CENTRO ACCADEMICO CANADESE IN ITALIA

McLUHAN E LA METAMORFOSI DELL'UOMO

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A cura di

DERRICK DE KERCKHOVE E AMILCARE A. IANNUCCI

what made review of the experimental results on the orienting reaction so interesting. If one reads only for *words* such as arousal, attention and memory, one misses the intimate and intricate relationship between them which has been *demonstrated* by the experiments and makes up the *language* of science. And what is even more important, one misses the feel and fun that science can be, the fun currently provided in such large measure by the sciences of mind.

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SEX, SYMBOLS, AND SENSATION

McLuhan's central thesis, that the mode of our sensory experience dramatically alters the way in which we construe the world, relates to the age old debate between tabula rasa theorists and the social Darwinists, who held that biology is destiny. Few people today would confess to either of these extreme views, and most would claim that they hold an « interactionist position ». However, this is not so much a solution as a retreat from the problem. The moment scientists attempt to go beyond interactionism, they are faced with their inherent predisposition to either biological or environmental determinism. McLuhan's argument puts us squarely on the fence, despite the innocence of his more subtle question of whether the 'form' of the message (the sensory experience) can modify cognitive appraisal. If we accept his argument then we must confront the obvious next step and ask the question: How would this be accomplished? In terms of brain systems, where these events are taking place, there are two possible scenarios.

The first is that different sensory inputs prime different higher order (cognitive systems) and *temporarily* create specific kinds of neural organization. This would be similar to the behavioral analogue of reading a newspaper, and subsequently 'seeing' the identical information on a television program. One could therefore exist in a 'reading mode' or alternatively in a 'television mode', and only be changed in the short term by these experiences. The second scenario has much more serious implications. In this case one might expect to find *permanent* changes in neural organization based on the nature of the sensory or

in tests measuring pitch discrimination when the years of musical training are taken into consideration.

These findings help to explain why studies on human infants have shown that females are much more likely to be comforted by the sound of their mother's voice, whereas males are much more likely to need physical reassurance. This allows the mother to be able to deal with her female infant at a distance (distal stimulation). Over time a greater vocal interaction takes place between mothers and daughters than between mothers and sons. This occurs also because the female responds to the inflection in her mother's voice, long before the actual understanding of speech has begun (Lewis, 1972).

By contrast, males develop a much greater ability to respond to visual detail, showing higher visual acuity from the earliest age this has been investigated, which is about 5 years of age. Males are also more sensitive to luminance, showing *less* tolerance of bright lights, exactly the opposite to the result of loudness tolerance.

Apart from these primary sensory differences, more noticeable differences in motor behavior have been observed. During childhood males participate in a type of whole body play called 'rough and tumble play', a self explanatory term. Throughout this period they develop greater strength, agility, and accuracy in visually guided movement. In mid-childhood their reaction time begins to improve relative to females, and by the middle teen years accelerates to a constant 50 milliseconds faster. The females by contrast develop greater skill in employing the fine motor systems, those systems which require the sequential fluency of action. They show an advantage in digital coordination, and coordination of speech mechanisms. Males are considerably more likely to demonstrate noticeable speech defects and monotonism, the inability to sing in tune.

During the early years, the sensory and motor systems begin to integrate into modes of ideation which Piaget has termed 'schemas'. His theory that sensory-motor schemas provide the transform operations essential for subsequent cognitive development has been borne out in a number of recent studies. Most impressive support for his formulation has been provided by research on reading failure, where it has been discovered that

the missing ingredient in the skills of poor readers is the failure to integrate phonemic analysis with the feedback from articulation. When this integration is trained, the reading problems disappear (see McGuinness, 1982).

Males, who have greater facility with gross motor skills, learn to combine this with their efficient visual ability into visuo-motor schemas. This, it appears, has considerable benefit for the cognitive skills essential to imagery of object relations and three-dimensional space, the very aptitudes that are important to higher mathematics, most especially geometry. On the other hand, females are more likely to show facility in integrating fine-motor systems with the auditory senses, which accounts for the fact that they show greater precocity in language development, and more advanced verbal skills at all ages, including elderly populations.

One of the more striking differences between the sexes is the consistent finding that males are more object oriented and females more person oriented. Goodenough in 1957 discovered that if you ask young children to tell a story based on an abstract visual pattern, the girls' stories all contain people, whereas this is far less likely in the boys' stories. Also, when asked to draw pictures based on a story, the girls' pictures contain people and the boys' generally do not. In one of my own experiments we asked college students to look at a screen where they saw two images, one which contained people and one which contained a common inanimate object such as a wrist watch, or automobile. The visual field was divided so that one image was presented to one eye, and the other image to the other eye. This has the effect of producing 'rivalry' where the most salient or interesting item dominates, and the brain actually suppresses the other image, an effect called « binocular rivalry ». The results of our study showed that women reported seeing people more than the males, and reported seeing people more than objects. The exaot reverse pattern was found for the men. The greater sensitivity to persons results in the finding that females are consistently more accurate in determining the meaning of facial expressions and other non-verbal signals.

It is not understood how this object/person difference arises, although it is obvious that the differences are in the appropriate

direction biologically. It is possible that the greater sensitivity of the female to speech sounds and prosodics leads to a greater interest in persons, but also possible that an interest in persons leads to greater attention to speech sounds and facial expression. However, it is not at all apparent why an organism would develop a preference for objects instead of species' members, a question which has puzzled me and my students for several years!

Functional Language Use in Men and Women

In the evolution of the human social organization, one of the primary adaptations that distinguished us from our ape cousins, was the capacity to *share*. A sharing community promotes an entirely different psychological awareness as well as a unique social organization. Some of the primary differences in human social behavior are set out below:

1. Sex role division of labor.
2. An 'economy' where work is shared and goods are transferred.
3. Sanctions, rewards and punishments leading to new concepts, such as generosity, greed, fairness and pride.
4. The evolution of complex social systems in all situations where sharing is difficult, especially where there is durable surplus.
5. A clear demarcation between 'self' and 'other'.
6. A system of signs to facilitate the above.

Thus I would conclude that the function of language is to facilitate sharing, and for this reason it has survival value. The question of interest here is: What kind of language user develops from a sex role division of labor? And further, given the findings on human sex differences outlined above, how might this knowledge help answer this question?

For whatever reason, males' superior strength was put to use in developing tools and weapons, for use in hunting and warfare. The fascination of males with objects may be part of a long

selection process for the visuo-motor expertise required in these endeavors. How then would a tool user and a competitive warrior and hunter use language? As males are attracted by objects, rather than people, the key lies in what can be done with objects. By and large they can be manipulated, assembled, analyzed, dissected and used. An object orientation leads to a language bias which has certain definable properties.

First it is essentially nominal and biased to semantics. In this approach, naming becomes embedded in « things ». This can be carried to extremes, as Cassirer has pointed out, where in ritual and magic, the name actually becomes what is named. The two are interchangeable. Secondly, nominalization tends to be context free. A rose is a rose is a rose, wherever and whenever it is found. Thirdly, this leads to a form of pragmatics in which *function* is the defining criterion. Language is important for what it will *do*. Language can be used to manipulate others and for exercising a common purpose. And for the same reason it is adopted in the service of dominance and dominance rituals. Fourthly, the same tendency that is used to analyze and dissect the world, when encorporated in language leads to taxonomies, and ultimately to classificatory schemes that have the secondary consequence of promoting rule-based and rigid systems. Such systems are hierarchical, and as has been noted by Eco and others, hierarchical systems are closed systems which lack flexibility. Lastly, meaning becomes definitional, and is considered to reside *IN* language, in the word itself.

There are of course many advantages as well as disadvantages in this approach to language use. Some of the advantages are precision, classificatory schemes essential to scientific thought, dictionaries, and so forth. The disadvantages, other than those alluded to already, are rigidity, dogmatism, and an insensitivity to context. This is especially relevant in interpersonal relationship, where context is of paramount importance in perceiving intent.

In a creature more disposed towards the world of persons, language comes to serve an empathetic function. This emphasis creates a pragmatic rather than semantic focus. But unlike a pragmatics directed towards the world of action, pragmatics here refers much more to the nature of determining other's

needs. Thus there is closer attention to the assessment or analysis of intentions, determining whether the utterance can be trusted, whether or not the person is *sincere*. Secondly an empathetic language system is particularly context sensitive rather than context free. Thirdly, females are particularly good listeners; there is an intensity in receptive encoding, which monitors not only prosodics, but non-verbal cues. Thus all social signals become incorporated in the analysis. Finally, and perhaps most interesting, is that for females *meaning* is almost entirely independent of language. Meaning deals with intentions and feelings, and language is merely one of a number of devices that enables people to approximate meaning. Women rarely define words; they are much more likely to rephrase an utterance using different words to find a closer approximation to what they 'mean to say'.

The advantages in this approach to language are the opposite to those cited above. Women *communicate*. They are accurate in decoding social signals and can generate effective behavior with respect to the needs and intentions of others. They also show an extreme facility in fluent encoding and speech production. But they also pay an emotional price, in that they are more likely to be oversensitive, to assume guilt or feel overly responsible for other people's needs and feelings.

How these findings might be applied to the impact of the media on these sex specific aptitudes can only be conjectured. Olson's results reported in this volume indicate that the effect of the written word on young children is to make them overly responsive to the superficial structure of the expression, as he describes it: sticking to the letter of the text, rather than seeing 'through' the text to the meaning. It has been securely established that men invented writing systems, in much the same way that they are currently inventing computer languages. In early societies such as Sumer, where writing was invented, the schools were filled entirely with males. Ironically, despite over 4,000 years of deprivation, females learn to read and write with considerable ease and it is the males who have problems. Despite the fact that as Olson observes: « writing breaks down the contextual world », females are not only better writers but *less* susceptible to the destruction of context.

This brings us full circle to our original problem. In a constant environment males and females are found to exhibit very different sorts of sensory-motor skills and cognitive aptitudes, a *biologically* determined effect. But it appears that the skills that are *least* supported by biology are *most* affected by the environment, whereas as those aptitudes with the greater biological underpinning are most resistant to adverse effects of experience. This means that the specific characteristics of innate sensory biases will interact with the form of the sensory experience. A clue to the nature of this interactive dynamic is related to the amount of *difficulty* encountered in coping with new cognitive demands. For example, males who for whatever reason have poorer language skills, but better visual skills, will be less attentive to the verbal or auditory components of messages, and more reliant on the visual component. This predicts that they will be slow to master a phonetic alphabet and be overly distracted by the visual appearance of the letters, exactly what is found. It would also predict that when viewing TV, males will respond maximally to the visual information but minimally to the auditory information. This same prediction would not hold for women, because one of the skills they demonstrate is the effective integration of auditory and visual codes.

It seems that a good deal of careful study is required to determine just how the various media influence cognitive processing, and it is clear that it will make a considerable difference whether the subject is male or female.

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SOGNO E METAMORFOSI DELL'UOMO

In che modo una riflessione sul sogno può avere accesso e contribuire positivamente ad un dibattito, ispirato del pensiero di McLuhan, sulla metamorfosi dell'uomo?

Il passaggio ad un'epoca post-industriale guidata dalla « razionalità » dell'elettronica, sembrerebbe ben estraneo a quel mondo bizzarro ed irrazionale con cui siamo soliti identificare il fenomeno onirico.

Ma « sogno » e « razionalità » appaiono oggi in una veste diversa da quella « indossata » fino a pochi anni fa. La tesi che, sia pur con sommarietà di analisi, cercherò di portare avanti in questa relazione, tende a sottolineare come, anche attraverso le moderne acquisizioni in campo biologico, la vera natura del sogno appaia emergere dal ripostiglio notturno del sonno per svelarsi come l'espressione appariscente di una modalità fondamentale e « diversa » dello psichismo umano.

In questa prospettiva ritengo che la valorizzazione odierna del sogno e delle modalità conoscitive che ad esso in qualche modo si collegano, possa non essere casuale, ma coerentemente connessa alle trasformazioni più generali in atto nella cultura contemporanea e, in certo senso, ad essa funzionale.

Per dare un minimo di plausibilità a questa ultima ipotesi, indubbiamente ardita (McLuhan dà coraggio all'immaginazione ...), è opportuno che mi soffermi a mettere in evidenza le più recenti acquisizioni e le prospettive che si sono aperte nello studio del sogno.

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Mechanism of Directional Selectivity in Simple Neurons of the Cat's Visual Cortex Analyzed With Stationary Flash Sequences

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SUMMARY AND CONCLUSIONS

1. The properties of simple neurons showing selectivity to direction of motion in area 17 of the cat cortex were examined. We analyzed in particular a sample of cells receiving a projection from 0 to 10° in visual angle from the area centralis of the cat retina. Three categories of simple neurons were examined: directionally asymmetric (DA) neurons, directionally selective neurons of the unimodal type (DS_1), and bimodal types (DS_2).

2. Poststimulus time histograms (PSTH) were obtained to moving white and black bars as well as to static onset sequences and static offset sequences. Our analysis involves a comparison of responses to single static flashes at various receptive-field locations with responses to sequence pairs of static flashes at those same locations.

3. We find that DA neurons are not sensitive to the direction in which a pair of stimuli are presented. Inhibitory and excitatory responses show properties of linear summation whatever the direction of the stimulus sequence. Their behavior is reminiscent of retinal and LGN neurons. The synergy model accounts well for a DA neuron's directional asymmetry.

4. If pairs of stimuli are close enough (usually an interstimulus distance of 20′ or less for the central 10° of the cat's visual field), then DS neurons show striking departures from linear summation. Specifically, this departure entails an anisotropic distribution of inhibition. The directional selectivity of DS neurons cannot be explained on the basis of a simple linear combination of their on and off region's responses. Directional selectivity is produced entirely within an on-excitatory discharge region or entirely within an off-excitatory discharge region.

5. The excitatory discharge center of even the simplest unimodal DS neuron can be shown to be decomposable into subunits smaller than that discharge center. The fact that the spread of this anisotropy of inhibition is often much more restricted than the entire extent of the DS neuron's excitatory discharge center argues strongly that underlying subregions or modules are contributing their inputs to DS neurons. A DS neuron does not analyze motion as an isolated unit; to the contrary, it is probably embedded in a pool of mutually "cooperative" DS neurons.

6. The basic module of directional analysis is responsive either to an on-on sequence or an off-off sequence but not to both. It is not selective to an on-off sequence. Therefore, unimodal DS neurons (DS1) are performing an analysis of single moving edges.

7. One result of the modular character of DS neurons' operation is that inhibition can be shown to be initiated when a pair of stimuli are presented and not when either S_1 or S_2 alone are presented. We term this sequence-direction-contingent inhibition.

8. Facilitatory (i.e., disinhibitory) responses, in which the response to the second of a pair of stimuli is larger than the linear summation of the responses to S_1 and S_2 presented separately, is sometimes present but quite often is absent. Hence we conclude it is not an essential part of the mechanism.

9. Bimodal DS neurons (DS2) probably integrate the outputs of both on and off uni-

modal DS neurons. In other respects, DS1 and DS2 do not appear to differ in any essential characteristics.

10. Since powerful mutual inhibition is manifested in DS neurons between the responses to pairs of stimuli presented synchronously, it is unlikely that the inhibition involved in directional selectivity must operate through a delay gate. However, once this inhibition is generated, it often displays sustained temporal characteristics.

11. The implications of our findings for various models of directional selectivity are elucidated.

12. We describe a schematic network involving asymmetry of inhibition and intense cooperative pooling among large numbers of directionally selective neurons.

INTRODUCTION

Neurons selectively sensitive to the direction of a moving object were first found in the cerebral cortex of the cat (20, 21), the optic tectum of the frog and pigeon (17, 24, 26), and the retina of the rabbit (1, 2). Various neural networks have been described that might account for this directional selectivity (2, 5, 8, 12, 16, 28, 36, 39). Barlow and Levick (2) described two candidate networks—one utilizing inhibitory processes and one utilizing excitatory processes—and demonstrated that in the rabbit retina, recording from ganglion cells, the mechanism was inhibitory. In the visual cortex the evidence, to date, has been contradictory. Using continuously moving edges as stimuli, Goodwin et al. (16) found evidence for a predominantly inhibitory network. Using sequences of short-duration flashes, facilitatory (29) or a combination of facilitatory and inhibitory processes (12) manifest themselves. These contradictions may result in part from the fact that different experimenters have employed quite different stimuli in order to analyze the putative motion network. Moving edges have the advantage of approximating natural moving objects more closely, they are powerful activators of visual cortex neurons, and they can separate the parts of a receptive field sensitive to on sequences (for example, regions responsive to a white leading edge or a black trailing edge) from those parts of the receptive field sensitive to off sequences, e.g., those regions response to a black leading edge or a white trailing edge (5). However, moving edges are relatively complicated as stimuli and the presence of confounding absolute luminance regions makes them less powerful for analytic purposes. Sequences of short light flashes are advantageous for analytic purposes, as Barlow and Levick (2) first demonstrated, but have the disadvantage of confounding the effect of turning on the flash with the effect of turning it off. To separate onset from offset effects, it is necessary to employ longer duration flashes in which the stimulus-onset asynchrony between the flashes is systematically explored; separately, the stimulus-offset asynchrony should also be explored. In the present paper, we have examined the response of cortical neurons both to moving edges as well as to static sequences of light pulses of long duration (400 ms or longer) where onset and offset asynchrony has been varied parametrically. Our specific goal has been to ascertain whether directionally selective cortical networks depend on inhibitory processes, facilitatory processes, or a combination of both. Our general aim has been to characterize the mechanism of directional selectivity in cat visual cortex.

METHODS

Microelectrode procedure

Thirty-four adult cats were used (average body weight of 2.0 kg). Before surgery, the cat was anesthetized, using the short-term anesthetic, ketamine hydrochloride (22 mg/kg). A Teflon catheter was inserted into the saphenous vein. This was followed by barbiturate anesthesia (sodium thiopental) administered intravenously in incremental doses sufficient to obtain and maintain a surgical depth of anesthesia. The trachea was then intubated. The long-lasting local anesthetic procaine in oil (Zyljectin) was injected at all incisions and pressure points. The cat was positioned in a stereotaxic apparatus that left almost the entire visual field free. Surgical procedures involved opening the cranium and dura about 5 mm along a mediolateral axis and about 10 mm along an anteroposterior axis. Microelectrode penetrations were made at stereotaxic coordinates P2.0–4.0 and L0.5–2.0 and within a 1.5-mm depth of the cortical surface in an attempt to ensure that the electrode was located in or near the projection of the cat's area centralis in Brodmann's area 17. In the cat, the center of the visual axis projects cortically to Brodmann's area 17 at Horsley-Clarke stereotaxic coordinates: posterior, 3.0 mm; lateral, 2.0 mm (22). An agar gel over the opening was utilized to minimize brain pulsation.

Following the completion of the surgical preparation, the administration of barbiturate anesthesia was discontinued. Muscle paralysis was induced using gallamine triethiodide (Flaxedil), administered by continous infusion at the rate of 50 mg/h. The animal was artificially ventilated with a constant-volume pump (stroke volume, 50–75 ml/stroke, 24 strokes/min) administering a mixture of 70% N_2O and 30% O_2. The concentration of CO_2 in the expired air was monitored with a Beckman CO_2 analyzer and was maintained near a level of 4%. Body temperature was maintained at 38 ± 0.5°C by an automatic thermostat.

Contact lenses were used to protect the cornea and correct for accommodation; the nictitating membrane was retracted with Neo-Synephrine; an ophthalmic procaine solution was used to dilate the pupil. Retinoscopy was performed and additional lenses were placed in front of each of the cat's eyes so as to bring their accommodation to 57 cm (the distance from the eye at which the stimulus screen was placed, a distance at which 1 cm = 1° of visual angle).

Following the surgical preparation, at least 1 h was allowed to elapse before beginning the recording to allow most of the effects of the barbiturate anesthetic to dissipate.

We used glass-coated, 70% platinum/30% iridium microelectrodes (44), with etched tips of between 1 and 10 μm in diameter. The electrode was initially constructed with the tip entirely covered by glass. Before recording, an electrical pulse was used to shatter the glass progressively at the tip until an impedance of between 2.5 and 5 M was obtained. Pulses of 1 ms were used to measure impedance.

Action potentials were amplified conventionally, then led to a voltage comparator, adjusted to pass only the largest amplitude spike activity, and finally to the Schmitt trigger input of a digital equipment PDP-8/I computer, where the spikes were counted and stored. Both visual and auditory real-time monitoring of the action potential was customary throughout the duration of an experimental series on a particular neuron.

Stimulus generation

The basic stimulus used here consisted of a single bar of variable width, orientation, and position, either brighter or darker than the background. In all the observations reported here, the bar or edge was oriented so as to stimulate the cell maximally. All traverses across receptive fields were at an angle perpendicular to that orientation. The stimulus rectangle was presented in three different classes of display. *1*) Continuous movement: The rectangle was moved first in one direction, then in the opposite direction, usually over a total traverse of some 5° of visual angle. Complete series were run for white and for black rectangles. In some of the experiments described below, the velocity of this movement was varied parametrically. In other series, the width of the rectangle was the parameter that was varied. *2*) Single-stimulus pulse: A single static rectangle was presented for a specified duration. A range of receptive-field positions was sampled. *3*) Stroboscopic sequence: Two static rectangles were presented in sequence, then in the opposite sequence. The sequence was as follows. S_1 was turned on. Then S_2 was turned on with S_1 remaining illuminated. Then S_1 was turned off. Finally, S_2 was turned off. The interval between S_1 and S_2 onsets is called the onset asynchrony (on-SOA). Correspondingly, there is an offset SOA (off-SOA). Typically the two SOAs were kept equal.

The bar was generated on the face of an oscilloscope having a P31 phosphor. A raster was produced by deflecting the beam vertically with a 100-kHz sawtooth wave (Y axis input), and horizontally with a 200-Hz triangular wave (X axis input). To generate a vertical stationary bright bar, a brightening pulse was produced at the Z axis of the oscilloscope synchronized to a particular value x_i on the X axis ramp voltage input. The digital-analog output of the PDP-8/I set the value x_i. Thus, by changing x_i linearly, bar movement was generated at a steady velocity. The width of the bar was set by the duration of the brightening pulse. To generate a dark bar against a bright background, the polarity of the brightening pulse was changed, making it a dimming pulse. Background luminance was maintained constant at 1.7 cd/m^2; the luminance of the bright bar was 17 cd/m^2. The oscilloscope was attached to a gimballed mounting so that it could be rotated to change bar orientation. It could be adjusted vertically and horizontally to bring the cathode-ray tube (CRT) display into a neuron's receptive field.

Data collection

Data collection was organized by the computer into blocks of 100 bins per stimulus presentation.

During continuous-movement stimulus displays, the duration of a spike-collection bin varied. For example, if a bar moved steadily at velocity of 10 deg^{-1} · s^{-1} for a total traverse of 5°, then the duration of the sweep was 5° · 10 deg^{-1} · s^{-1} = 0.5 s and one bin collected spikes during a time window of 0.5 s/100 bins = 5 ms per bin. More generally, bin duration (in milliseconds) = (extent of traverse/velocity) × 1,000/100. During stimulus displays involving a single stimulus pulse, data collection was organized into a prestimulus period of 200 ms, a stimulus-on pulse of 400 ms, and a stimulus-off period of 400 ms. Here each spike-collection bin had a duration of 10 ms. The third type of display involved a stroboscopic sequence of pulse pairs presented at some specific stimulus asynchrony

(SOA) between the members of the pair. In this last category of stimulus presentation, the duration of data-collection bin (in milliseconds) equaled 200 + SOA_v + 400 + SOA + 200/100.

Typically, 25 stimulus sweeps constituted a block of trials for one set of stimulus parameters. The basic response measure used here is the average spike rate in action potentials per second, as sampled during a single bin duration, averaged over the 25 stimulus sweeps.

RESULTS

Classification of neurons

The material discussed here is taken from two samples of visual cortex neurons. In the first sample, 70 neurons from 23 cats were recorded during stimulation with rectangularly shaped stimuli of standard intensities. A second sample of 21 neurons was collected from an additional 11 cats using stimuli varying in contrast. In our sample, 81% showed either directional selectivity or readily discernible directional asymmetry (2, 33).

A battery of measurements comprised the presentation of *1*) a series of white rectangles varying in width (or in some cases varying in velocity), moving first in the preferred direction and then in the opposite direction over the neuron's receptive field; *2*) a replication of *1*, now with black rectangles; *3*) a series of single narrow bar-shaped static flashes, usually covering progressively the neuron's receptive field in 0.5° steps; *4*) a series of stroboscopic pairs of sequenced bar-shaped flashes, again covering the neuron's receptive field in 0.5° steps, both in preferred direction sequences and in null direction sequences.

We classified the neurons in our population using a set of criteria derived directly from Hubel and Wiesel (20, 21), Pettigrew, Nikara, and Bishop (33), Bishop, Coombs, and Henry (4–6), Schiller, Finlay, and Volman (36), Emerson and Gerstein (11, 12), and Palmer and Davis (31, 32). With regard to the classification of simple and complex cells, the work of Enroth-Cugell and Robson (13), Hochstein and Shapley (18, 19), and Movshon, Thompson, and Tolhurst (27–29) has been particularly helpful.

Simple cells are those whose receptive fields exhibited one or more subfields, within each of which a response could be obtained to either a light or dark edge, but not both. Within this categorization several subclasses could readily be distinguished, in agreement with Bishop, Coombs, and Henry (5) and with Schiller, Finlay, and Volman (36). Although our classification scheme is closely related to Schiller et al.'s (36) for the monkey visual cortex, we use the terms DS-type 1, DS-type 2, etc. as exact substitutes for their S_1, S_2, etc. We hope by this substitution to avoid confusion with our stimulus nomenclature, where we use the terms S_1, S_2, . . . to denote successive stimuli in a sequence.

Our directionally selective simple cells fell into the following two main groups. *1*) Directionally asymmetric (DA) neurons, which show a marked asymmetric arrangement of their receptive fields: an elongated on-excitatory discharge center flanked by a closely abutting elongated off-excitatory discharge center. First described by Hubel and Wiesel (20, 21), these neurons respond preferentially to one direction of motion when a black bar is moved across their receptive fields and reverse their directional preference when a white bar is substituted. Their directional propensities derive in a straightforward way from the spatial characteristics of their receptive fields (11, 12). Their receptive-field sizes are at the small end of the range. They constituted 14.8% of our sample of simple cells. *2*) Directionally selective (DS) neurons are defined by their maintaining the same directional preference across contrast reversal (viz., white versus black bar). There are several discernible types. DS-type 1 (Schiller S_1): single-field, unidirectional cells (unimodal). These neurons respond selectively to either a light edge or a dark edge but not to both. Such neurons are unidirectional. They respond briskly to static stimulus onsets or offsets but not both. They show little spontaneous activity. Their receptive fields are, on the average, in the smaller range, although there are notable exceptions. Aside from their directional selectivity, they respond much like X-type lateral geniculate nucleus (LGN) neurons. This categorization is probably identical to Bishop et al.'s (5) "single moving edge, unidirectionals." They constituted 24.6% of our sample of simple cells. DS-type 2 (Schiller S_2): these are double-field (bimodal), unidirectional cells. Moving edge stimuli revealed two spatially separated response areas, one of which was excited by a light leading edge and the other by a dark leading edge. Both regions

responded selectively to the same direction of movement. Stationary flashes revealed separate light and dark excitatory regions. On the average, the DS-type 2 receptive fields were about twice the size of DS-type 1. This categorization is probably identical to Bishop et al.'s (5) "both edges, unidirectionals." They constituted 19.7% of our sample of simple cells.

There are miscellaneous other groups in Schiller et al.'s (36–39) classification of simple cells, in Bishop et al.'s, (5, 6), and in Pettigrew, Nikara, and Bishop's (33), in which multiple separate subfields are manifested. These categories are proportionately smaller and will not be dealt with in this paper.

Complex-type cells did not manifest distinct differences in their response to light versus dark leading edges. Flashing stimuli elicited both on- and off-responses throughout the receptive field. They constituted 67% of our total sample.

A comparison of the proportions of each classification type with those found by Pettigrew, Nikara, and Bishop (33), Bishop, Coombs, and Henry (4), and Schiller, Finlay, and Volman (36) is shown in Table 1.

An illustration of the terms used in the analysis of a sequence-selective neuron in the present study is shown in Fig. 1. The top row (Fig. 1*A*, *B*) shows two single stimulus histograms collected from neuron *am-36*. An impulse response is a poststimulus histogram (PSH) obtained here by presenting a single (0.25° wide) stationary rectangle at an optimal orientation relative to the receptive-field axis, at a particular position within the receptive field. The PSH in *A* is obtained from presentations at 2° from the cat's area centralis and the PSH in *B*, from presentation at 3°. Since this is a heuristic figure, only the histogram for the 300 ms following stimulus onset is shown. Each data point represents the average

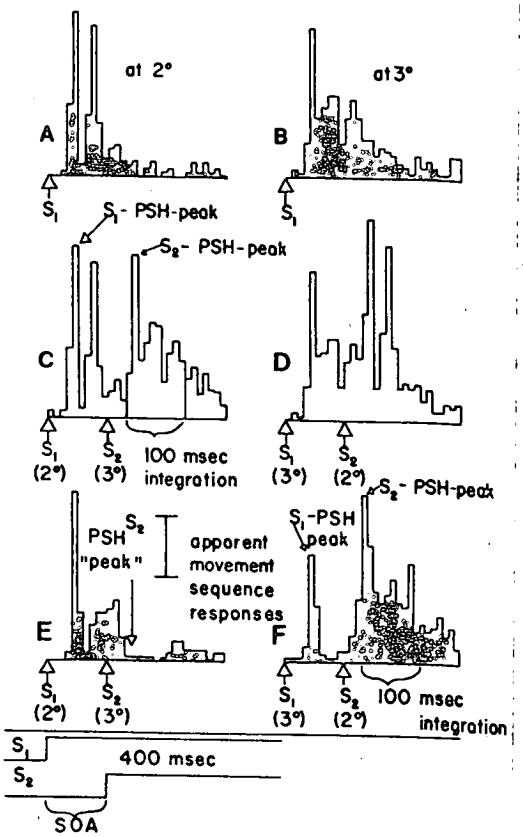


FIG. 1. Illustration of terms used in the analysis of a sequence-selective neuron used in the present study.

spike rate in a data bin of 10 ms duration. In the middle row, linear superposition histograms are depicted. The PSH in *C* is merely the addition of the PSH in *A* to the PSH in *B*, with *B* delayed by 100 ms. The addition is performed bin by bin. Thus, the 11th bin in *A* is added to the 1st bin in *B* to give the 11th bin in *C*, the 12th bin in *A* is added to the second bin in *B* to give the 12th bin in *C*, etc. The *C* linear superposition histogram simulates what we should expect to obtain

TABLE 1. *Percentages of simple cells in various categories*

References	Total Sample Size	DA-Type: Contrast-Interaction	DS-type 1: Unimodal	DS-type 2: Bimodal	Misc Types	Simple:Total Ratio
Our data	91	14.8	24.6	19.7	41.0	0.67
33	99	37.4	44.4	16.2	2.0	0.67
4	43	4.7	20.9	51.2	23.3	
36	245	14.7	27.3	19.2	38.8	0.43

from a static stimulus sequence 2 then 3° (SOA = 100 ms), if only simple linear summation of the two single-stimulus response occurs. Correspondingly, the *D* linear superposition histogram depicts the linear summation expectation for a 3 then 2° (SOA = 100 ms) sequence. The bottom row depicts corresponding poststimulus histograms empirically obtained from neuron *am-36* to the pairs of actual static stimulus presentations. The figure also demonstrates the three response measures referred to in the text: the magnitudes of the S_1 PSH peak and the S_2 PSH peak in units of spikes per second and average spikes per second calculated over a 100-ms interval of integration. The latter interval begins 30 ms and continues until 130 ms after S_2 onset (or S_2 offset where appropriate).

Inhibitory interactions between on and off regions

Because the mechanism of directional selectivity has been theorized to involve a synergy of response between the excitatory center of a receptive field (RF) and its antagonistic surround (20, 21), we were interested in examining how simple neurons respond to various sequences of stimulation presented to these two RF regions. Note that in this section the stimuli are relatively far apart (1–1.5°).

INTERACTIONS BETWEEN ON AND OFF REGIONS IN DIRECTIONALLY ASYMMETRIC NEURONS (DA TYPE). DA cells, which were categorized as simple by the usual criteria (20, 21), showed one directional preference when a white bar on a gray surround was moved across its receptive field and a preference for the opposite direction when a black bar was substituted (11, 33, 36, 39). For example, neuron *am-55* responded more strongly to rightward motion of a white 0.5-deg-wide bar than to leftward motion; this directional preference switched to leftward motion when a black bar of the same width was moved. It is of interest to know how these cells respond to single flashes and to sequences of flashes presented to their on and off regions. For example, neuron *am-55* had shown, when presented with single flashes to different portions of its receptive field, a main on region at 7° from the area centralis and an off region centered at 5.5°. Figure 2*I* depicts the response of the cell to single white bars (0.25° wide) at various loci. We see then, that *am-55* has a classic asymmetric receptive field. Figures 2*A–H* and 3*A–H* show the results of a series of experiments in which two flashes (long white rectangles, 0.25° wide and optimally oriented) were shown in sequence, one at 7° in the on region and one at 5.5° in the off region. The response at stimulus onset is shown in Fig. 2. The left column of histograms depicts responses to onset sequences in a rightward direction (the preferred direction for continuous movement of a white bar for *am-55*). The column of histograms on the right are from sequences in the opposite direction. Results for different stimulus-onset asynchronies (SOA) are shown in the various rows. The on-response is evidently stronger in the right column of histograms. The results depicted in the left column of histograms suggest that turning a stimulus on in the on region is inhibited by first turning a stimulus on in the off region. This result is in accordance with the well-known antagonism of center and surround found at many levels of the visual system (see, for example, Refs. 20, 23, 34, 35, 41).

Turning to the right column of histograms in Fig. 2, we see that a fairly large response is given to the first stimulus at 7° (on region) when the onset of the second stimulus at 5.5° (off region) is delayed by 300 ms (Fig. 2*H*). Note that as the SOA is reduced to 75 ms (Fig. 2*G*), then to 25 ms, and then to 10 ms (Fig. 2*E*), the response to the first stimulus is successively curtailed. Thus, the on-response is also strongly inhibited by an aftercoming stimulus onset in the off region. It appears that for a DA neuron such as *am-55*, strong inhibition can be generated both by a preceding and by a later stimulus onset in the off region. To this extent, the cortical neuron is showing the results of on-off region antagonism that is not sensitive to the direction of the sequence in the sense that spatial summation is present in both sequence orders. This also means the inhibition generated by on-off regions' interactions is not sensitive to the timing of the sequence.

Figure 3 displays histograms collected at stimulus offset from neuron *am-55*. The results are to a first approximation analogous to those in the previous figure except that the sequence direction is now reversed. The re-

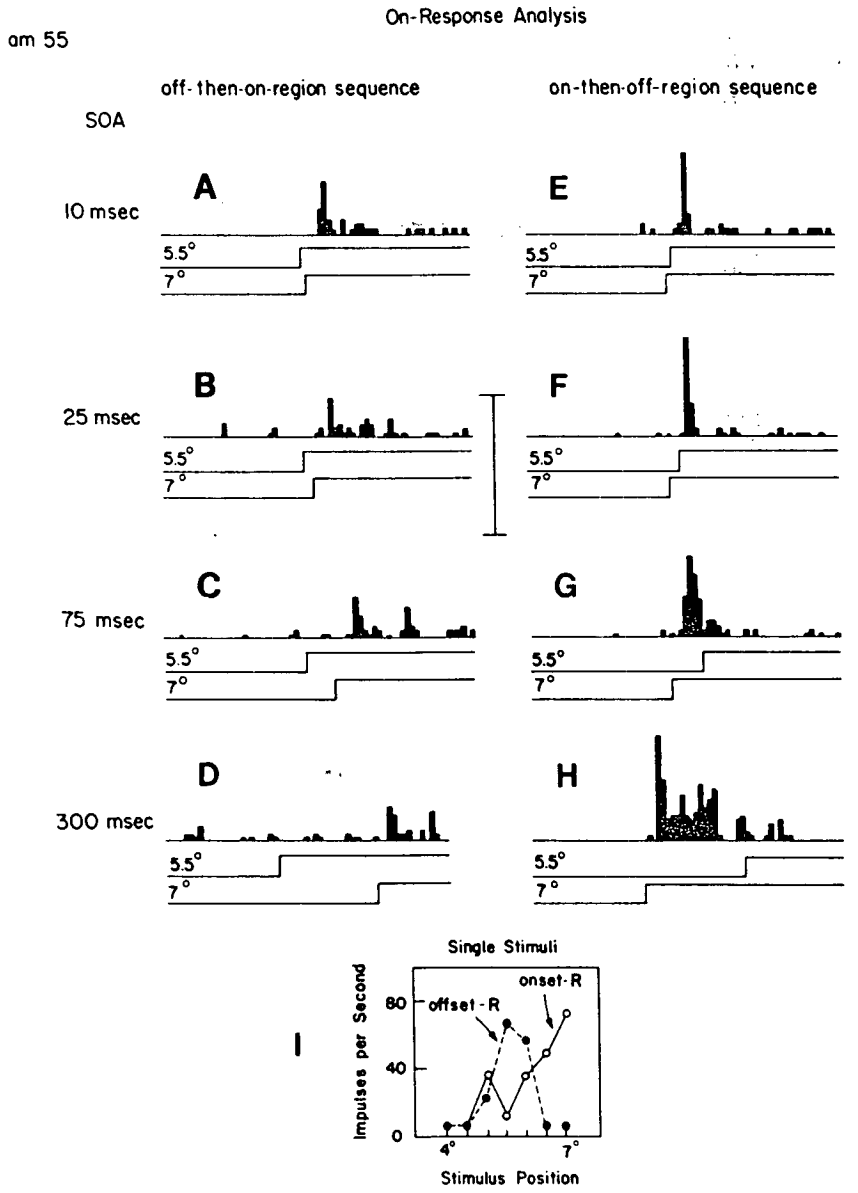


FIG. 2. Analysis of the interaction between an on region and an off region in a directionally asymmetric neuron (DA). *A–H*: onset responses of neuron *am-55* to a sequence of two static flashes presented to an on region and then to an off region, or in the reverse order. Stimulus-onset asynchronies between 10 and 300 ms are shown. Neuron *am-55* showed rightward motion preference for a white bar and leftward motion preference for a black bar. Vertical calibration, 100 impulses/s. *I*: peak response rates to single flash onsets and offsets are depicted at a number of receptive-field positions.

sponse to offset sequences in a rightward direction are now stronger (Fig. 3*B, C, D*). Also, *1*) the right column of histograms shows that an off-response by stimulus offset in a off region is strongly inhibited by a preceding stimulus offset in an adjoining on region (Fig. 3*E–H*); *2*) the left column (especially Fig. 3*C, D*) shows that a strong off-response is shown if the inhibiting stimulus (stimulus offset in an on region) is delayed by 75–300 ms; *3*) the left column of histograms shows that the aftercoming inhibiting stimulus can still be shown to exert an inhibitory effect. This is shown by a delay in the initiation of inhibition

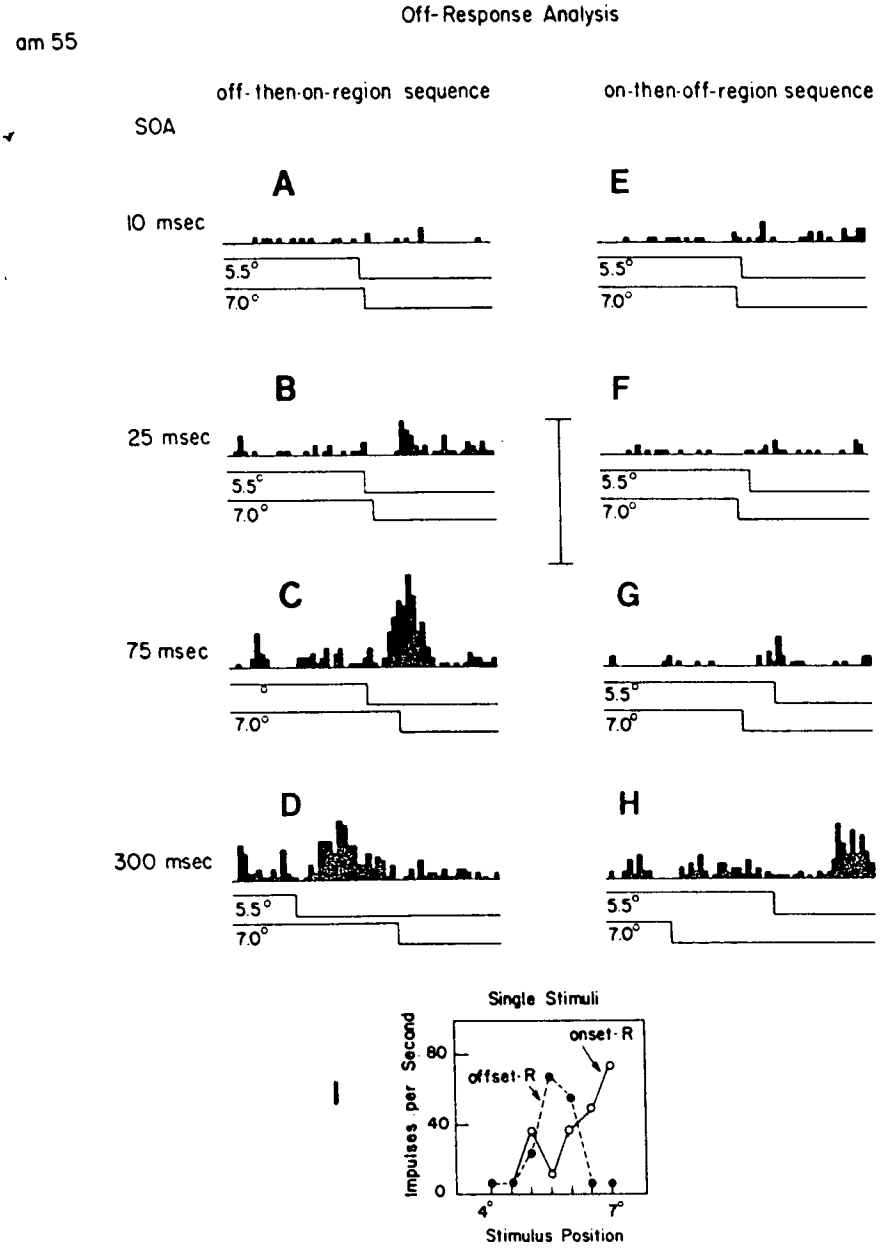


FIG. 3. Exactly as in Fig. 2 but for stimulus offsets.

when SOA is longer. The delay in inhibition is inferred from the progressive curtailment of the off response as one proceeds from an SOA of 300 ms (Fig. 3*D*), to 75 ms (Fig. 3*C*), to 25 ms (Fig. 3*B*); *4*) to this extent, we are seeing the operation of an antagonism between the on and off flanks of the DA neuron's receptive field. This antagonism is not selectively tuned to a specific temporal sequence.

INTERACTIONS BETWEEN ON AND OFF REGIONS IN DS-TYPE I NEURONS. Neuron *am-37* provides an illustration of a typical DS-type 1 neuron. We note in Fig. 4*A* that the neuron responds preferentially to rightward motion of a white rectangle. The excitatory discharge center is estimated to extend from 3 to 4.5°. Note that the region of responsiveness on the histogram does not change sub-

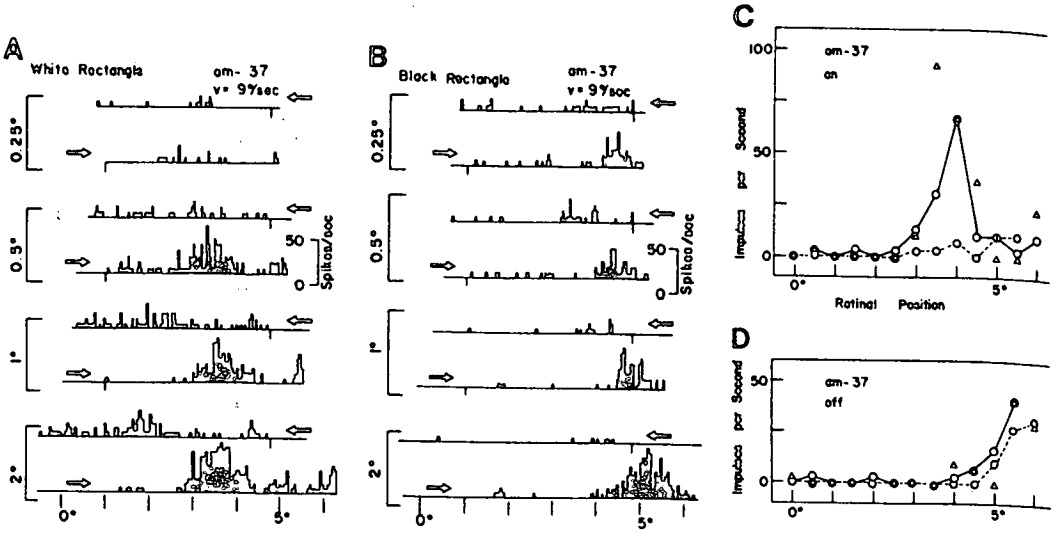


FIG. 4. Average response-rate histograms obtained from *am-37*, a DS-type 1 sequence-direction-selective neuron. *A*: a white bar is moved over a traverse of 4–5° at a velocity of 9°/s, first in a forward direction and then in a reverse direction. Both directions of movement are perpendicular to the axis of optimal orientation for the neuron. Each histogram is compiled from 25 traverses. During a traverse, action potentials are assigned to 100 bins of computer memory locations. The duration of a bin is 5 ms. Bar width is labeled on the left. The starting position of the leading edge in the visual field was maintained constant as bar width changed both in the forward and reverse direction. The downward vertical stem on the horizontal axis indicates the leading edge's starting position. The horizontal axis represents retinal distance in degrees of visual angle from the cat's retinal area centralis. *B*: As in *A* but recorded during the traverse of a black bar. *C*: triangle symbol, magnitude of the onset response to a single thin static flash. The vertical axis represents the magnitude of the peak of the PSTH. Stimuli were presented at locations 0.5° apart along neuron *am-37*'s receptive field. Open circles, magnitude of the peak of the onset response PSTH to the second of a pair of static flashes in a preferred direction. Filled circles, magnitude of the PSTH peak to the second of a pair of static flashes sequenced in a nonpreferred direction. Flash duration, 400 ms; stimulus-onset asynchrony, 100 ms; bar width, 0.25°; interbar separation, 0.5°. *D*: as in C but for stimulus offsets. Stimulus-off asynchrony, 100 ms.

stantially in Fig. 4*A* as the width of the moving rectangle is reduced from 2 to 0.5°. Since the response histograms are displayed in Fig. 4*A* with the stimulus' leading edges aligned vertically, this proves it is predominantly the leading edge of the moving white rectangle that is exciting the cell (4, 5). The leading edge of a white rectangle initiates an on-response. Therefore, neuron *am-37* probably received its input predominantly from on-excitatory retinogeniculate afferent fibers.

The response to a black rectangle is shown in Fig. 4*B*. It is clear that *am-37* retains its rightward movement preference when the contrast of the rectangle is reversed. It should be noted that the peak response region changes toward the left (i.e., toward 4°) as the width of the black rectangle is reduced. This suggests it is the trailing edge of the black rectangle that is primarily responsible for activating neuron *am-37;* the trailing edge of a black rectangle initiates an on-response. Therefore, we again have evidence that *am-37* is predominantly on-excitatory. Thus, the spike activity shown in Fig. 4*B*, bottom row, when the 2° wide, rightward-moving black rectangle's leading edge is at 5–6°, is predominantly caused by the simultaneous presence of the trailing edge increasing luminance levels in an on region located at 3–4° from the area centralis.

Neuron *am-37* was also analyzed with single, static light flashes. Each flash was a thin rectangle, 0.25° in width and 8° in length, presented for 400 ms. Poststimulus time histograms (PSTHs) were generated from averages computed from 25 iterations at each receptive-field location. In Fig. 4*C* and *D*, each of the triangle symbols depict peak response rate to a single static flash. The response to stimulus onset (Fig. 4*C*) and stimulus offset (Fig. 4*D*) are shown separately. We note that there is a fairly delimited on region at 3.5–4° and a much weaker off region at 5–6°. (The

results depicted by the circle symbols will be discussed in a section further below.) The position of the receptive field measured with static stimulus onsets and offsets corresponds fairly well to the position of the excitatory discharge center inferred from the continuously moving leading edge of the white rectangle (Fig. 4*A*).

Knowing the response of neuron *am-37* to moving stimuli and having some notion of the location of the on and off regions, we now turn to an analysis of the response to stimulus sequences presented to both the on and off regions. In Fig. 5, neuron *am-37*'s responses to sequences of stimulus onset are shown. The left column of histograms (Fig. 5*A–C*) depict responses to onset sequences in the preferred direction. Since *am-37* responds better to rightward continuous motion (see Fig. 4*A, B*), a comparable sequence of static flashes would also be in a rightward direction, viz., 4 then 5°. This corresponds to the stimulation of an on and then an off region. The column of histograms on the right are from sequences in the opposite direction (5 then 4°), a nonpreferred direction. Results for different stimulus

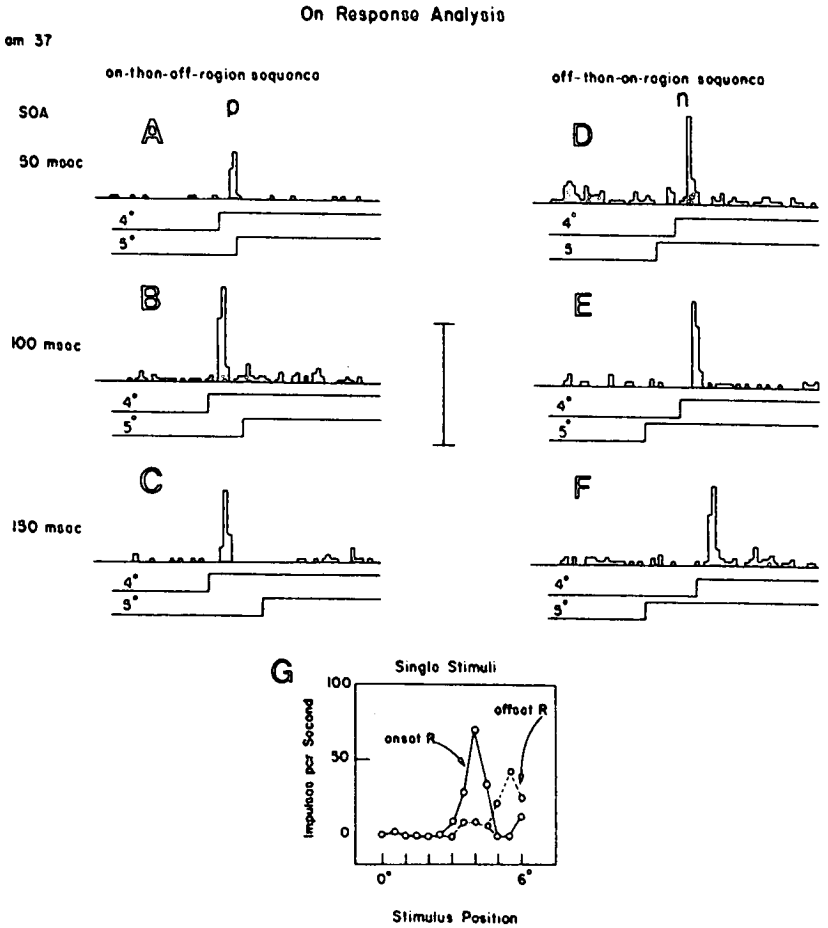


FIG. 5. Analysis of the interaction between an on region and an off region in a DS-type I directionally selective neuron. The figure depicts the onset response to a sequence of two static flashes presented to an on region and then to an off region, or in the reverse order. Conventional poststimulus response rate histograms are depicted, each histogram representing the average of 25 presentations. *A–C*: a rightward sequence 4 then 5°, which corresponds to an on then off region sequence and corresponds to the neuron's preferred direction (p) of continuous motion (see Fig. 4*A* and *B*). *D–F*: a leftward sequence 5 then 4°, which corresponds to an off then on region sequence and corresponds to the neuron's nonpreferred direction (n) of continuous motion. Stimulus-onset asynchronies, 50, 100, and 150 ms; vertical calibration, 100 impulses/s. *G*: for purposes of comparison, the peak response rates to single flash onsets and offsets are depicted for a number of receptive-field positions.

asynchronies, 50, 100, and 150 ms stimulus onset asynchronies (SOA), are shown. It may be noted that the preferred-direction sequences do not yield larger peak response rates than the nonpreferred-direction sequences. In fact, at 50 ms SOA the preferred-direction sequence results in a smaller response. Therefore, even though *am-37* has a predominantly on-excitatory discharge center (see Fig. 4*C*), there is no synergy of response (i.e., enhanced responsiveness) for onset sequences presented to the on and off regions in the preferred direction. This holds for all three SOAs.

Next, we turn to the analysis of the off response to stimulus sequences presented to the on and off regions. Figure 6 depicts a column of histograms from preferred-direction sequences (4 then 5°) on the left and a column of histograms from nonpreferred-direction sequences (5 then 4°) on the right. For the stimulus-offset sequences, the responses in the right-column histograms are larger than the responses in the left-column histograms. Thus responsiveness is actually larger in a direction opposite to the neuron's preferred direction at all three SOAs. Therefore, at stimulus offset

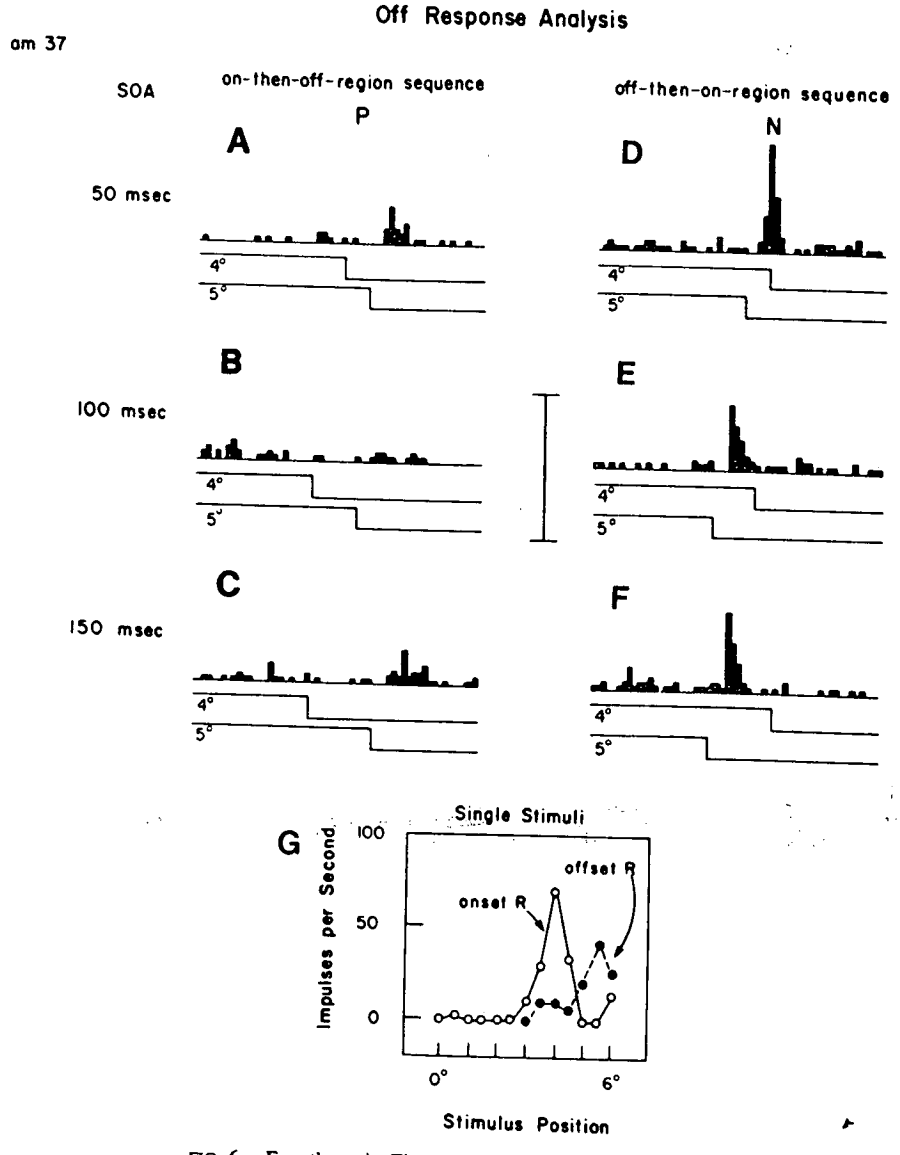


FIG. 6. Exactly as in Fig. 5 but for stimulus offsets.

the reverse of a synergy is found in neuron *am-37*, namely a depression of responsiveness for stimulus sequences in the preferred direction.

It is clear that the directional selectiveness of DS neurons cannot be explained on the basis of a simple linear combination of their on and off regions' responses. Furthermore, in contrast to retinal and LGN neurons (34, 35) and cortical DA neurons, the response to pairs of flashes even in "simple" neurons is not predicted from the response to moving contours and vice versa. These prediction failures suggest directional selectivity must involve basic and substantial nonlinearities. We found these results to be quite consistent within the category of DS-type 1 neurons.

One further point may be emphasized here. Figures 5 and 6 prove that for DS-type 1 neuron *am-37*, a pair of strobed stimuli at an interstimulus distance of 1° is too large for directional selectivity though well-positioned for on region versus off region analysis (below we show that directionality does appear when interstimulus distance is reduced to 0.5° in this same neuron). Therefore, since the excitatory discharge center is 1–1.5° wide, the subunit responsible for directional analysis is smaller in size than the excitatory discharge center. In other words, at this level in the hierarchy of directional selectivity (36, 39), simple neurons have receptive fields made up of multiple subunits or directional modules smaller than receptive-field size. As we will show further below, directionality of a consistent sort is only demonstrated when sequences of static flashes are not distanced greater than the module size.

INTERACTION BETWEEN ON AND OFF REGIONS OF SIMPLE BIMODAL DIRECTIONALLY SELECTIVE NEURONS (DS-TYPE 2). A similar analysis was performed on simple directionally selective neurons that had two strong excitatory discharge centers, an on and an off region, of which both regions showed directional selectivity for the same direction of motion (4, 5, 33, 36, 39). Again, we ask the general question, can the directionality be explained by the synergistic action of antagonistic on and off regions?

For example, DS neuron *am-53* responded more strongly to centripetal motion, i.e., motion toward the area centralis. It showed the same motion directionality to a white 1° bar as to a black 1° bar. Responses to single 400-ms flashes (Fig. 7*I*) revealed an off region at about 5.25° from the area centralis and an on region at 5.75–6°. Figure 7 shows the response given to stimulus-onset sequences at 5.3 and then 6.1°, or in the reverse sequence. The histograms in the left column depict sequences in the same direction as the preferred direction for continuous motion; the histograms in the right column depict responses to a nonpreferred sequence direction. Response rates are higher in the left (preferred) than in the right (nonpreferred) column. (It should be noted that the responses to 150- and 200-ms SOAs were obtained somewhat later in the session with this neuron, when responsiveness as a whole was lower. Nevertheless, the left-column histograms are still higher than those on the right.) It might be noted that the nonpreferred direction for continuous motion (i.e., centrifugal) is the same as would show inhibition on the basis of a center-surround antagonism between an on and an off region: stimulus on in an off region (viz., 5.3°) is followed by stimulus on in an on region (viz., 6.1°). Therefore, at stimulus onset, the nonpreferred direction is the same as the sequence direction we would expect would produce more inhibition from center-surround antagonism; correspondingly, the preferred direction is the one that we would expect to produce less inhibition simply on the basis of retinogeniculate center-surround antagonism.

At stimulus offset, neuron *am-53*'s results show quite a different picture. In Fig. 8 the left column of histograms (preferred direction) indicates higher responsiveness than the right column. But now this goes counter to what is expected on the basis of center-surround antagonism. In the left column of histograms (Fig. 8*A–D*), a stimulus is first turned off in an on region and then turned off in an off region, which should generate inhibition of the off region's off-response. Yet, the off-response is enhanced relative to the off-response for stimulus sequences in the opposite direction (right column of histograms). Therefore, at stimulus offset, preference for direction of continuous motion is somehow compatible with a stimulus sequence, which, on the basis of simply the operation of a simple center-surround antagonism mechanism, would lead us to expect strong inhibition. As with DS-

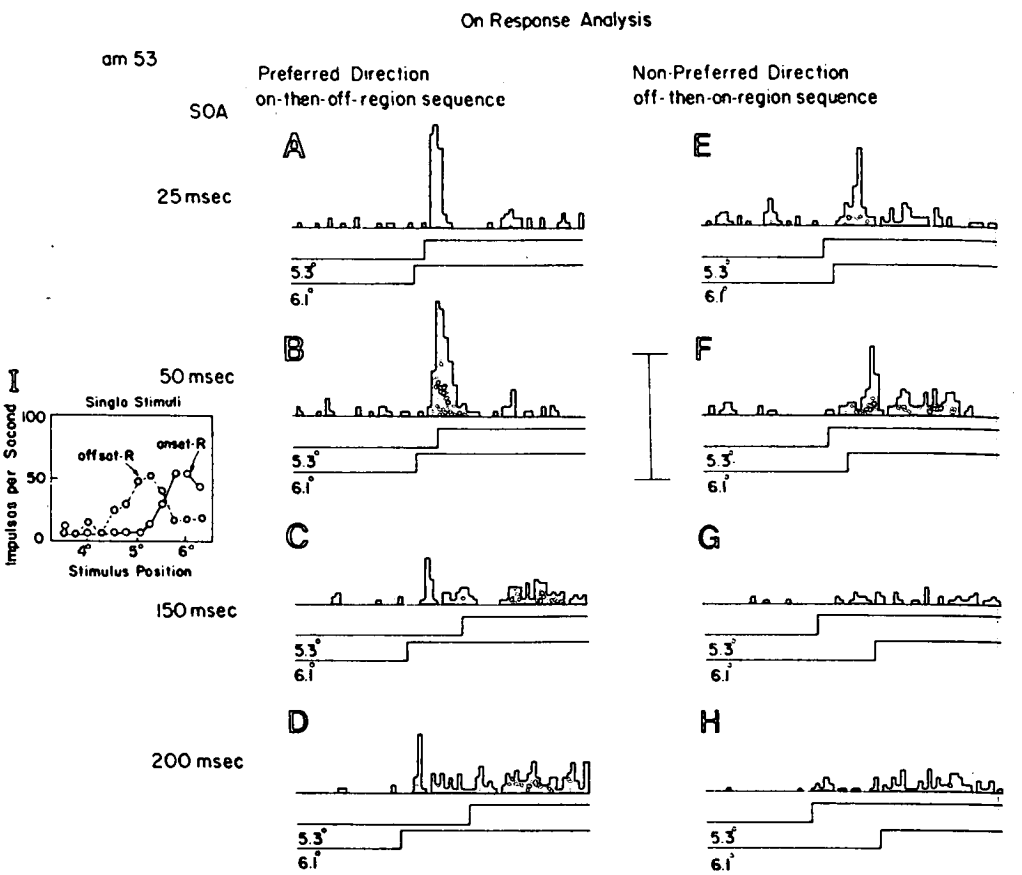


FIG. 7. Analysis of the interaction between an on region and an off region in a DS-type 2 directionally selective neuron. *A–H*: onset responses of neuron *am-53* to a sequence of two static flashes presented to an on region and then to an off region, or in the reverse order. Stimulus-onset asynchronies between 25 and 200 ms are shown. The sequence direction 5.3 then 6.1°, i.e., centrifugal motion, corresponds to the cell's nonpreferred direction for continuous motion. Vertical calibration, 100 impulses/s. *I*: peak response rates to single flash onsets and offsets are depicted at a number of receptive-field positions.

type 1 directionally selective neurons described in the section above, we again find that a neuron's directional selectivity actually goes counter to the interaction of on and off regions expected from a linear superposition of retinal and LGN center-surround antagonism. Therefore, some other presumably nonlinear mechanism is clearly at work. Note that for this DS-type 2 neuron, a striking nonlinearity is present for a preferred-direction offset sequence.

CONCLUSIONS FROM ANALYSIS OF INTERACTION BETWEEN STIMULI PLACED IN ON REGIONS AND STIMULI PLACED IN OFF REGIONS. We have seen in our results that the two major classes of simple directionally selective neurons (DS-type 1 and DS-type 2) show signs of an antagonistic relationship between receptive-field regions. However, *1*) this antagonism has no predictable relationship to the neuron's direction of movement preference (sometimes in accord sometimes counter to it) and *2*) this antagonism is not sequence sensitive. In other words, it displays the approximate spatial and temporal superposition found characteristic of retinal and lateral geniculate body (LGB) stages of the visual system (23, 34, 35, 41). Hence the antagonistic on-off relationship found at these levels cannot form the only basis for the mechanism of directionality. This is taken up further in the DISCUSSION section.

Analysis of responses to sequences of stimuli presented entirely within an on or entirely within an off region

WITHIN-REGION ANALYSIS IN DS-TYPE 1 NEURONS. We attempted, in a number of experiments, to cross most of the receptive field

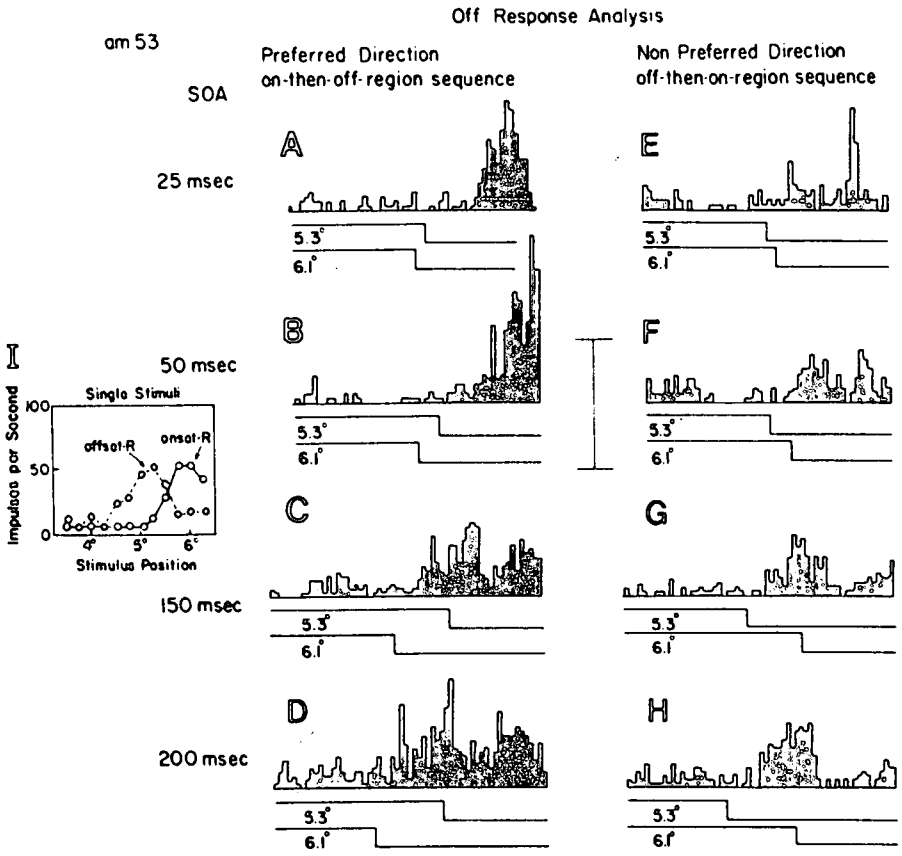


FIG. 8. Exactly as in Fig. 7 but for stimulus offsets.

with pairs of stimulus sequences separated by only small distances. Typically, each pair of thin (0.25°) rectangles was separated by 0.5° in distance (0.25° in some cases) measured from center to center. SOA was kept constant at 100 ms. The results of one such series are shown in Fig. 4*C, D*. Several aspects of the results are noteworthy, we believe. Neuron *am-37*, it will be recalled, had shown a directional preference for continuous motion in a centrifugal direction that remained consistent even when a black bar was substituted for a white one. The analysis of the responses to stimuli presented sequentially to the centers of the on and the off regions had not yielded results consistent with that directional preference. The picture changes substantially when smaller interstimulus distances are used. The circle symbols in Fig. 4*C, D* show the magnitude of the peak response to the second stimulus. The open circles represent S_2 response peak magnitudes when the S_1-S_2 sequence was in a preferred direction (viz., a direction consistent with the preferred direction of continuous motion, centrifugal for this cell); the filled circles represent response peak magnitudes for S_2 presented to the same retinal regions, but as part of an S_1-S_2 sequence in a direction opposite to the preferred direction. In the on-excitatory region, 3–4.5°, we see that at stimulus onset (Fig. 4*C*) the S_2 response (depicted by the filled symbols) is markedly reduced when that stimulus is part of a non-preferred-direction sequence. The results depicted in Fig. 4*D* show that at stimulus offset, neuron *am-37* shows only rather weak directional selectivity, although it is still consistent with the neuron's direction preference for continuous motion. The fact that directional selectivity to static flash sequences is for the most part restricted to stimulus onset is consistent with the analysis of the cell's response to white and black bars, shown in Fig. 4*A, B* and discussed in a section above. We see that a DS-type 1 neuron's ability to respond to white and black bars with the same directional preference is related to the unimodal characteristic of the receptive field, viz., the fact that *am-37* has primarily an on-excitatory discharge center and that it is this on-center that

contains the preponderant directional selectivity. Therefore, when a white bar moves through its receptive field aligned along its axis, it is primarily the leading edge that the neuron responds to with directional selectivity; when a black bar moves through its receptive field, it is primarily the trailing edge to which the neuron responds with directional selectivity.

Since DS-type 1 neurons, such as *am-37*, show directional selectivity almost exclusively at stimulus onset, it is clear that the mechanism underlying the directionality cannot be simply dependent on a synergy of action between stimulus onset and stimulus offset. Directional selectivity is produced entirely within the DS unit's on-excitatory discharge center to a simple sequence of two onsets.

Correspondingly, in other recordings we have found that other DS-type 1 neurons with off-excitatory discharge centers show directional selectivity at stimulus offset alone. Again, this argues against a mechanism solely based on on-off synergy.

Another important point to note is that the excitatory discharge center of a DS-type 1 neuron such as *am-37*, a category of simple cells it will be recalled, can be shown to be decomposable into subunits smaller than the excitatory discharge center, each subunit still showing directional selectivity for sequences of static flashes. For example, we saw in Fig. 4*C* that *am-37* had an on-excitatory discharge center in the region 3–4.5°. Figure 9 shows that the response to the second stimulus in the sequences 3.5 then 3°, 4 then 3.5°, 4.5 then 4°, and 5 then 4.5° is more strongly inhibited than the response to that same second stimulus when shown in pairs of stimuli presented in the reverse order 3 then 3.5°, . . . , etc. This suggests that the mechanism of directionality is developed within subregions of the excitatory discharge of a simple unimodal neuron. A stimulus such as a thin rectangle presented to the position 3.5° of *am-37*'s receptive field (see Fig. 9) exerts powerful inhibition toward 3° (i.e., centripetally) but little inhibition toward 4° (i.e., centrifugally), and

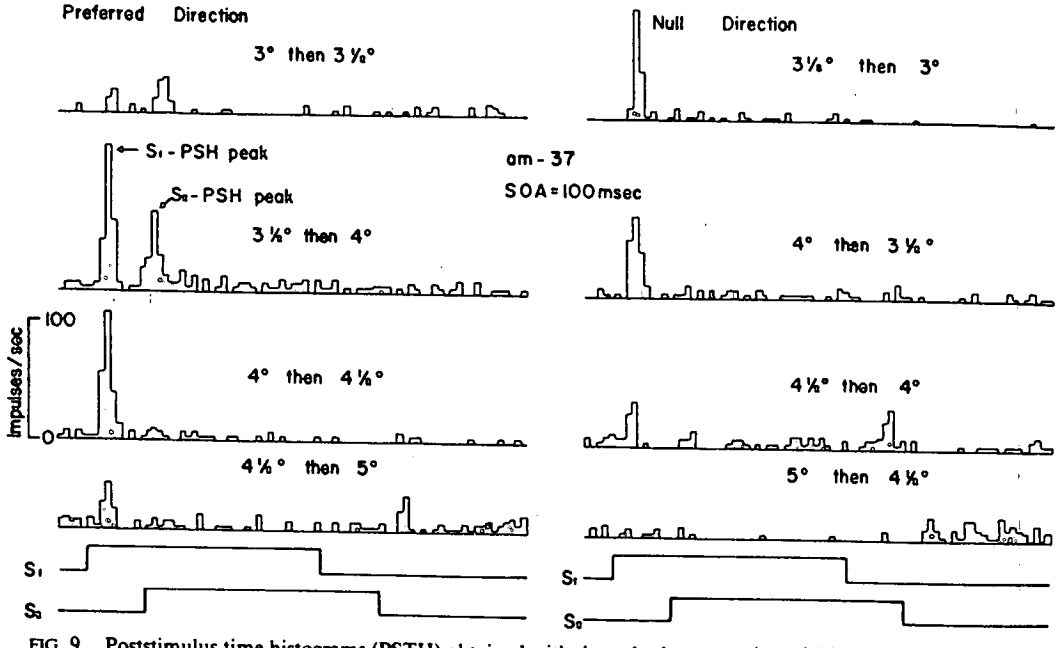


FIG. 9. Poststimulus time histograms (PSTH) obtained with the pulsed presentation of thin rectangles (0.25° wide) optimally oriented in neuron *am-37*'s receptive field. Each PSTH is obtained from a sequence of two such stimuli presented at a stimulus-onset asynchrony of 100 ms and at an interstimulus separation of 0.5°. The left and right columns of PSTHs depicts results for preferred-direction sequences and nonpreferred- (or null) direction sequences, respectively. Preferred and nonpreferred are defined by results such as shown in Fig. 2*A* and *B*, obtained with continuous movement. Results are shown for receptive-field locations from 3 to 5°. The sequence is as follows: 250 ms of data are collected prior to stimulation (only 50 ms are shown here), S_1 is turned on, after 100 ms S_2 is turned on, after another 300 ms S_1 is turned off, and after another 100 ms S_2 is turned off. Data continue to be collected for another 250 ms. Thus, each PSTH represents 1 s of data collection. Bin duration, 10 ms.

the same holds for a first stimulus presented at 4 or at 4.5°. In other words, the inhibition that underlies the directional selectivity is generated by smaller subunits or modules that show directional anisotropy; these modules are spatially asymmetric with respect to inhibition.

Another interesting observation emerges from a comparison between Figs. 5 and 6 and Fig. 9. When a relatively large interstimulus distance of 1° was used (Figs. 5 and 6), no strong directional sequence preferences were obtained to stimulus pairs. When identical stimuli were presented to the same general region but with a smaller interstimulus distance of 0.5°, a strong directional preference was obtained (Fig. 9). In other words, smaller interstimulus distances are associated with stronger spatial sequence selectivity (see also a section further below). Hence the putative selective subunits or modules have an optimal size (usually quite a bit smaller than the excitatory discharge center), which when exceeded no longer displays spatial sequence selectivity.

FREQUENT ABSENCE OF ONSET-ONSET OR OFFSET-OFFSET FACILITATION IN DS-TYPE 1 NEURONS. If the mechanism underlying the directional selectivity of neuron *am-37*'s on-response depended in an essential way on facilitation (or disinhibition) of the S_2 response by the S_1 response in the preferred direction, then we would expect the preferred direction S_2 PSTH peaks (open circles in Fig. 4*C*) to be substantially above those of the linear superposition-function S_2 PSTH peaks (triangles in Fig. 4*C*). This is clearly not the case in Fig. 4*C*. Therefore, the mechanism of directional selectivity appears, in this instance, to depend primarily or solely on inhibition.

Figure 10 depicts the results of a similar analysis on another DS-type 1 neuron. Neuron *am-44* responded to stimulus onsets over virtually its entire receptive field. It had an on-excitatory discharge center, which was found to extend from the center of the area centralis to more than 5° in the retinal periphery. The off-excitatory region was much smaller and much weaker. Figure 10 compares the observed response to static flash sequences in the preferred and nonpreferred directions, with linear superposition histograms shown in outline. (Linear superposition functions and their derivations are explained in Fig. 1 and accompanying text.) Note first that the PSTH peaks to the second stimulus in a nonpreferred direction are invariably smaller than the linear superposition functions, no matter what the asynchrony between the two. It can also be seen that neuron *am-44* showed no signs of facilitation of the response to the second stimulus in a preferred direction sequence at any asynchrony. This can be seen from the fact that in the preferred direction, the filled circle symbols do not exceed the outline. From these observations one can conclude that the mechanism of directional selectivity in neuron *am-44* depends in an essential way on inhibition. We have found this to be generally true in our sample of DS-type 1 neurons.

One additional point might be of interest. Figure 10 makes it clear that at small SOAs, i.e., 0- to 25-ms SOA, the inhibition is found about equally in both directions. In general, we have found that it requires an SOA of as much as 50–75 ms to obtain an optimal degree of discrimination between preferred- and null-direction sequences.

Analysis of responses to sequences of stimuli presented entirely within on or entirely within off regions of bimodal neurons (DS-type 2)

Figure 11 depicts the response of a DS-type 2 neuron, cell *am-36*, to a 2-deg-wide rectangle, 10° long, moving across its receptive field at a velocity of 2°/s. We note first that the cell is more responsive to leftward movement, both for a black bar on gray surround and for a white bar on gray surround (Fig. 11*A*).

The response histograms obtained with the white rectangle suggest an on-excitatory area at a retinal position of 2–4°; the black rectangle elicits responses suggesting an off-excitatory region at a retinal position 4–5°. These suggestions are confirmed more directly by obtaining responses to single flashes, as shown in Fig. 11*B*. Each response in this protocol was obtained with a light pulse that lasted 400 ms, at 16 locations across the receptive field, the measurements taken 0.5° apart. Only the magnitude of the peak of the on poststimulus time histogram (PSTH) and the peak of the off PSTH are shown here. We can clearly see two separate response areas, an on-excitatory and an off-excitatory area, each sharply de-

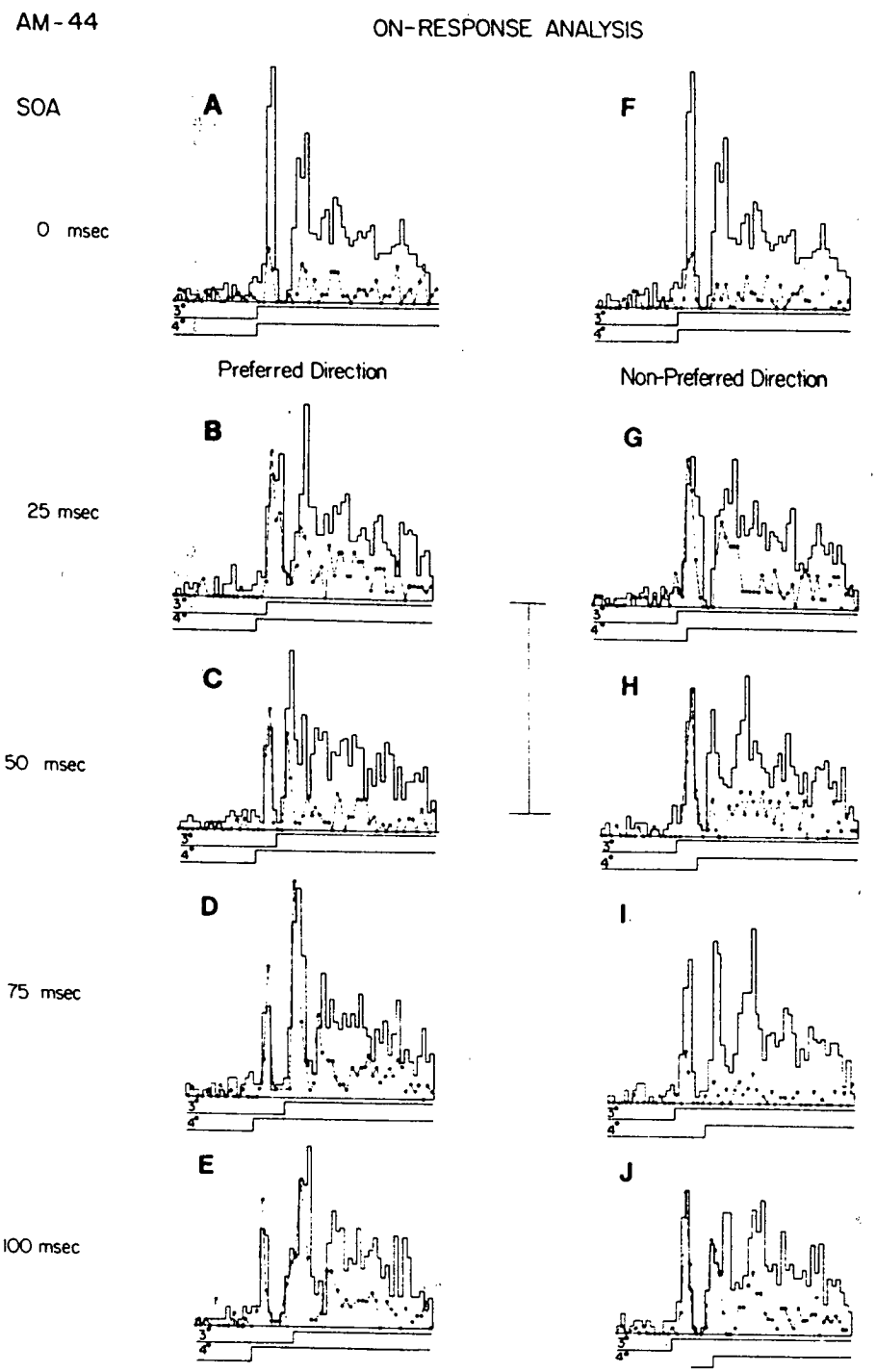


FIG. 10. A comparison between predictions of a linear superposition function and observed results from sequences of two static flashes. Records obtained from *am-44*, a DS-type 1 directionally selective neuron with on-excitatory discharge center extending from the area centralis to 5°. The outline histograms are linear superposition functions obtained as described in Fig. 1 from single-flash data and then summed, bin by bin, at various asynchronies of S_1 and S_2. The solid circles depict observations from two flash presentations. In the nonpreferred direction the suppression of the S_2 response peak is easily discerned at SOAs of 50 and 75 ms (*H* and *I*, respectively). No facilitation manifests itself (which would appear as solid symbols above outline histogram) at any SOA. The presence of strong inhibition at SOA = 0 should also be noted. Vertical calibration, 100 spikes/s. Each histogram was generated from 25 stimulus presentations.

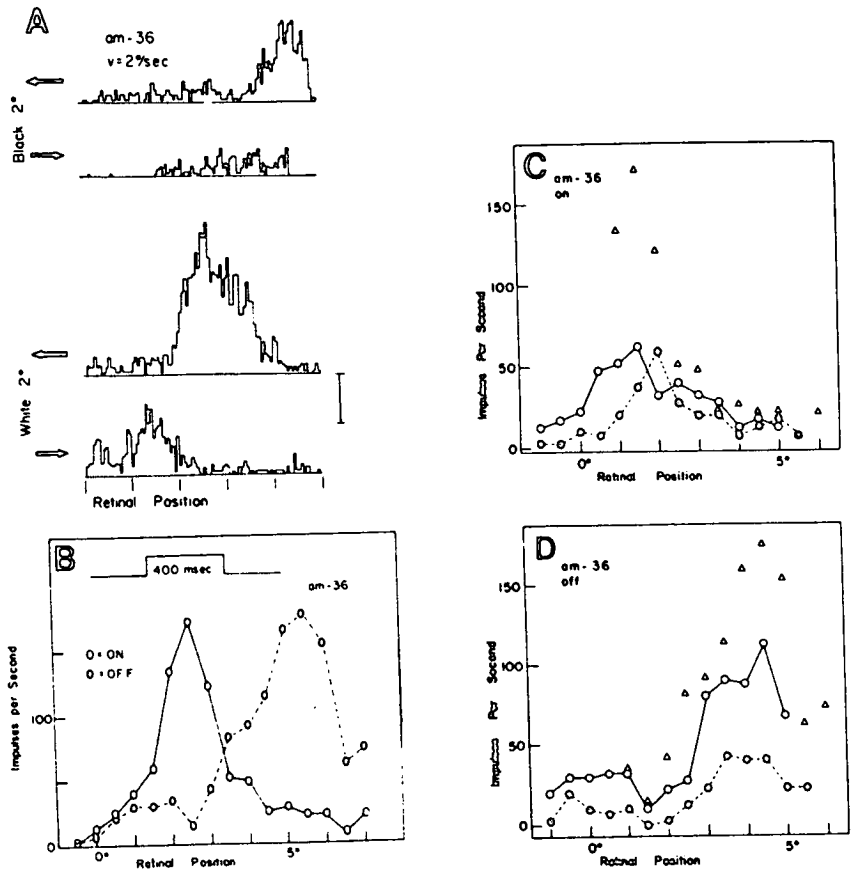


FIG. 11. Analysis of a DS-type 2 directionally selective neuron (*am-36*). *A*: average response rate histograms obtained with a bar in continuous movement. A bar 2° wide is moved continuously over a traverse of 5° at a velocity of 2°/s first in a forward and then in a reverse direction. Both directions of movement are perpendicular to the axis of optimal orientation for neuron *am-36*. Each histogram represents average spikes per second taken over 25 traverses. Action potentials were assigned to 100 bins, each bin 25 ms in duration. The horizontal axis represents the position of the bar's leading edge in *am-36*'s receptive field in units of degrees of visual angle (0° represented at the left). Vertical calibration mark, 20 spikes/s. *B*: single static flashes. The average magnitude of the impulse response peak obtained from single (0.25° wide) rectangle presentations presented at various positions across *am-36*'s receptive field. Open and filled symbols represent the impulse response peak magnitude at stimulus onset and at stimulus offset, respectively. Averages are computed from 25 stimulus sequences. *C*: distribution of sequence selectivity across the receptive field of neuron *am-36* as measured by the magnitude of the peak response to a sequence of two thin (0.25°) stationary white rectangles. Only the on-responses are shown here. Circles represent S_2 PSTH peak magnitudes: filled and open circles represent sequences in the nonpreferred and preferred directions, respectively. The position of the second stimulus is plotted along the horizontal axis. SOA = 100 ms; interstimulus separation, 0.5°. Triangle symbols represent the on PSTH response peak obtained with a single stimulus presentation. *D*: exactly as in *C* except that the magnitude of the off S_2 PSTH response peak is shown here.

lineated while partially overlapping with discharge centers about 3° apart.

The next step in the analysis involves *am-36*'s response to stroboscopic stimulus sequences. SOA was kept constant at 100 ms for this next series. We examine the magnitude of the response peak to the second stimulus as it is affected by the S_1-to-S_2 sequence direction. These peak measures are shown in Fig. 11*C*, *D*. We see that the neuron shows a greater S_2 responsiveness to one direction of sequence (open circles) than to its opposite (filled circles), a preference that is spread over a considerable portion of the cell's receptive field. In Fig. 11*C* there is an on-excitatory region at retinal position −1 to 1.5° where the stimulus-on S_2 PSTH peak is larger in the preferred direction. In Fig. 11*D*, we see that there is an off-excitatory region especially strong from 3 to 5° where the stimulus-off S_2

PSTH peak is larger in the preferred direction. Note that, as essential for a DS-type 2 neuron, this directional preference is shown both at stimulus onset and stimulus offset. The retinal location of directional selectiveness is different for the on-response (located at retinal positions 0–1.5°) than for the off-response (located mainly at retinal positions 3–6°). The results indicate that movement selectivity in a DS-type 2 neuron is developed independently for the on and off regions. Therefore, once again it is clear that the basis for movement selectivity, i.e., the underlying analytic mechanism, cannot be simply a synergy of action between an on and an off region, such as when a black bar moves from an on to an off region (20, 21). Each region, on or off, has its own independent sequence-analyzing mechanism.

FREQUENT ABSENCE OF ONSET-ONSET FACILITATION AND ABSENCE OF OFFSET-OFFSET FACILITATION IN DS-TYPE 2 SIMPLE, DIRECTIONALLY SELECTIVE NEURONS. To ascertain whether in bimodal neurons sequence selectivity is based on inhibition or on facilitation, or possibly both, we compared responses to static pairs of light pulses with linear superposition functions (see Fig. 1) obtained from single pulses.

In Fig. 11*C* and *D*, the S_2 PSTH peaks obtained from preferred (open circles) and nonpreferred (filled circles) direction sequences are compared to linear superposition peaks derived from single-stimulus presentations (triangles). We see first that single stimuli elicit large responses (triangles) compared to the response to second stimuli. Second, the response to the second stimulus in the preferred direction is not substantially above the response to the single stimulus. Third, second-stimulus responses in null-sequence directions are lower than second-stimulus responses in preferred-sequence directions. These three properties are true for both on and off regions and hold across extended portions of the receptive field. All three imply that *am-36*'s directional selectivity is based only on inhibition and is not dependent in an essential way on disinhibition (2). We have found this to be true generally for simple bimodal directionally selective neurons. Within the scope of our limited sample, we have found that directional selectivity is not based on disinhibition.

With regard to subunits within *am-36*'s receptive field, note the extended region between 2 and 6° in Fig. 11*D* wherein a 0.5° sequence pair in the nonpreferred direction (filled symbols) yields low response rates to the S_2 presentation. In other words, there is no single dividing line in *am-36*'s receptive field that must be crossed to yield directional selectivity. Nor are there in Fig. 11*D* small lacunae, that we have been able to measure, within the directionally selective region within which selectivity is absent or reversed. We believe this indicates *am-36* is pooling the outputs of numerous directionally selective subunits of some kind.

Our basic analytic tool in examining directional selectivity has been to look at the response to the second stimulus for various sequence directions and asynchronies. Specifically, we have measured the peak of the response to the second stimulus. We have also explored other response measures to see whether our basic findings are invariant across various measures. For example, we have measured average response rate integrated over a 100-ms time frame following S_2 onset or following S_2 offset. This response measure is depicted in Fig. 1. Typical results taken from neuron *am-36* are shown in Fig. 12.

Our three basic findings for DS-type 2 neurons are found to be replicated with the 100-ms integration measure depicted in Fig. 12. First, the response to single-stimulus presentation (triangle symbols) is substantial. Second, the response to the second stimulus is smaller in the nonpreferred direction (filled circles) than in the preferred direction (open circles). There is no facilitation (or very little) of the response to the second stimulus in the preferred direction. This can be gleaned from the fact that the open circle symbols are not substantially above the triangle symbols. Hence, our basic conclusions using a peak response measure are confirmed when a different response measure utilizing a more extensive time frame is examined.

Spatially asymmetric inhibition in simple neurons

All simple directionally selective neurons in our sample, including DS-types 1 and 2, exhibited inhibition to static stimulus flashes that was contingent on the sequence direction of stimulus pairs. Sequence-direction-contingent inhibition is illustrated in Fig. 13. From recordings of bimodal simple neuron *am-36*,

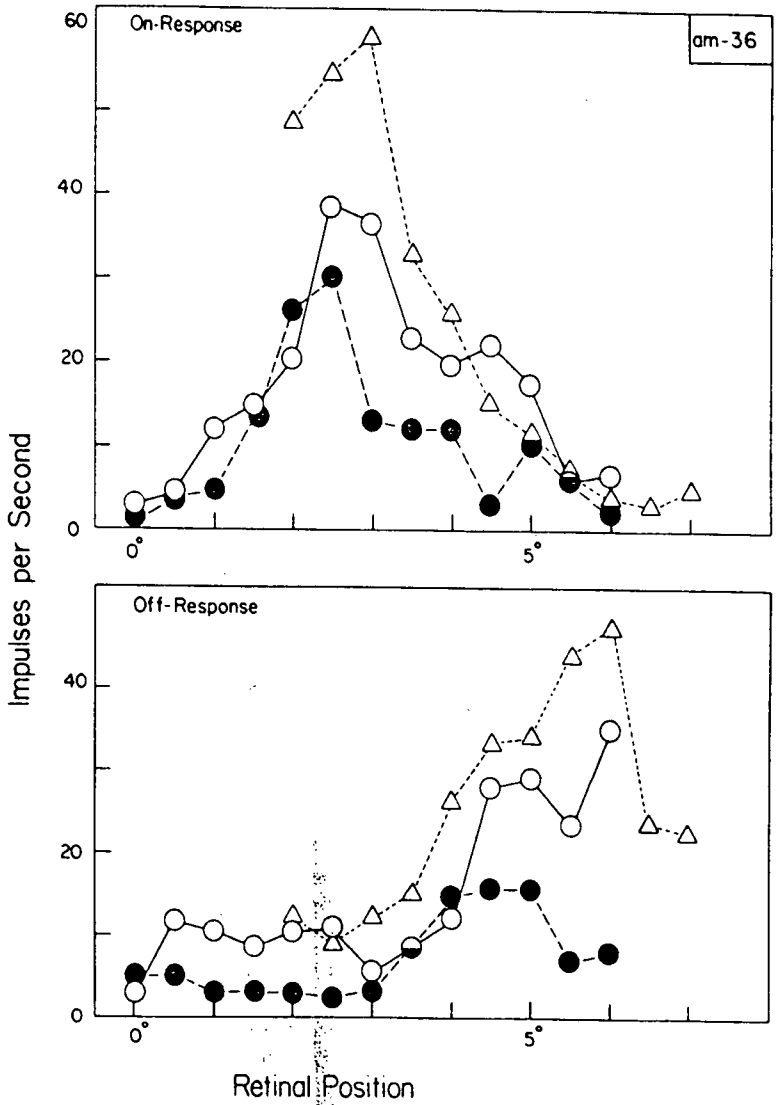


FIG. 12. Analysis of directional selectivity in neuron *am-36* using a 100-ms integration measure (described in Fig. 1). Each symbol stands for the average spike rate for an interval of 100 ms, starting 30 ms after the initiation of S_2. Open and filled circles represent preferred and nonpreferred sequences of flash pairs. Triangle symbols represent single flash presentations. Stimuli were 0.25° thin white rectangles, optimally oriented and 0.5° apart. Stimulus duration, 100 ms.

we analyze the effect that a thin white rectangle presented at 2° (an on-excitatory discharge center) has on a subsequent stimulus. We compare that effect in two different sequence directions: preferred and nonpreferred. In other words, we contrast the effect of presenting a first stimulus at retinal position 2° on a second stimulus as a function of where that second stimulus is. Only the on-response is analyzed. It should be noted that in Fig. 13, the outline histogram represents, for purposes of comparison, a response to a single stimulus. Specifically, the outline histograms in the left column represent on-responses to single stimuli at 1° and the outline histograms in the right column represent on-responses to single stimuli at 3°. Where the filled symbols are lower than the outline histogram, inhibition is probably present.

Consider first sequences in the preferred direction. We see in the left column of Fig. 13 that when a stimulus is presented at 1° in a sequence 2 then 1°, we obtain a response to the 1° stimulus approximately equal to (or

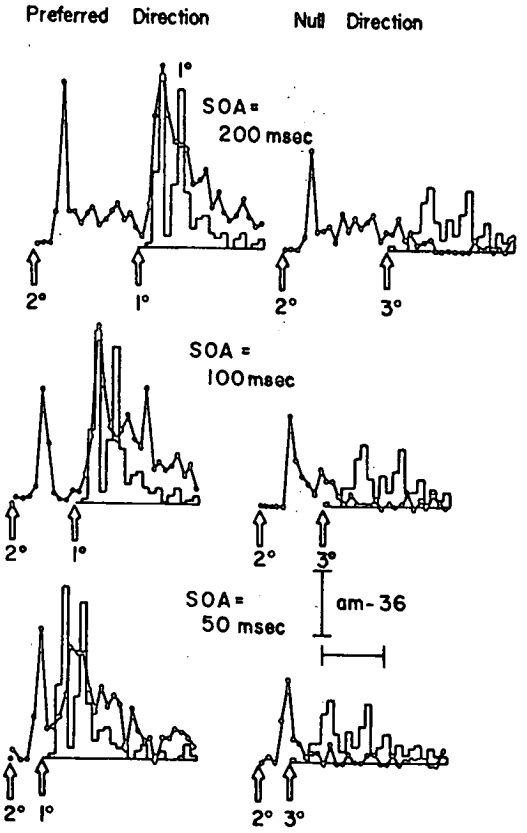


FIG. 13. Illustration of sequence-contingent inhibition in a DS-type 2 simple neuron (*am-36*). The effect of presenting a thin white rectangle at 2° on a second stimulus rectangle is depicted. Only the on-response has been analyzed here. Filled circles represent response histograms obtained from displays of sequenced static stimulus pairs. The outline histograms were obtained from single stimulus presentations presented at 1° in the left column and at 3° in the right column. The figure demonstrates that the effect of a stimulus at 2° is either inhibitory on a subsequent stimulus or not, depending on the sequence direction of the pair in which the 2° stimulus finds itself. In other words, the inhibition is sequence contingent. These results were obtained at all three stimulus asynchronies (SOA). Note also that the inhibitory effect of S_2 in a null-direction sequence only begins when the second stimulus has been presented. Vertical calibration, 50 impulses/s; horizontal calibration, 100 ms.

even slightly larger than) the response obtained by presenting a single stimulus at 1° (outline histogram). Therefore, the effect of the 2° stimulus is not inhibitory on the response to the 1° stimulus. Next, we analyze sequences in the null direction. We note that when a stimulus is presented at 3°, in a sequence 2 then 3°, we do obtain a much smaller response to 3° than when 3° is presented alone (outline histogram). Therefore, the effect of the 2 stimulus is inhibitory on the 3° stimulus response. Therefore, the inhibitory effect of presenting a stimulus at 2° on neuron *am-3(* depends on the direction of the pair of flashes of which 2° will be a part. In other words, the inhibitory potential elicited by the 2° stimulus displays spatial asymmetry or anisotropy. There is an inhibitory effect by stimulus onset at 2° in the nonpreferred direction (viz., centrifugal) and an excitatory effect in the preferred direction (viz., centripetal). The fact that simple neurons demonstrate inhibition with spatial asymmetry has a number of implications for models of directional selectivity. These will be elaborated in the DISCUSSION.

Another important fact can be gleaned from Fig. 13. The outline histograms in the right column depict the response to a single static stimulus presented at retinal location 3°. It is clear from the outline histogram that such a stimulus elicits an on-response (see also Fig. 11*B*, the 3° position). But when a 3° stimulus is presented as part of a nonpreferred direction sequence 2 then 3°, the sequence pair arouses an inhibitory response. Thus, the polarity of the response to the 3° stimulus—whether excitatory or inhibitory—is contingent on the sequence of which it is a part. We call these effects sequence-direction–contingent excitation and sequence-direction–contingent inhibition. Such sequence-direction contingency we believe constitutes an essential aspect of DS neuron operation and, furthermore, is not generally characteristic of DA neurons.

Furthermore, these sequence-direction contingencies constitute clear examples of a failure of linear superposition for these simple directionally selective neurons. In other words, in contrast to retinal and LGN findings (34, 35), the response to the sequence 2° then 3° is not simply the linear summation of the response to a stimulus at 2° alone plus the response to a stimulus at 3° alone.

There is a dynamic property, which we believe is important, that sequence-contingent inhibition manifests. It is illustrated in Fig. 13. Note that the inhibitory effect of the (2 then 3°) sequence on neuron *am-36* appears to be time-locked with the onset of the 3° stimulus. Figure 13 shows three different onset asynchronies between S_1 and S_2. As SOA increases, from 50 to 200 ms, the onset of inhibition is correspondingly delayed, coming

each time some 30 ms or so after the onset of the 3° stimulus. Therefore, preceding a 3° stimulus by a 2° stimulus changes the excitatory effect of 3° into inhibition and, moreover, this effect begins only with the onset of the 3° stimulus. This is again a clear indication that the neuron is, in part, responding to the combined 2 then 3° stimulus pair sequence rather than to their separate components. In other words, the inhibitory response is sequence contingent; the action of the two stimuli on *am-36* are decidedly nonindependent and nonlinear. The delay of the inhibition has implications for the network that we describe in the DISCUSSION section.

We performed the same analysis of the directionally asymmetric properties of inhibition of the on-response of neuron *am-36* at one other receptive-field location, viz., 4°, and obtained the same results. Therefore, it is not the case that this phenomenon is only located at a precise receptive-field position; rather, it is reduplicated at a number of sites.

It will be recalled that in an earlier section we reported that in DA neurons, inhibitory interactions generated by pairs of stimuli were independent of sequence direction. The quality of inhibition, whether it is selective to direction of sequence or independent, appears to be an essential difference between DS and DA neurons. In the DISCUSSION section we will consider under what conditions one or the other of these contrasted types is obtained.

Disinhibitory interactions between on and off sequences in DS-type 2 neurons

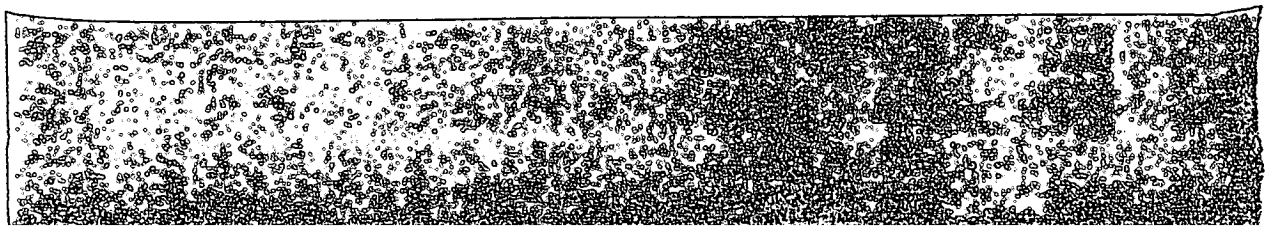
While disinhibition does not appear to be essential to the mechanism of directional selectivity, we have observed it under a variety of circumstances (see also Refs. 11, 12).

An analysis of an on-off disinhibitory interaction is illustrated in Fig. 14. Neuron *am-53*, it will be recalled (see Figs. 7 and 8), was directionally selective, preferring centripetal motion. It was a DS-type 2 neuron with a bimodal receptive field having an off-excitatory discharge center at 5.3° and an on-excitatory discharge center at 6.1°. In Fig. 14*A*, the dashed-line functions with the circle symbols depict histograms of response rates from experiments involving two static flashes, one to 5.3° (off region) and one to 6.1° (on region). The left column of dashed-line histograms depicts presentations in which 6.1° was the first position stimulated and 5.3° was the second. This corresponded to the neuron's preferred direction for continuously moving stimuli. The right column of dashed-line histograms depicts the reverse sequence. Only the off-response is depicted. The figure shows five different asynchronies between S_1 and S_2, chosen from a total of eight used in the actual experiment. The data deleted agree in every essential respect with those presented in the figure.

The outline histograms, presented for purposes of comparison, are linear superposition functions generated from single, static, flash presentations and then combined with the appropriate asynchrony by simple addition.

We will look first at the right column of histograms (Fig. 14*F–J*), which all depict sequences in a nonpreferred direction in which the 5.3° stimulus is turned off and then the 6.1° stimulus is turned off (recalling that 5.3° is an off region and 6.1° an on region). We note first that removing a thin white rectangle positioned at 6.1° elicits an inhibitory response. In these figures, inhibition is manifested by a significant diminution of the dashed-line (filled circle symbols) function below the outline histogram. In other words, the observed stimulus sequence (dashed-line functions) yields lower response rates than the linear superposition estimates (outline histogram). The right-hand column histograms (i.e., nonpreferred direction) suggest a stimulus offset at 6.1° elicits an inhibitory effect that begins about 30–40 ms after 6.1° is turned off and lasts approximately 300 ms. Moreover, the inhibition is progressively delayed as the second stimulus is progressively delayed. Hence, not surprisingly, turning a white line off in an on-excitatory discharge center generates inhibition at some level of the network.

The left-column histograms (Fig. 14*A–E*) represent sequences in the opposite direction in which the 6.1° stimulus (on region) is turned off first and then the 5.3° stimulus (presented to an off region) is turned off. This sequence direction corresponds to the neuron's preferred direction of continuous motion. We see that the 6.1° offset when it comes first elicits an off-response of large magnitude. It is clearly elicited by the 6.1° stimulus offset because it occurs proportionately earlier in time if the 6.1° stimulus is presented longer times before the 5.3° stimulus, as SOA in-



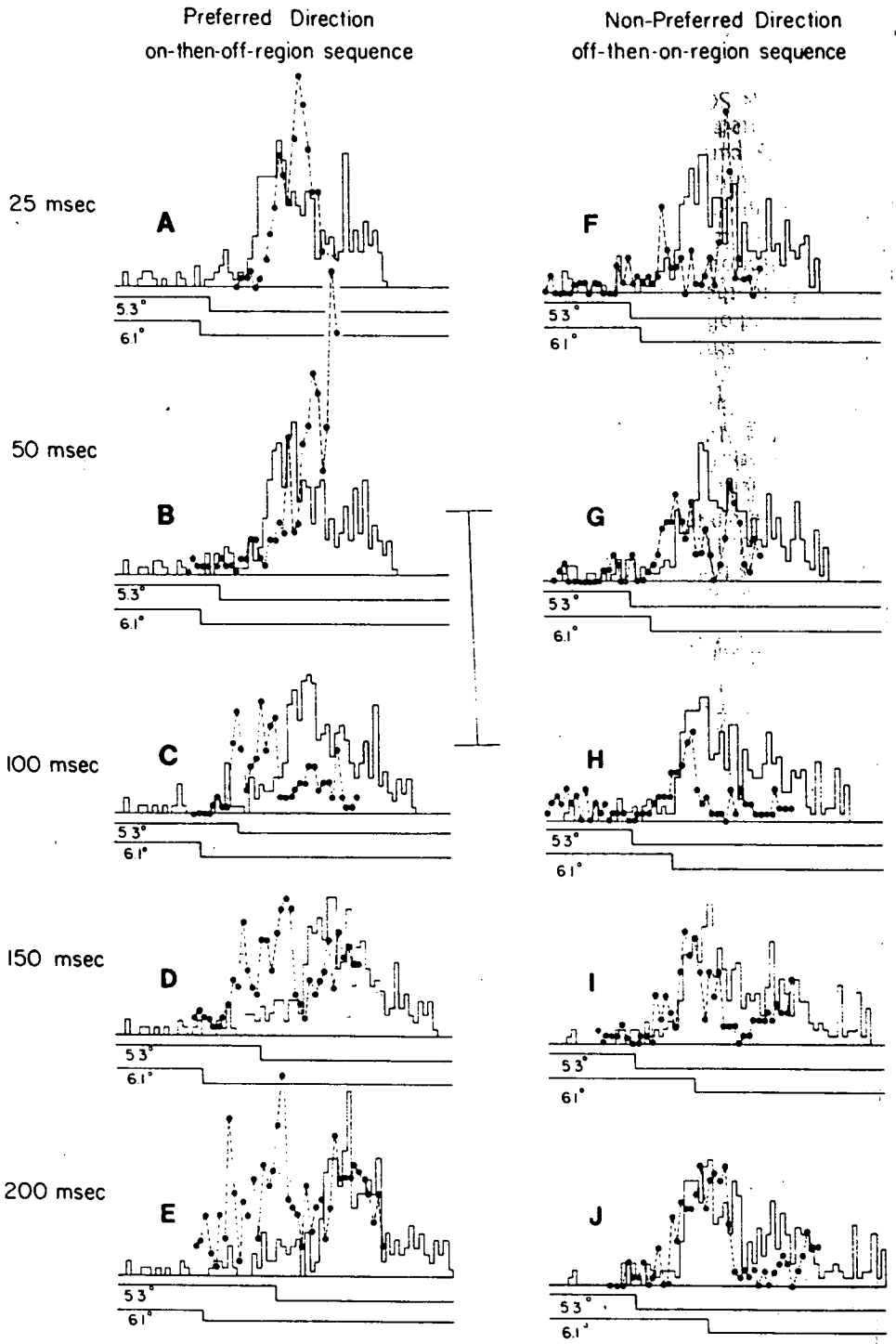


FIG. 14. Disinhibition of an off-response. Neuron *am-53* (DS-type 2) had on- and off-excitatory discharge centers at 6.1 and 5.3°, respectively, from the area centralis (see Figs. 7 and 8). Both regions were directionally selective, preferring the same direction of motion. Filled symbols represent response histograms to the static pairs of white lines turned off in sequence. Outline histograms are taken from single stimulus presentations at 5.3 and, separately, at 6.1°, added together with corresponding asynchronies. Neuron *am-53* responds selectively to centripetal motion 6.1 then 5.3°. Stimulus-offset asynchronies, 25–200 ms. In *F–I*, turning the white line off in an on region (viz., 6.1°) generated an inhibitory response locked in time to the 6.1° offset. In *A–E*, turning the white line off in an on region (viz., 6.1°) generated strong facilitation.

creases. The outline histograms do not depict a strong off-response to the 6.1° stimulus offset when single stimuli are used. As a single, static stimulus, the 6.1° receptive-field region does not yield a strong off-response. (This is particularly clear from the histogram at the 200-ms SOA preferred direction frame (Fig. 14*E*.) Hence, the 6.1° off-response depends on the 5.3° off region being illuminated. The sequence of events is approximately as follows. It is likely that the on region at 6.1° has an antagonistic relation to the off region at 5.3°, as demonstrated at LGN (41). Turning the illumination off at 6.1° turns off the inhibitory action of the 6.1° on region. This generates a transient disinhibition of the off-response at 5.3°.

It should be noted that the disinhibitory effect of turning the stimulus off at the 6.1° on region depends on the 5.3° off region being still illuminated. Hence, the disinhibitory effect is markedly temporal sequence contingent. It occurs in the temporal sequence (6.1° off then 5.3° off) and not vice versa.

It might be of interest to note that these essentially nonlinear disinhibitory interactions between on and off sequence, since they follow only a preferred-direction sequence and are in a direction that would enhance comparable sequences of stimuli in continuous motion. Specifically, for *am-53*, a white bar moving in a preferred direction (centripetal motion) would give rise to a sequence of events comparable to the ones we have presented stroboscopically, whereas a black bar would not. Hence, the disinhibitory effect may make some direction-selective neurons contrast selective, e.g., responding preferentially to a white bar moving toward the center of the visual axis.

DISCUSSION

We begin by briefly summarizing our main findings.

1) DA neurons (20, 21) are defined as cells that show one directional preference when a white bar is moved across its receptive field and a preference for the opposite direction when a black bar is substituted (11, 33, 36, 39). Thin static, single stimulus bars reveal a bipartite field with an on region and an off region (11, 12, 20, 21). In other words, they obey Hubel and Wiesel's classical definition of a simple cell as having a response to stimuli predictable from spot maps. DA cells are fairly linear in response properties, reminiscent of retinal and LGN neurons analyzed by Rodieck and Stone (34, 35). We demonstrate in this paper that in DA neurons the mutual antagonism between on and off regions—which resembles that found by Singer and Creutzfeldt at LGN (41)—is not sensitive to spatial sequence in the sense that spatial summation is present in both sequence directions. Hubel and Wiesel's (20, 21) synergy model predicts the behavior of DA neurons successfully.

2) Unimodal DS neurons are defined as those cells that maintain their directional preference when contrast is reversed. They are decidedly nonlinear by that simple fact. We show specifically that the directional selectiveness of DS neurons cannot be explained on the basis of a simple linear combination of their on and off regions' responses. The use of thin static lines in sequences and at various distances demonstrates that the DS unit's directionality is a function of inhibition generated primarily in one direction and over a short distance (estimated at 15–30′ of arc for the central 10° of vision), typically a distance that is much shorter than the entire excitatory extent of the excitatory discharge center (see also Refs. 12, 16). We interpret this to mean that a typical DS neuron receives the outputs of multiple directional modules in intense cooperative pooling, in agreement with Creutzfeldt et al. (8).

3) Unimodal DS neurons pool the outputs of either onset-sequence analytic modules or offset-sequence analytic modules, but not from both. In other words, the mechanism is edge selective (see also Ref. 16). Directional selectiveness is not dependent on an onset-offset sequence, as suggested elsewhere (12).

4) Given that a sequence of two static stimuli are presented within the range of the underlying sequence-analytic module, inhibition will be highly spatial-direction contingent. If larger distances are employed, the neuron's behavior loses this directional contingency and reverts to a more linear behavior characteristic of retinal and LGN interactions.

5) We present evidence that suggests that DS neurons receive inhibitory inputs from other DS neurons sensitive to the opposite direction of motion (see also Ref. 8).

6) While inhibition is always found, disinhibition is not always present. Hence, we conclude that disinhibition, while it probably plays a subsidiary role, is not an essential part of the mechanism of directional selectivity.

7) For pairs of static lines presented simultaneously or at very small asynchronies (SOA = 0–25 ms), we invariably find deep inhibition of DS neurons' responses. This makes it impossible that inhibition acts through a delay gate at the level of the analytic module (2).

8) The use of long-duration stimuli demonstrates that the anisotropic inhibition responsible for directional selectivity is often quite sustained in character, contrary to other reports (12) and the predictions of certain models (25).

9) Bimodal DS neurons responses to sequences of static stimuli is probably the result of their receiving the outputs of some onset analytic modules and also some offset analytic modules. Often, these two inputs come from different receptive-field locations. The total extent of their excitatory discharge regions are typically larger than unimodal DS neurons. Analysis with sequences of static stimuli fails to reveal any fundamental difference between bimodal and unimodal DS neurons.

Our results, partly corroborative of previous investigators and partly new, help us to narrow the range of candidate neural networks responsible for directional selectivity. We first discuss the shortcomings of models offered to date and then offer our own candidate model.

The on-off synergy model of directional selectivity is based on the asymmetry of arrangement of flanking on and off regions found in many simple receptive-field neurons (20, 21). According to this model, a moving bright line would be particularly effective at the moment it was leaving an off area and entering an on area of an asymmetric receptive field. A black line would then be optimally effective in the opposite direction. DA neurons do respond to a large extent in accordance with the synergy model. They do summate the responses of their on regions and off regions in an approximately linear manner and they do switch their directional preference when the contrast of the moving edge is switched from white to black (11, 12). We also find that the interaction between on and off regions is not spatial-sequence sensitive: on and off regions interact in the same way whether one region is stimulated first, or vice versa. Therefore, the directional asymmetry of some simple cortical neurons is predicted by the synergy model.

By way of contrast, several sources of data lead to the conclusion that DS neurons—including types 1 and 2 in Schiller's classification—do not appear to derive their directional selectivity simply from a synergy of action between the on and the off regions of their receptive fields. The strongest evidence against the on-off synergy model is that cortical DS neurons demonstrate directionality entirely within the on-excitatory discharge center for moving white edges and entirely within the off-excitatory discharge center for moving dark edges (see also Refs. 4, 5, 11, 12, 16, 36, 39). Furthermore, we have shown in this paper that this directionality for continuous edge motion generalizes to the presentation of static sequences of flashes. For example, an on-excitatory discharge center preferentially sensitive to rightward continuous motion will often show greater responsiveness to a thin pair of static stimulus onsets sequences in a rightward direction and presented entirely within the on-excitatory discharge center. Furthermore, we show that this directionality is maintained within subregions of the excitatory area. For example, if the on-excitatory discharge area is some 1.5° in width, one can find 15–30′ subregions, each of which will show the same consistent directional preference of thin static flashes presented in sequence. In fact, we find that directional preference for sequence pairs is often stronger when the pair are confined to a small subregion than when they are segregated to on and off regions. Clearly, these facts argue strongly against a mechanism of directionality being dependent solely on a synergy of action between on regions and off regions. Rather, the mechanism of directionality is developed separately within the on region and/or separately within the off region.

It is clear why a DS-type 1 neuron with an on-excitatory discharge center will respond to the same directional preference, whether the bar is white or black. The reason is that it will respond mainly to the leading edge of a white bar and mainly to the trailing edge of a black bar. Conversely, a DS-type 1 neuron with an off-excitatory discharge area will respond to the leading edge of a black bar and the trailing edge of a white bar. DS-type 2 neurons, having the same directional preference in the on and

off regions, will respond both to the trailing and the leading edges, but at different receptive-field positions.

Suppose we accept, as have Goodwin et al. (16), Emerson and Gerstein (12), and Schiller et al. (36, 39), the notion that directional selectivity is generated separately within the on region and separately within the off region. We can now inquire whether the mechanism depends on inhibition of activity when a stimulus moves in the nonpreferred direction or whether it depends on disinhibition of activity during preferred-direction motion, or some combination of both.

The delayed-inhibition model (1) was first formulated to explain the mechanism of sequence selectivity at the rabbit retina. An object moving in the null direction initiates activity possibly in horizontal cells (43), which then, in effect, generates a delayed anisotropic inhibition, possibly at the level of the bipolar dendrites located at the outer plexiform layer of the retina. Barlow and Levick (2) showed that for the rabbit retina, the evidence supported the delayed-inhibition model. Our results also support the inhibitory model for cortical DS neurons but without a delay gate, since we often find inhibition for zero asynchronies.

If the mechanism of motion selectivity is based on inhibition, then the following should occur when pair of static flashes is presented. When the sequence is in the null direction we should expect the S_2 PSTH peak to be lower than the linear superposition (LS) function. If the mechanism of motion selectivity is based on disinhibition of the second stimulus when the sequence is in the preferred direction, then we should expect the S_2 PSTH peak to be higher than the LS function. Empirically, both an inhibitory and facilitatory mechanism could be found. Our experiments demonstrate that onset-onset sequences and offset-offset sequences always yield the first prediction. Disinhibition in the preferred direction is obtained only under special conditions.

In our experiments with static sequences of stimulus onsets and static sequences of stimulus offsets, we have found that DS-type 1 neurons often fail to show any signs of facilitation or disinhibition, as here defined, either for onset-onset sequences or for offset-offset sequences. We find that the S_2 PSTH peak for the second of a pair of static onsets (or offsets) in the preferred direction is, in fact, typically smaller than the PSTH to that stimulus presented by itself.

There is this additional point. If directionally selective neurons were critically dependent on disinhibition of S_2 by S_1 in the preferred direction, then responses to single flashes should have been generally small. We found most directionally selective neurons responded with substantial response rates to single flashes. This provides further doubt as to the prevalence of substantial disinhibition or facilitation as an essential mechanism of directional selectivity. We conclude that the essential basis of directional selectivity is probably always inhibitory in cat primary visual cortex neurons.

Our conclusion that the basic selective mechanism is inhibitory is supported by Creutzfeldt, Kuhnt, and Benevento's (8) observation from intracellular recording in cat visual cortex that motion in the null direction elicits IPSPs. Similar conclusions derive from Sillito (40), who demonstrated that iontophoretic application of bicuculline eliminates directional selectivity in cortical neurons. Bicuculline is an antagonist of γ-aminobutyric acid (GABA). GABA is a presumptive inhibitory neurotransmitter. Goodwin, Henry, and Bishop (16) have also recently provided evidence supporting the role of inhibition in directional selectivity.

Our results also have implications for a more recent model of directional selectivity (16). It is based on the fact that both retinal ganglion cells and LGN cells show a radial directional selectivity to stimulus movements directed either toward or away from the centers of their receptive fields (34, 35). For example, a white spot will elicit a stronger response moving toward the center of an on-excitatory discharge center or out of an off-excitatory discharge center. Goodwin et al. (16) postulate a sustained bar of inhibition generated possibly at the visual cortex, which effectively eliminates one-half of the receptive field, leaving a cortical neuron sensitive to motion in one general direction.

A critical prediction that the bar-inhibition model (16) makes is that since the directionality is attributed to retinal and/or LGN receptive-field properties, the cortical neuron

should act like a retinal and/or LGN neuron if a static sequence of flashes is presented within the half of the excitatory discharge center over which the bar inhibition has little effect or when the bar is absent. In other words, it should show linear superposition for static sequences of thin lines exactly as demonstrated by Rodieck and Stone (34, 35) for retinal ganglion cells: the response to a pair of static flashes is equal to the sum of their individual responses, whatever their sequence or position. We find that this is not true: DS cortical neurons depart markedly from linear superposition in their response to static pairs of flashes within subregions of their receptive fields, depending on the direction of the sequence. By way of contrast, DA neurons do resemble retinal ganglion and LGN neurons in their responses.

A further weakness of Goodwin et al.'s, model (16) is that it yields true directionality independent of brightness contrast only for edges (which are needed to provide sustained suppression of one-half of the receptive field). However, we show in this paper that directional inhibition is found even for paired sequences of thin white lines (only at their onsets in the on part of the receptive field and only at their offsets in the off part of the receptive field). Hence, neurons show directionality in the absence of extended edges in their visual field (see also Refs. 11, 12).

Recording from ganglion cells in the rabbit eye, it was found that small subregions of the receptive fields—20′ of arc within a 2° receptive field—retained their directional preference (2). Barlow and Levick (2) interpreted this finding to mean that the sequence-discriminating mechanism must be reduplicated many times to cover the whole receptive field. By using pairs of stimuli sequentially, as in a stroboscopic-movement paradigm, they were able to show that sequence discrimination is actually better over 20′ of arc subregions than when the two light pulses were presented at opposite ends of the receptive field. They concluded that the ganglion cell is acting as a higher order pooling mechanism receiving activation from a fairly large number of lower order sequence-discriminating mechanisms (which we call modules), all sensitive to one direction of motion (see also Refs. 11, 12).

Using an argument analogous to Barlow and Levick (2), we conclude that the fact that an excitatory discharge region of 1.5° and sometimes greater is found to be most sensitive to direction differences of 15–30′ at several subregions of that receptive field implies that the receptive field even of a purely simple receptive field, as classically defined, is receiving inputs from the outputs of multiple analytic modules tuned to the same direction.

Another facet of the mechanism of directional selectivity derives from the finding that inhibition is sometimes sequence contingent. For example, Creutzfeldt et al. (8) find inhibitory postsynaptic potentials (IPSPs) in simple cells to be sensitive to dynamic factors. This along with our own evidence of sequence contingency implies, we believe, that DS neurons are being inhibited by the outputs of adjoining DS neurons sensitive to motion in the opposite direction. Thus, the directional selectivity of a single DS neuron being recorded from is actually a function of an entire network of neurons pooling their inhibitory sensitivities.

A "delay gate" for inhibition is not needed to account for the fact that the second stimulus can be delayed by some hundreds of milliseconds and still be inhibited by the action of a sustained first stimulus in the nonpreferred direction. This can equally be explained by the sustained characteristic of much of that inhibition (15). If inhibition were actually delayed by orders of magnitude of 50–100 ms, then we would not find extensive reductions in response to S_2 at short SOAs. But, as illustrated in Fig. 10 for example, we typically find profound inhibition of both the S_1 and S_2 responses at 0 ms SOA. Hence, inhibition does not appear to be substantially delayed.

An asymmetry of inhibitory strength astride the excitatory discharge center comprises, we believe, the basic module of directional selectivity. Bishop, Coombs, and Henry (6) and Emerson and Gerstein (11, 12) also provide evidence of a similar asymmetry. This module, in turn, is embedded in a hierarchical network.

Figure 15 illustrates a possible neural network that accounts for some of the properties of directionally selective neurons. Three hierarchically organized levels of interaction are depicted. Figure 15*A* illustrates LGN interactions, such as described by Singer and Creutzfeldt (41). A pyramidal LGN cell (triangle shape labeled 1.0) receives an excitatory input from a retinal ganglion cell that has a circular receptive field, an on-excitatory dis-

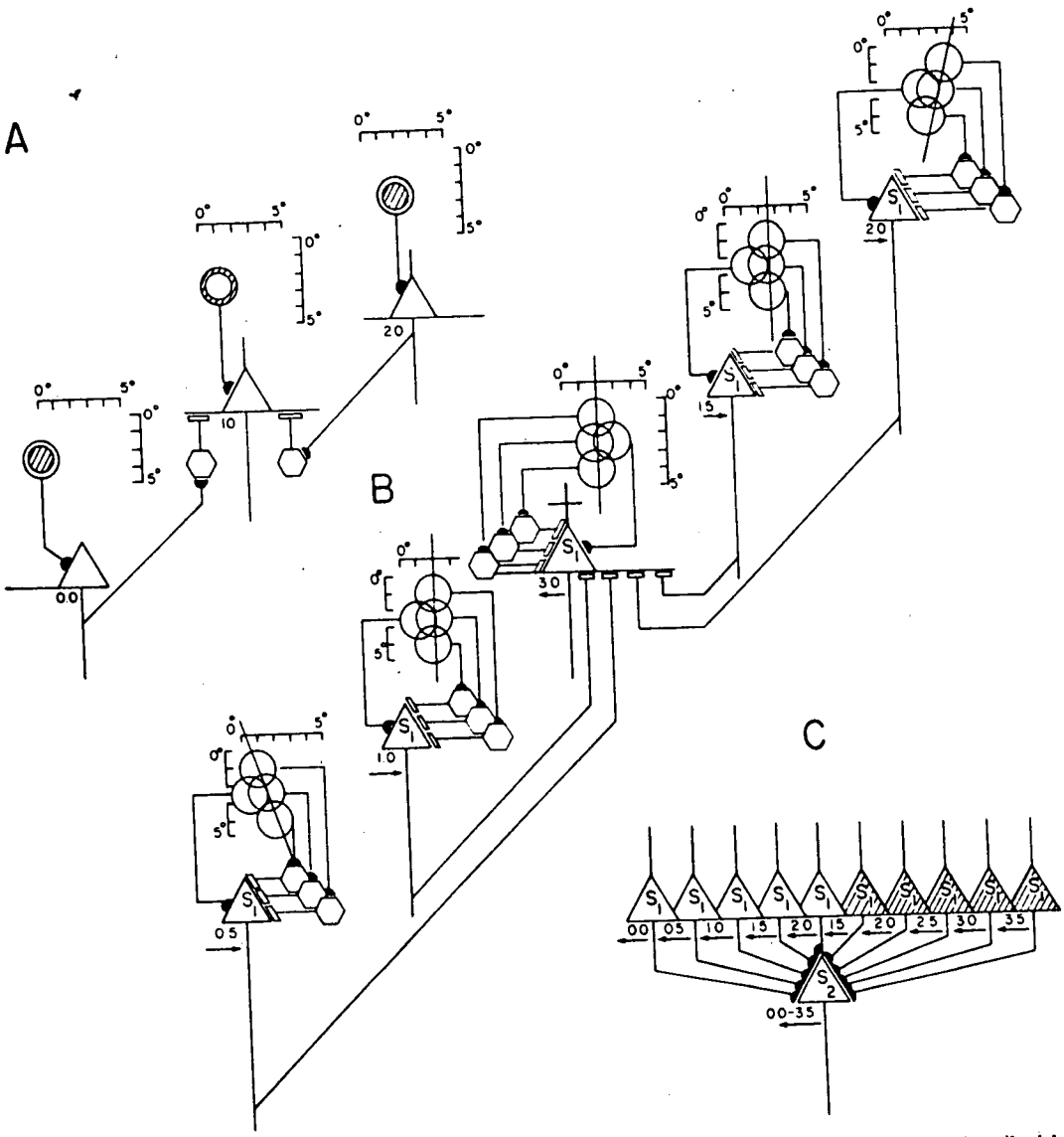


FIG. 15. A schematic network with three hierarchically organized levels. *A*: LGN interactions as described by Singer and Creutzfeldt (41). *B*: a cortical row of mutually interacting directionally analytic modules. A directionally selective neuron S_1 (3.0) is shown to receive three different types of inputs: *1*) circular-symmetric direct excitatory input from LGN, *2*) a highly localized linear array of inhibition anisotropically distributed (depicted by the hexagonally shaped internuncial cells), *3*) inhibition that is directionally in character from other S_1 units tuned to the opposite direction of motion. *C*: a directionally selective unit one level further up in the hierarchy. In this figure, all inhibitory synapses are depicted by open rectangles or open parallelograms; all excitatory synapses are depicted by black semicircles.

charge center, and an off-excitatory surround. The vertical and horizontal scale indicates this circular receptive field is located 1° right of and 2° below the area centralis. We also see that this 1.0 pyramidal receives inhibitory synaptic input (all inhibitory synaptic inputs are depicted by open rectangles and open parallelograms) from two adjoining internuncial cells. Internuncial neurons are depicted by hexagons in this figure. These in turn are excited by pyramidals 2.0 and 0.0, whose off-excitatory discharge centers are at 2.0° right of the area centralis and at the area centralis, respectively. This network is identical to that analyzed by Singer and Creutzfeldt (41). It is sufficient to account for many of the powerful

inhibitory and disinhibitory interactions we have observed here, particularly those not sensitive to sequence direction.

In Fig. 15*B*, cortical interactions responsible for directional selectivity are depicted for a DS-type 1 neuron (36). Pyramidal cell S_1 (3.0) is directionally selective only to onset sequences preferring leftward movement. All its inputs are from on-center LGB and on-center cortical neurons. We suggest such a cell receives at least three qualitatively distinct inputs. First, we see that the cell receives a direct excitatory input from a single (or a few) LGN neuron(s) with a circular receptive field, located at 3° right of the area centralis. Second, it receives three inhibitory inputs (three hexagon-shaped cells) that receive their inputs from (+2°, −1°), (+2°, −2°), and (+2°, −4°). Hence, neuron S_1 receives inhibition from a vertical flank of cells to the left of its excitatory discharge center. This simple spatial anisotropy of inhibition is sufficient to render the cell directionally selective. However, if this were all there was, the neuron would show three properties. *1*) There would be a portion of the receptive field that was on-excitatory and a portion that was on-inhibitory, and a boundary between them. To show directional selectivity to a pair of thin static flashes, the first would have to be shown to the inhibitory region and the second to the excitatory zone. *2*) The inhibition would show linear superposition; it would not depend on the timing of the two stimuli. A static stimulus could be placed in the inhibitory region either before or after the one placed in the excitatory regions and the inhibition would occur in both instances. *3*) The inhibition would be temporally related only to the onset of the one stimulus placed in the inhibitory zone. The latency of the inhibition would not be dependent on the onset of the stimulus placed in the excitatory zone. For a pair of static stimuli presented in a null direction, the inhibition should depend temporally on the onset of the first stimulus and be completely independent of the onset of the second stimulus.

We find that DS-type 1 neurons show all three implications of a simple arrangement of excitation and inhibition to be invariably incorrect. *1*) We do not find an inhibitory-excitatory boundary. Directionality is distributed without a seam throughout the receptive field. *2*) Inhibition is dependent on the timing of the two flashes; it is sequence dependent. *3*) The inhibition can sometimes be shown to depend on the onset of the second flash. Thus, at the lowest directionally selective level (viz., a DS-type 1 neuron) in the hierarchy, a more complicated network is required. We postulate that this third level of input into S_1 (3.0) comes from recurrent collaterals from the outputs of surrounding type 1 neurons tuned to the opposite direction. Figure 15*B* shows that S_1 (3.0) receives inhibitory inputs from adjoining S_1 (0.5), S_1 (1.0), S_1 (1.5), and S_1 (2.0), among others. They, in turn, are all excited by movement in a rightward direction. Hence, rightward movement stimulates S_1 (0.5), S_1 (1.0), S_1 (1.5), and S_1 (2.0), which, in turn, all inhibit S_1 (3.0). This latter inhibition, because it derived from the outputs of motion-selective neurons, is sequence dependent or sequence contingent, as we call it. Figure 15*B* shows some of these S_1 pyramidals turned to a slightly different orientation, S_1 (0.5) and S_1 (2.0), but that is not an essential aspect of the model. It is presumably these inhibitory recurrent collaterals from adjoining directionally selective S_1 pyramidals that accounts for Creutzfeldt, Kuhnt, and Benevento's (8) recording of IPSPs obtained only by null-direction movement. It is possible that recurrent collaterals from higher in the hierarchy (e.g., S_2 neurons shown in Fig. 15*C*) also inhibit the lower level S_1s.

The fact that small excursions (as small at 4′ of motion) still show directional selectivity is thought to derive from the multiple recurrent collateral inhibitory input from other type 1 neurons, each sensitive to a slightly different receptive-field location.

Although we have shown, in Fig. 15*B*, an on sequence directional analyzer, we assume identical networks exist that are directionally selective only to an off sequence, receiving solely off-excitatory discharge center input.

Figure 15*C* depicts a possible network for a DS-type 2 neuron (Schiller S_2), thought to be higher in the hierarchy. It is bimodal, having separate regions of on-directional selectivity and off-directional selectivity. It is generally found that S_2 neurons have larger receptive fields, depicted as 0.0–3.5° in Fig. 15*C*. We suppose, simply, that a group of S_1 on sequence-selective neurons (open triangles) and off sequence-selective neurons (shaded triangles) converge excitatory synaptic inputs

onto S_2. We assume the neural network of a DS-type 3 neuron (Schiller S_3) is essentially identical to that shown in Fig. 15*C*, except that the direction of the on sequence analyzers (on S_1's) is reversed from the direction of the off sequence analyzers (off S_1's). For example, all the shaded S_1's in Fig. 15*C* might prefer rightward movement, whereas all the unshaded S_1's in Fig. 15*C* would prefer leftward movement (39).

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