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7. The exact forms of the fitted functions were: linear, $RT = a + bM$; logarithmic, $RT = a + b\log_2 M$; exponential, $RT = a - be^{-cM}$; and bilinear, $RT = a + bM$ if $M \leq M^*$ and $RT = a + bM^* + c(M - M^*)$ if $M > M^*$, where M is the number of items in the memory list and a, b, c, and M^* represent parameters of the various functions. For the bilinear function a is the intercept and b the slope of the lower limb, M^* is the point at which the lower and upper limbs cross, and c is the slope of the upper limb.
8. The RMSD's for the other functions for experiments 1 and 2, respectively, were: logarithmic, 12 and 21 msec; exponential, 12 and 25 msec; and linear, 50 and 31 msec. Deviations from each fitted function were tested for significance by using an F test as described by D. Lewis [*Quantitative Methods in Psychology* (McGraw-Hill, New York, 1960), pp. 351-379]. Only the linear fit for experiment 1 yielded a significant deviation [$F(6, 28) = 5.42$, $P < .01$].
9. The logic of these slope and intercept tests is described by N. Draper and H. Smith [*Applied Regression Analysis* (Wiley, New York, 1966), chap. 1].
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11. See R. C. Atkinson and J. F. Juola [in *Attention and Performance IV*, S. Kornblum, Ed. (Academic Press, New York, 1973), p. 583] for an example of a model in which list length-dependent and list length-independent processes are mixed and the proportion of each determines the slope values for memory retrieval functions.
12. A detailed comparison of bilinear and logarithmic fits was made by analyzing subsets of the data. Each of the five subjects served in ten sessions for experiment 1 and five sessions for experiment 2. Breaking down the data for each subject into two blocks of five sessions for experiment 1 and a single block of five sessions for experiment 2 yielded 15 subsets of data. For each of the 15 subsets the RMSD was smaller for the bilinear than for the logarithmic function. However, the generally good fit for both functions suggests that some caution be used in asserting that the bilinear is preferable to the logarithmic fit.
13. A formal description of such a classification process is provided by information theory [see E. Edwards, *Information Transmission* (Chapman and Hall, London, 1964)]. In information theory terms, the logarithmic relationship results from a process of reducing the uncertainty in the memory list ensemble. For an example of the application of information theory concepts in the Sternberg memory retrieval task, see G. E. Briggs and J. M. Swanson [*J. Exp. Psychol.* **86**, 296 (1970)].
14. Supported by National Research Council of Canada grant A8266. We thank L. Butler for experimental assistance.

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Focal Attention in the Frog: Behavioral and Physiological Correlates

Abstract. *The prey-catching response of frogs toward small moving objects can be facilitated by small movements of the same stimulus a few seconds earlier, even though initial movements seldom trigger the feeding response. This focal attention phenomenon may be related to the observation that one class of tectal unit continues to discharge for a few seconds following a brief stimulus motion. Together with anatomical data of other investigators, results of the present study suggest that self-exciting neural loops within the tectum mediate this type of selective attention.*

Although the long-standing interest of psychologists in phenomena of selective attention has produced, within the last decade, many new experimental paradigms for human and animal subjects, neurophysiological studies have provided few insights into the underlying mechanisms of those neural filters responsible for selective attention. Among vertebrates, studies of the optic tectum have provided one model of habituation. For example, Lettvin *et al.* (*1*) first noticed that many neurons within the frog tectum habituated rapidly to repeated movements of small buglike objects. Such data seem to correlate well with the locus-specific habituation of feeding behavior by frogs and toads during repeated movements of actual prey objects (*2, 3*). In these species, habituation seems to depend upon extrinsic inhibition of tectal neurons, since appropriate thalamic lesions abolish habituation effects both in overt prey-catching (*4*) and among single tectal neurons (*5*). Habituation effects are prominent in many neurons within the tecta of mammalian species as well (*6*).

The control of visual attention, mediated in part by the optic tectum, is not limited to inhibitory phenomena, since facilitatory effects have also been described. Lettvin *et al.* (*1*) reported that certain tectal neurons in the frog could be "awakened" by one or more short movements of a small spot within the receptive field, and these neurons would continue to respond if the spot continually moved to new portions of the field. Sprague *et al.* (*7*) found that neurons within the cat's tectum could show sudden periods of facilitated response related to signs of arousal in the cortical electroencephalogram. A more definitive study of facilitatory effects on tectal neurons by Goldberg and Wurtz (*8*) relates short-term increments in neural responsiveness to the preparedness of the conscious monkey to make directed eye movements. These observations provide an important entrée into attentional mechanisms, but so far no specific neural circuitry can be identified as the basis of focal attention. The present report includes two experiments which provide further insight into the neural mechanisms of this phenomenon. The first indicates that focal attention occurs during the frog's feeding behavior, and the second reveals a new class of unit in the frog's optic tectum, whose discharge pattern suggests a specific neural model of focal attention.

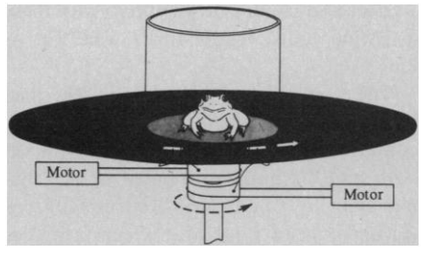

Fig. 1. Apparatus used to study snapping frequency toward dummy prey stimuli. Each yellow wormlike object was independently moved through a short arc when a single pulse activated the corresponding motor. The frog, confined by a transparent cylinder, remains at a nearly constant distance from the stimuli during a series of trials.

My initial observation of attentional effects in the frog's feeding behavior came from tests in which two small prey-objects were manually moved in synchrony 2 to 3 seconds after one object had moved slightly. In this experiment ten frogs directed 85 of 100 snaps toward the stimulus that had moved first, although the initial motion was too small to elicit a snap. In order to gain objective control over these stimuli, I adapted the test method of Ewert (*3, 4*) (see Fig. 1). The 2-cm-long wormlike stimuli were moved by means of motors that were activated by pulses from Textronix pulse and waveform generators. Since frogs were selected for persistent feeding behavior, motions of less than 0.5 second in duration were required to maintain a low frequency of snaps at the initial motion. In the first paradigm, ten frogs (7 to 8 cm long) were tested for snapping responses toward a single object moving for only 0.3 second through a 5° excursion. This motion was then repeated after a 3.2-second delay. During 100 test trials, these frogs snapped at the initial stimulus motion only eight times, but 75 out of 100 times at second motions. That frogs can be alerted by such a brief motion is obviously adaptive for feeding on insects or worms that move discontinuously.

In order to decide whether the facilitatory effect of prior stimulus motion was a generalized arousal effect or whether it was limited to a spatial locus near the first motion, I repeated the test paradigm five times with the same ten frogs, but interspersed five trials with a new double-stimulus paradigm. In the second case, two prey stimuli were set 30° to 40° apart, and the frog was induced to orient the head directly toward a hand-held stimulus, set momentarily between the test objects. After a 10-second pause one stimulus moved

as usual for 0.3 second, and after the 3.2-second pause the second stimulus moved in the same direction for the same 0.3-second duration. I again observed an increase in snap frequency from 12 to 86 percent for successive movements of one object. However, when the double-stimulus paradigm was used, the snapping rates were 12 and 10 percent, respectively. From these data I conclude that the facilitation effect is absent when the second stimulus is more than 30° distant from the first.

This focal attention effect may be related to my previous observation (*5*) that tectal neuron discharge in frogs disinhibited by thalamic lesions could sometimes be escalated by two or three successive motions of a buglike stimulus within the receptive field of that unit. Since these facilitatory effects can be unmasked either by thalamic lesions or by topic application of 0.5 percent curare (*9*), I have made additional recordings in the tecta of frogs disinhibited by both of these means. Using tungsten microelectrodes, I found a previously unreported class of units within the most superficial 200 μm of the tectal neuropil whose properties seemed to be related to the focal attention phenomenon. These "attention units" were found in every tectal penetration in each of 20 disinhibited frogs, but they were noticed only occasionally in seven normal frogs. Attention units were activated consistently only by small black spots, less than 10° wide, when these spots were moved within the same region in which receptive fields of simultaneously recorded retinal class 2 ("bug-detector") units were found. All attention units could easily be distinguished from retinal axons because they always gave a delayed discharge following a brief in-out movement (Fig. 2), whereas retinal unit discharge stopped abruptly as the stimulus left the receptive field. In the 19 attention units whose spike height was larger than that of any retinal fiber (Fig. 2C), one could see that the response began only after the stimulus had left the field. Since these attention units could also be activated by leaving the spot within the receptive field, the stimulus withdrawal was not a required feature. In most cases, the large signals from retinal units masked a possible initial response of attention units.

In order to study attention units in a quantitative manner, I used as a stimulus a 2° black square fixed to a white background, which was moved behind a window by an X-Y recorder. Each in-out motion was triggered by a 0.5-second square wave input delivered each 60 seconds to the recorder, and unit discharge was converted into pulses, by the oscilloscope's internal trigger mechanism, for storage and summation by a Fabritek instrument computer. From more than 100 identifiable attention units, post-stimulus histograms were summed from at least four repeated trials. From this array of data, I distinguish two unit types: (i) those giving a slow steady discharge for 3 to 6 seconds after a delay of 1 or 2 seconds (Fig. 2A) and (ii) those responding with a short delayed burst, as in Fig. 2B. Histograms of 15 units in the latter group showed reliable peaks of discharge which always occurred at 3 or 4 seconds after the stimulus had left the field (Fig. 2D). No obvious differences were found in units recorded in frogs disinhibited by surgical or by drug methods. However, the 15 attention units that I examined in normal frogs did show more rapid habituation than those in disinhibited animals—a result similar to that found earlier during recordings of newness neurons at a deeper tectal level (*5*). However, newness neurons typically had receptive fields of at least 20° in the disinhibited tectum and cannot be identified with these attention units, whose fields were 10° or less.

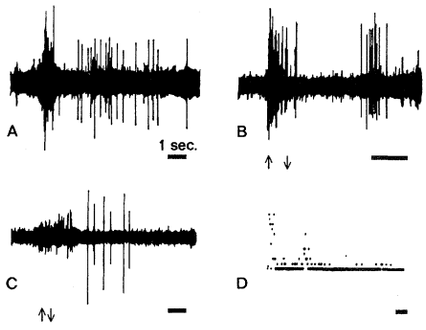

Fig. 2. (A) A brief class 2 burst followed by a 6-second discharge of an attention unit. (B) One of the few attention units that discharged during the stimulus entry, and again with a delay. (C) One of 19 cases where the class 2 discharge was so low that one could see only a delayed response from the attention units. (D) Post-stimulus histogram of one attention unit showing a delayed peak at 3 to 4 seconds. The first peak reflects the sudden discharge of class 2 fibers.

The attention units that I have described have three important characteristics in common with focal attention behavior: (i) both unit discharge and behavior are elicited only by small prey-sized moving objects; (ii) behavioral aftereffects are spatially restricted, while attention units have small receptive fields; and (iii) both behavioral and physiological phenomena are manifest a few seconds after the priming event. In fact, the occurrence of a 3- to 4-second peak discharge among some attention units coincides with earlier evidence (*10*) that delayed snapping responses by toads toward stationary stimuli are most likely to occur at 3 or 4 seconds after cessation of movement. Taken together, these coincidences suggest (but do not prove) that those tectal efferent neurons that trigger prey-catching behavior are primed by tectal events following a brief motion so that their threshold remains lowered, for at least a few seconds, to stimuli within a specific portion of the visual field. Although simultaneous recording of unit discharge and overt orientation are needed to prove the hypothesis for the frog, the events described in this report do resemble focal facilitation phenomena observed in the monkey tectum (*8*).

The frog's tectum may prove a useful model for detailed analysis of focal attention phenomena, since it appears simpler in architectonic design than the mammalian tectum (*11*) and since it functions without direct extrinsic input from the telencephalon (*12*), as does its mammalian homolog. Because the rather frequently recorded attention units are located within the nearly cell-free neuropil, they are probably axon terminals from either extrinsic or intrinsic neurons. The known thalamotectal input (*13*) is not a likely candidate since attention units are actually unmasked by large caudal thalamic lesions. However, intrinsic axons arising from deeper tectal neurons (*14*) are plentiful and seem the most likely source of the attention units.

As yet, there is insufficient data available on response properties of deeper tectal neurons to either confirm or reject this hypothesis. However, Szekely (*14*) has suggested, on the basis of Golgi and electron-microscopic analysis of the frog tectal neuropil, that the termination of intrinsic axons upon apical dendrites could provide the basis for reexciting circuits within the tectum. If such recurrent axons lowered the dendritic threshold for subsequent retinal input, our behavioral observations might be predicted. According to this model, reexciting circuits are partly held in check by tonic inhibitory input from thalamic neurons (*5*) and would discharge with seizure-like intensity only when the inhibitory influence is surgically (*5*) or chemically (*8*) removed. Further analysis of such circuitry may be of value in understanding recurrent axon function in other brain structures, such as the mammalian neocortex, where more subtle attentional effects are thought to occur during perceptual activity.

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Neuromimes: Self-Exciting Alternate Firing Pattern Models

Perkel and Mulloney (*1*) described an elegant model for production of alternating bursts of impulses in a neuronal network. Models of circuits producing alternate single impulses go back to McDougall (*2*), who proposed separate continuous inputs to two neurons which mutually inhibit each other. Later, Reiss (*3*) reintroduced McDougall's ideas and modified his model to a reciprocally inhibiting pair of neurons driven by a common, constant frequency source. Using electronic neuron models similar to Harmon's (*4*) with a few modifications, we designed and tested three circuits exhibiting alternate firing patterns (*5*). Our purpose was (i) to arrive at a simple scheme that will simulate alternate firing and (ii), as suggested by Perkel and Mulloney (*1*), to create a self-exciting circuit. Our circuits represented one, two, and three neurons, and all but the one-neuron model can be triggered by a single pulse, whereupon the systems become self-perpetuating.

Figure 1a shows the output pattern of a self-exciting, three-neuron network. A single pulse input (Fig. 1a, top trace) to any one of the three neurons will trigger the system. Essentially the same network in the non-self-exciting mode was proposed by Wilson (*6*) to explain motor neuron function in flight, and was later modeled by Harmon (*7*). The output of neurons 2 and 3 in Fig. 1a can be varied to give alternating bursts of various durations and pulse numbers by adjustment of synaptic input rise and decay times.

This network can be simplified for a two-neuron model (Fig. 1b). The two neurons are linked by mutual excitation and inhibition inputs. Adjustment of the characteristics of each pair of synapses impinging on one neuron produces an alternating burst output, as shown in the two upper traces of Fig. 1b. The inhibitory synaptic inputs to neurons 1 and 2 are shown in the lower two traces of Fig. 1b. To get an alternating output, the inhibitory input of neuron 1 must be in phase with the excitatory input of neuron 2, while the two inputs to any one neuron must have a phase shift between them. Duration of bursts and degree of overlap of the output of the two neurons will depend on the phase shift between the inputs to each neuron. This model is very similar to the one proposed by Perkel and Mulloney (*1*). However, whereas their model is based on the postinhibitory rebound phenomenon, ours incorporates a biphasic (inhibitory-excitatory) synaptic input.

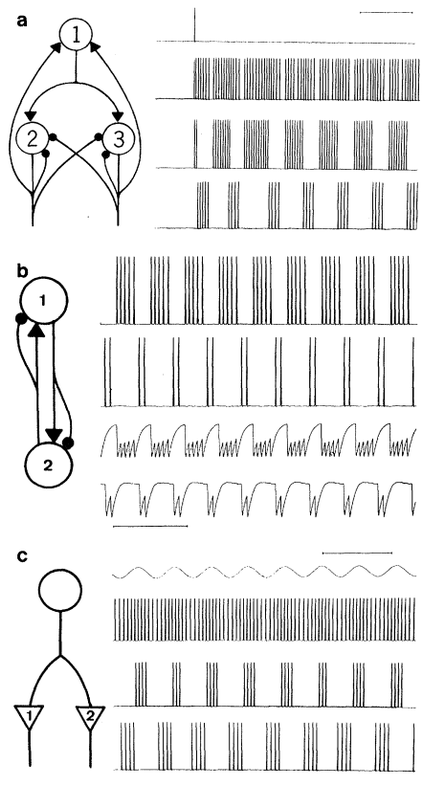

Fig. 1. Neuron schemes and alternate output patterns; solid circles depict inhibitory inputs, solid triangles excitatory inputs. Calibration bar, 300 msec. (a) Three-neuron model is triggered by single pulse (top trace) to any of the neurons 1, 2, or 3. Activity of neuron 1 is shown in second trace from top. Alternate firing of neurons 2 and 3 is shown in the bottom two traces. (b) Two-neuron model showing alternate firing (top two traces). Bottom two traces show inhibitory synaptic inputs to neurons 1 (bottom trace) and 2 (second trace from bottom). (c) Single-neuron scheme with branching axon. Top trace shows d-c analog of the cell body's firing frequency; second trace shows the exponential firing of the soma. Triangles 1 and 2 are frequency band-pass filters. The alternating outputs of the axon branches are shown in the bottom two traces.

The scheme in Fig. 1c depicts a hypothetical neuron with two branches. Each branch is shown with a band-pass filter—a low-pass filter on the left and a high-pass filter on the right. Thus, the soma of a neuron which generates a sinusoidal frequency pattern (*8*) will show alternating bursts of spikes as an output of its two branches. The branch with the low-pass filter will pass the initial part of the sinusoidal burst cycle and then will reach its cutoff point, while the branch with the high-pass filter will pass the remaining high-frequency part of the cycle. The driving frequency can be varied to produce bursts of various durations, while the degree of burst overlap or delay between alternate bursts may be adjusted by the filter bandwidth Q factor. Although this single-neuron model is hypothetical, different outputs from branches of one neuron have been described (*9*). This one-neuron scheme may be incorporated into the previous models to generate a self-exciting system, in agreement with Perkel and Mulloney's (*1*) proposal for systems without tonic driving inputs.

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5. The following modifications were made in this study. (i) Inhibitory input to the neuromime was connected via a negative-positive-negative transistor. (ii) Synaptic inputs were fed through resistance-capacitance networks with adjustable rise and decay times. Three types of synapses were used: two with a rise time of 0 to 2 msec and a decay of 25 to 500 msec, and a shorter-duration one with a rise time of 0 to 1 msec and a decay of 2 to 100 msec. (iii) A high input impedance to synaptic inputs was found desirable in limiting the load on neuromimes when several synapses were used. Outputs of neuromimes into synapses were recorded on magnetic tape and played back at a reduced speed to enable display on a paper recorder.
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