisecond transport delay resides in the neuromuscular apparatus. Neurons whose activity correlated either with constriction or with dilatation phases of change in the pupil area were observed.*

In reporting single-unit activity in the midbrain of the cat, Nisida and Okada (*1*) described an oculomotor unit with a spontaneous firing rate of 12 pulse/sec (*1*), and, Terdiman, Smith, and Stark (*2*) described a midbrain single unit with an average firing rate of 20 pulse/sec, the variations of which correlated with the dilatation phase of the pupil response to light.

In order to maintain a stable consensual (contralateral) pupil response to light the following techniques were used. Cats were first injected intraperitoneally with 20 mg per kilogram of body weight of sodium pentobarbital and were positioned in a stereotaxic frame (after the trachea and femoral vein had been cannulated). These animals were then placed in a shielded cage and were respired artificially while succinylcholine chloride (Anectine) was administered intravenously (20 mg/hour) in order to avoid any extraocular activity that might interfere with the actual recording of the pupil response. All experiments were performed with the on-line use of the IBM 1800 computer with a teletype to communicate with the computer from the remote laboratory (20 m). The desired time-varying voltages generated by the computer drove a linear light-function generator (glow modulator 1131C) (*3*). This light signal was conducted through fiber optics to the retina of the input eye where the incident light ranged from 0.001 to 10 mlu/m^2. The pupil of the input eye was completely dilated with cyclogyl (cyclopentolate hydrochloride); this resulted in an open-loop condition, that is, the iris in no way interfered with

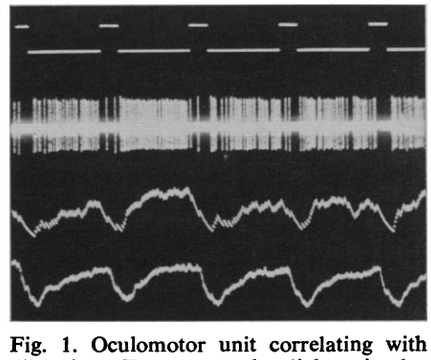

Fig. 1. Oculomotor unit correlating with dilatation. Top trace, the light stimulus changing from 0.01 to 5 mlu/m^2 for 800 msec every 4 seconds; second trace, light-off as well as spontaneous firing; third trace, these same pulses after passing through a simple model of a pupil that consists of only a low-pass filter (this allows one to predict roughly the expected response of pupil area); fourth trace, actual response of the pupil with the pupil changing (last response) from a dilated base line of 20 mm^2 to a constriction peak of 15 mm^2.

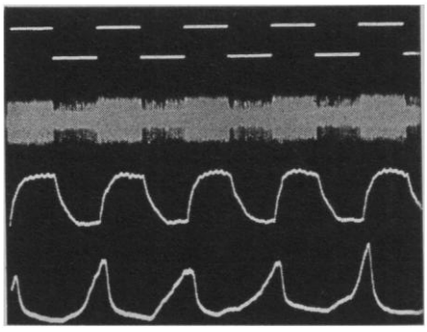

Fig. 2. Pretectal unit correlating with constriction. Same display as in Fig. 1. Time for all traces and stimulus amplitude can be calibrated by noting that the light stimulus changes from 0.001 to 1 mlu/m² for 2.5 seconds every 5 seconds. The fourth trace can be calibrated as above by noting that the last response changes from a dilated base line (really a peak) of 17 mm² to a constriction level of 10 mm².

light stimulation. The contralateral or ouptut eye was illuminated with infrared light, and a photodiode was positioned 1 cm in front of the responding pupil. The photodiode responded sensitively to variations in reflected infrared light from the iris of the output eye (*3*), and the resultant signal in pupil area was then amplified with a d-c coupled device. Electrodes of insulated (Insl-X) tungsten wire were used for extracellular recording (*4*). The electrode path was determined stereotaxically with the result that both neural and pupillary records were taken from the same side of the animal. The electrodes were advanced by means of a hydraulic system, and recording sites were coagulated with direct current. With the aid of histological verification, stimulation and recording sites were determined for 32 units in the pretectal area and for 41 units in the anterior oculomotor nucleus and oculomotor tract. Records of light flux input, pupil area, and single-unit activity were recorded on a tape recorder and on the digital computer for subsequent analysis.

Our results demonstrate that oculomotor units in the cat generate spike trains which, when integrated on a simple lag circuit, correlate with the light-driven response in pupil area and with the noise of the pupil area (noise denotes all pupil fluctuations not driven by the light stimulus). The activities of these midbrain neurons correlate with either pupillary dilatation (firing rate increases as pupil area increases) or with pupillary constriction (firing rate increases as pupil area decreases). The iris-muscle response of the pupil occurred after the nerve train with a delay of approximately 200 msecs; and direct stimulation of ciliary nerve endings also show this 200-msec delay for iris muscle (*5*). Figure 1 shows the unit activity recorded from the oculomotor nucleus. These units exhibited fairly regular spontaneous activity ranging from 8 to 20 pulse/sec. A total of eight dilatation-correlated oculomotor units were found. In three of the units found, the area adjacent to the unit was investigated by focal electrical stimulation with the same recording electrode being used. Pupil responses to electrical pulse trains (30 pulse/sec, 2 μa) were always the same as that seen during high firing rates of the particular unit during stimulation with light. Sometimes focal stimulation of the oculomotor area resulted in constriction of the pupil; no data on single units was obtained with the results of this type of stimulation. Only two questionable single units for constriction were observed at all.

Most single-unit activity recorded from the pretectal area exhibited a response pattern similar to those of the optic nerve and lateral geniculate body, namely, "on" (nine units), "off" (five units), and "on-off" (12 units) (*6*). Figure 2 shows the activity of such a unit correlated with the constriction phase of the recorded response of the pupil area.

Almost all units in the pretectal area responded to light; however, spontaneous activity from many units in the oculomotor region (approximately 31) did not appear to correlate with either the light stimulus or pupil area. These units characteristically maintained regular spontaneous activity; it is possible that they are associated with the lens accommodation system, the nictitating membrane, or even with extraocular motor neurons, all of which would presumably have no direct sensory input from the visual pathway.

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Discrimination Learning as the Summation of Excitation and Inhibition

Abstract. *Pigeons received either excitatory, inhibitory, or combined excitatory and inhibitory (intradimensional) training to discriminate line-tilt stimuli. Algebraic summation of relative-generalization gradients obtained after separate excitatory and inhibitory training sessions was used to predict characteristics of gradients after intradimensional training. The good agreement between obtained and predicted gradients provided support for gradient-interaction theory.*

After an organism learns to make a response to one value along a stimulus dimension and to withhold response to another stimulus value, the organism may then be tested with entirely new values in order to determine the stimulus properties which controlled performance on the original discrimination. Pavlov (*1*) discussed behavioral outcomes from such experiments in terms of two competing cortical processes, "excitation" produced by the association of reinforcement with the positive stimulus (S+) and "inhibition" produced by the association of nonreinforcement with the negative stimulus (S−). Pavlov's interpretation was vague and overspeculative in its accounts of brain function, but in 1937 Spence proposed a more specific and testable theory of discrimination learning by treating the concepts of excitation and inhibition in an essentially nonphysiological manner (*2*). This theory posited a summation of separate stimulus-generalization gradients of excitation