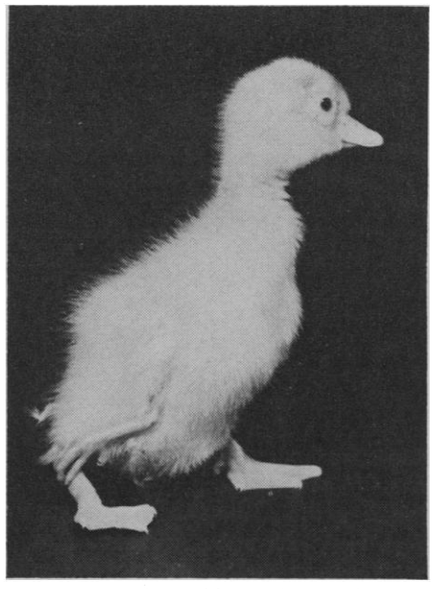

Fig. 2. A White Pekin duckling which as an embryo received a leg bud transplant from a White Leghorn embryo to its wing site. The duckling has now become a mature drake and has retained the transplant.

bryo. The duckling which hatched is shown in Fig. 2. The transplanted leg is rather loosely attached and nonfunctional. Nevertheless, the bird is now a mature male and the transplant is still maintained. In part 4 of Fig. 1, a Khaki Campbell duckling is shown. As an embryo it received a wing bud from a White Leghorn embryo to the site left by the removal of its own wing bud. This transplanted bud became the right wing of the duckling. In this case the color of the host prevailed in the feathers of the transplant but the fast feathering phenotype of the White Leghorn is evident. This wing was reasonably functional. However, when the duckling reached the age of 6 weeks the transplant started to disintegrate and in a short time was completely eliminated as a leathery piece of tissue with attached feathers.

In part 5 of Fig. 1 a White Leghorn chick which as an embryo received a wing bud from a Japanese Quail embryo is shown. This transplant was functional but survived for only 5 weeks. In part 6 of Fig. 1 a turkey poult of a white variety is shown. As an embryo it received a wing bud transplant from a Brown Leghorn embryo. Unfortunately, this poult died at 4 weeks of age but had retained the transplant to that time.

We seem to have little trouble with the retention of transplants between birds of different varieties within domestic chickens (*Gallus domesticus*) where the birds have received early conditioning to the donor antigens either by parabiosis or by embryonic transplants. In the case of transplants between species of birds it is indeed frustrating to see transplants which appear perfect in attachment and condition finally disintegrate and die after a few weeks. One can only speculate as to the reason. Does some slight antibody formation develop even when the antibody system is passive and then become more pronounced as the system becomes more active? This is only one of a number of questions which reasonably might be asked concerning this behavior. However, the fact remains that occasionally transplants to a host from a donor of another species will be tolerated until the host reaches maturity.

A case in point is the now mature Pekin drake shown in Fig. 2, which still retains a White Leghorn transplant. To our knowledge this represents the most diverse tissue ever tolerated for so long a time in a warm-blooded animal. It is true that the cheek pouch lining of the hamster will accept and nourish very diverse tissue (*6*). Here it appears that the lining of the pouch acts as a unidirectional barrier, screening the antigens from the antibody system, yet allowing nutrients to pass through from the host to nourish the donor tissue. In a sense no true tolerance develops. This is indicated by the fact that if some duplicate donor tissue is placed in another location on the body of the hamster, that transplant will be sloughed and that on the pouch lining will be sloughed as well (*7*).

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Unit Responses in the Frog's Tectum to Moving and Nonmoving Visual Stimuli

Abstract. *"Movement-detecting" units that respond little or not at all to illumination without movement, respond well to change in position under stroboscopic light even when relatively large jumps in the visual field occur during a dark pause between two flashes. The threshold angle and angular velocity are different for different classes of units. They are higher for the periphery of the receptive field and increase with decreasing contrast. An inhibitory effect of a large surrounding of the receptive field could be demonstrated in class-2 neurons.*

Various workers (*1*) have described single neurons in the frog's optic nerve which respond to moving visual stimuli but little or not at all to nonmoving stimuli. The present investigation confirms and adds quantitative information on this "movement-detection" and shows it to be actually "change-of-position-detection."

By means of metal-filled micropipettes 1 to 3 μ in diameter (*2*) the spike activity of single axons in the stratum superficiale of the optic tectum was recorded in *Rana pipiens*. The curarized and fixed animals looked through a window at the visual stimuli 24 cm away, carried on a specially constructed perimeter. The stimulus pattern could be moved by a mechanical stage and the movement recorded by means of a potentiometer circuit on one beam of the oscilloscope. The stimuli were large cards bearing spots, stripes, and so forth, illuminated diffusely, or a spot of light 0.2° to 2° in diameter, provided by an assembly of bulb, lenses, and shutter mounted on the perimeter. By the use of stimulating patterns comparable to those of Maturana *et al.* (see *1*) the four classes of units of these authors could be confirmed, as well as some other types not discussed here which were probably tectofugal fibers. The more quantitative stimulation technique gave additional information about these classes.

Class-1 responses (called by Maturana *et al.* "sustained edge detection") are obtained immediately below the tectal surface and are strongest to moving dark spots on a white background. Neurons of this class show no response to diffuse uniform illumination

or darkening. We find in all cases that a small spot of light in the receptive field (defined as the field from which active discharge can be obtained) elicits response, predominantly of the "on" type. The receptive field is 2° to 4°, often oval.

No inhibitory zone surrounding the excitatory field could be detected with the single light spot technique. The degree of activation by moving dark spots is smaller, the lower the contrast between spot and uniform background (tested with spots of different grays on white or darker or brighter gray backgrounds). Within the photopic range, change of the general illumination has no effect or only a very small effect on the response of the neurons to moving spots. A spot that is moved into the receptive field and stopped elicits a relatively long-lasting firing, in accordance with the findings of Maturana *et al.* The minimal angle (α) of displacement which elicited a response was 0.03° to 0.05°; the minimal angular velocity (A) necessary to elicit a response with a movement of 0.2° was 0.2° to 1°/sec^{-1}. Both of these thresholds apply to the center of the receptive field and are higher in the periphery and with reduced contrast. Patterns larger than the receptive field have a markedly increased threshold. The maximal velocity which elicited a response from a small (1° to 2°) spot moved through the receptive field was 15° to 25°/sec^{-1}.

Class-2 neurons (called "convex edge detectors" by Maturana *et al.*) are similar in many ways (Fig. 1), and most sensitive to small dark spots moving on a white background. They do not respond to diffuse illumination. As in class 1, punctiform light stimuli within the receptive field (2° to 5°) elicit a response, but chiefly "on-off" after a dark period and chiefly of the "off" type after several flashes. Again no special and constant construction of the receptive field, with respect to inhibitory or excitatory zones as described by Kuffler (*3*) in the cat's retina, could be found. Small spots moved into the visual field elicit a longer-lasting activation, which is erased by darkening and, as a rule, in most of the neurons this activation does not reappear after reillumination, in contrast to the case with class 1. Moving white spots on a black background elicited a response in all investigated neurons of this class too, but a significantly smaller response than a black spot on a white background. α was 0.05° to 0.1° for the center of the receptive field; A was 0.2° to 1°/sec^{-1}. If there is contrast in the receptive field, some of the units respond to general change of illumination with a short burst of discharges, but some do not. The response to moving stimuli is very feeble if the size of the smooth contoured stimulating object is larger than the receptive field of the unit; a smooth border between a large white and a large dark field causes almost no response when moved across the receptive field. A single straight movement within the field gives less response than the sum of the responses to two successive movements each a half of the first movement (if the angular velocity is larger than 2A). The maximal angular velocity which elicited a response from a small spot moved through the receptive field was 20° to 30°/sec^{-1}.

Class-3 neurons are the "on-off" units of Hartline (see *1*), called "changing contrast detectors" by Maturana *et al.* Diffuse illumination of the receptive field and its surrounding, as well as partial illumination of the receptive field by means of small light spots, elicited a short burst of discharges at "on" and "off." The size of the receptive field was 5° to 9°. Small light spots, projected to most parts of the receptive field, elicit an on-off response; in other words, in these units too, no special construction of the receptive field could be detected by means of this method. α and A were significantly higher than for classes 1 and 2: α was between 0.12° and 0.25° for the center of the field, while A varied between 2° and 4°/sec^{-1}. The highest angular velocity of a moving small spot which elicited a response was between 50° and 70°/sec^{-1}. All three preceding classes adapt rapidly to repetition of a given movement but are re-excited by a new movement in another part of the receptive field.

Class-4 neurons are the "off" units of Hartline, the "dimming detectors" of Maturana *et al.* Their fibers are localized in the deepest layer of the stratum superficiale of the tectum. In the same layer recordings of single

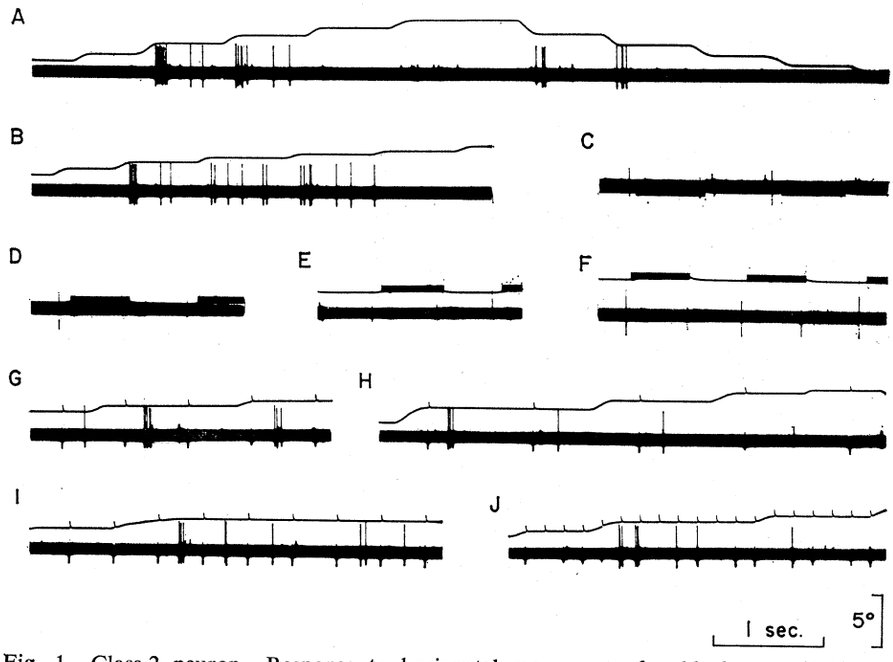

Fig. 1. Class-2 neuron. Response to horizontal movement of a black spot (1.2° in diameter; white background; illumination 2.5 ft-ca) through the center of the receptive field. One channel of the oscilloscope marks the movement of the stimulus; upward = toward left. (*A*) Movement through the receptive field from left to right and back. The activation of the unit is different for the two directions. (*B*) A smaller angular velocity and size of the small movements influence the discharge rate and discharge pattern. (*C–F*) Illumination (black bars) with the spot in different positions, whether inside or outside the receptive field, elicits no response of the unit. (Apparent spikes are artifacts.) (*G–J*) Movement of the spot during stroboscopic illumination with flashes of different frequency; flash duration less than 10 μsec. A response of the unit is elicited whether illumination occurs during the periods of movement or not. This example shows that "change in position" is the true exciting stimulus for this unit.

nerve cell somata could be obtained. Class-4 units have large receptive fields (15° or more) and small moving stimuli elicit no response or only a weak response. Values for α are 3° to 5° with a dark spot of 1° to 3°; A is about $10°/sec^{-1}$. Very effective stimuli for these neurons are large dark objects or shadows moving rapidly through the receptive field.

To test the possibility that, not movement itself, but successive positions stimulate the "movement" detectors, short flashes (<10 μsec) of light were used as the only illumination. The brief duration guaranteed that virtually no image movement occurred during illumination of the moving spot. With low flash frequency the movement of the spot could be completed during the interval between two flashes (Fig. 1). All neurons investigated of classes 1 to 3 respond under these conditions to "movement" of small dark or white spots within the receptive field. Furthermore, the discharges during the activation period after change of position within the receptive field (object stationary) are grouped in the rhythm of the light flashes, if the flash frequency was not higher than 10 to 15 flashes per second. These results indicate that change of position within the receptive field is the "true" stimulus, which is, of course, under normal conditions, identical with movement within the receptive field. However, there was a maximum time interval for this response to change in position; values depend on other parameters but flashes can be at least 1 second apart. Because large jumps during the interval between two flashes (so long as they are within the receptive field) still elicit a response, the change in position necessary to elicit a "movement" response can be said not to require the successive activation of neighboring or adjacent-but-one receptors.

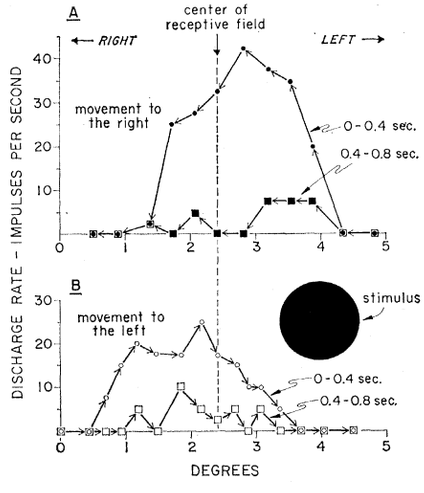

Fig. 2. Class-2 neuron. Horizontal movement of a black spot (1.2° in diameter, white background, 2.5 ft-ca illumination) through the center of the receptive field, at an average angular velocity of $3.5°/sec^{-1}$. (Threshold of response in the center of the field = $0.1°/sec^{-1}$.) (*A*) Movement of the spot toward the right. Ordinate: discharge rate (per second) during the first 0.4 second and the second 0.4 second after the beginning of the single movements. The difference between the two values shows the relatively fast adaptation of the response. Abscissa: Position of the stimulus in degrees. The arrows indicate the direction of the movement. (*B*) Same stimulus. Now movement to the left. An axis is drawn through the geometric field center. *A* compared with *B* shows that the response to an object moved through the receptive field may be different for different directions and is larger with centripetal stimuli than with centrifugal ones. The vertical extent of the receptive field was for this neuron 5.1°.

With respect to direction sensitivity, only one rule could be found in all neurons investigated of classes 1 to 3: centripetal stimuli, that is, spots moved toward the center of the field, were more effective than centrifugal stimuli. Sometimes movement in one direction, for example, to the left or upwards, was consistently more effective than the opposite, for example, to the right or downwards (Fig. 2). But no neuron was found similar to those described in the rabbit retina by Barlow and Hill (*4*), which responded to movement in one direction and not to movement in the other under "symmetrical" stimulus conditions. However, if black and white half-fields, with a vertical border, are moved horizontally through the receptive field, the neurons of class 1, 3, or 4 often respond only to movement in one direction. In these cases the asymmetry clearly was introduced by the stimulus.

The well-known negative correlation between discharge rate and latency of response to stationary visual stimuli (*5*), is also found for the response to moving stimuli. The latency of the response under the same conditions was higher if a spot was moved in the periphery of the receptive field than if it was moved with the same angular velocity in the center of the field. The latency was within certain ranges shorter, the higher the angular velocity of the stimulus. Class-3 units, as a consequence of the larger minimal angle and the higher threshold (A), have a longer latency to relatively slow movements than classes 1 and 2, but not to fast movement.

Stimuli outside of the receptive field can exert effects (though a single nonmoving light spot does not). For class-2 and class-3 neurons, certain patterns moved outside of the receptive field have an inhibitory influence, that is, decrease the discharge rate elicited by a spot moved in the receptive field. This inhibitory effect is detectable whether the movement of the surround is the same as the movement of the spot in the field or is different in direction or velocity. The visual pattern and the direction of movement of the surround determine the amount of inhibitory influence.

The responses of the class-1, -2, and -3 neurons cannot be explained with the "classical" excitatory and inhibitory zones, even if some kind of asymmetry in the receptive field is assumed. However, if it is assumed that there are in the bipolar layer of the frog's retina on-neurons with an excitatory center and an inhibitory receptive field periphery and off-neurons with an excitatory surrounding and an inhibitory receptive field center, a simple explanation in terms of different convergence may be possible for the neurons of classes 1 to 3. This will be fully developed in another place (*6*).

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