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SINGLE UNIT RECORDINGS OF CELLS RESPONSIVE TO VISUAL, SOMATIC, --ET
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ABSTRACT

SINGLE UNIT RECORDINGS OF CELLS RESPONSIVE TO VISUAL, SOMATIC, ACOUSTIC, AND NOXIOUS STIMULI IN THE SUPERIOR COLLICULUS OF THE GOLDEN HAMSTER

James P. Dixon, M.S.

Medical College of Virginia - Virginia Commonwealth University, 1978

Major Professor: Dr. Barry E. Stein

→ Responses of single neurons to sensory stimuli were studied in the superior colliculus of the golden hamster. A laminar organization was observed with cells in the superficial layers responding exclusively to visual stimuli, whereas the intermediate and deeper layers contained cells which responded to visual, somatic, acoustic, and multimodal inputs. Electrophysiological and pharmacological evidence is also presented which shows that cells of the lower laminae respond to nociceptive inputs.

The internal organization of visual receptive fields was studied in both upper and lower laminar cells with parametric variation of stationary and moving stimuli. Generally, optimal stimuli had low velocities ($< 50^\circ/\text{sec}$), were less than 50% of the receptive field diameter, and moved toward the upper nasal quadrant of visual space. Stimulus size and velocity were found to affect a cell's directional preference, which was a factor influencing the discharge frequency of 65% of the cells studied.

A somatotopic map was apparent in the intermediate and deep layers of the superior colliculus. Receptive fields of the head and forelimbs were located rostrally in the superior colliculus and

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SINGLE UNIT RECORDINGS OF CELLS RESPONSIVE TO VISUAL, SOMATIC, ACOUSTIC, AND NOXIOUS STIMULI IN THE SUPERIOR COLLICULUS OF THE GOLDEN HAMSTER.

Patrick's thesis

BY

⑩ James C. Dixon

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B.S., United States Air Force Academy, 1972

Thesis

Patrick

submitted in partial fulfillment of the requirements for the Degree of Master of Science in the Department of Physiology at the

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A somatotopic map was apparent in the intermediate and deep layers of the superior colliculus. Receptive fields of the head and forelimbs were located rostrally in the superior colliculus and

receptive fields of the hindquarters were located caudally. The somatic representation in the superior colliculus is in topographic register with the overlying visual representation. "Nociceptive" cells which were activated by pinch, pin-prick, and heat were found in the intermediate and deep layers of the superior colliculus. The resultant responses of these cells differed from the brief discharges commonly evoked by innocuous stimuli by showing a wind-up and a long, sustained train of spikes which often lasted over 60 seconds. Etorphine, a morphine-like analgesic, blocked responses to noxious stimuli while naloxone, a narcotic antagonist, reinstated responses.

A major function of the superior colliculus in all vertebrates is the orientation of the eyes, pinnae, head and body to visual, acoustic and somatic stimuli. Since characteristics of neurons in the hamster superior colliculus are not unlike the responses of superior colliculus cells in other mammals already studied, it is concluded that this is accomplished by similar neurophysiological processes in different species.

This thesis by James Patrick Dixon is accepted in its present form as satisfying the thesis requirement for the degree of Master of Science.

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INTRODUCTION

The behavioral consequences of destruction of the superior colliculus and visual cortex attest to the separate yet complementary functions of these two neural structures. It was once thought that removal of either the superior colliculus or visual cortex caused total blindness. It is now known, however, that neither structure alone is critical for visual perception, but that both are required if visual following and the perception of shapes, sizes and patterns is to take place.

The clearest functional division between the superior colliculus and visual cortex has been demonstrated in the golden hamster⁹⁰. If the superior colliculus is ablated in this species, disruption in visual orienting and following behavior occurs; yet the ability to differentiate shapes and patterns still exists (presumably because the geniculostriate system is intact). If the visual cortex is removed and the retinomesencephalic system is left intact, shapes and patterns are not identifiable but moving objects can be followed. Attempts have been made to relate these behavioral phenomena to the activity of single neurons. Since little is known about the physiology of superior colliculus neurons in the hamster, the present investigations were undertaken in order to document the characteristics of these cells.

LITERATURE REVIEW

BEHAVIORAL EFFECTS OF COLLICULAR LESIONS

The functional roles of many structures in the central nervous system have been inferred from investigations in which the structure was removed and the residual behavioral capacities of the animal tested. For instance, early studies reported that blindness occurred after either superior colliculus^{9,23} or cortical⁷¹ lesions. As Schneider^{90,91} and others^{10,43,58,100} point out, though, destroying the superior colliculus does not produce total blindness and neither does lesioning the visual cortex. Schneider has demonstrated that destruction of the superior colliculus in the hamster results in an "orienting" blindness. The animal can neither fixate nor follow a moving object. However, the hamster is able to discriminate between two stationary visual patterns. On the other hand, when the visual cortex is destroyed, the ability to discriminate patterns is lost but the animal can orient to and follow a moving object.

The ability to fixate upon a moving object is related to the function of those superior colliculus neurons which discharge prior to eye movements. Wurtz and Goldberg¹¹⁹ have shown in alert monkeys that the latency for moving the eyes after a light is presented in visual space increases when the superior colliculus is ablated. From these observations they concluded that the superior colliculus participates in the facilitation of eye movements, probably by decreasing the time necessary to acquire the visual stimulus.

Sprague and Meikle^{67,97,100} showed that superior colliculus lesions also produce certain abnormal responses to acoustic, tactile,

and nociceptive stimuli. These experiments showed that contralateral tactile and acoustic stimuli were not localized very easily, if at all. Noxious stimulation evoked strong emotional response, but the source of stimulation was poorly localized. Thus, in addition to having a visual orienting role the superior colliculus is implicated in acoustic and somesthetic orienting behavior.

EFFECTS OF ELECTRICAL STIMULATION OF THE SUPERIOR COLLICULUS

Electrical stimulation within the central nervous system is another technique used in documenting the function of a neural structure. In the superior colliculus some investigators^{30,85,87,88,118} found that certain intermediate and deep layer cells discharge prior to eye movements in the absence of a visual stimulus. Stimulation studies showed that eye movements can be elicited in both the cat^{7,106} and monkey^{84,88,89} by electrically activating these areas. Thus, the superior colliculus may be an integration center for directing the eyes. In fact, an integrated orientation of all sensory receptors was noted during electrical stimulation of the superior colliculus. It was noticed that the motor map of the deeper layers is topographically arranged and is in register with the sensory map of the superficial layers⁸⁹. Depending upon the stimulation site within the superior colliculus, particular movements of the pinnae, neck, body and limbs were produced^{40,86}. Thus, when the deeper layers of the superior colliculus are electrically stimulated, the turning of the head and body corresponds to the response of an animal when the hair or skin is touched. This stimulation of the superior colliculus produces excitatory

postsynaptic potentials in contralateral neck motoneurons and inhibitory postsynaptic potentials in ipsilateral motoneurons⁴; consequently, the animal turns to the side on which a stimulus occurs. Presumably, natural sensory stimuli act similarly via the same circuit.

Electrode stimulations in the superior colliculus of humans and cats in the early 1950's have implicated the superior colliculus in pain. Reyes *et. al.*⁸² showed that under local anesthesia humans complained of localized pain on the contralateral side of the body in response to electrical stimulations in the superior colliculus. Similar reactions indicative of pain were elicited in unanesthetized cats when the superior colliculus was either electrically stimulated or injected with strychnine⁹⁵. This line of investigation, however, was not pursued further due to the increasing interest generated by the superior colliculus' role in vision. Yet this provides evidence for implicating the superior colliculus in orienting behavior associated with pain.

ANATOMY

In vertebrates the retina projects to the optic tectum of the midbrain. In animals without a well-developed cortex the optic tectum is the primary termination site of these retinal fibers⁵⁵. If an animal has a visual cortex, however, some of the function of the superior colliculus may be appropriated by cortical neurons, and visual pattern discrimination is no longer dependent upon the superior colliculus⁹⁰. This is the case in mammals, which, in addition to the retinomesencephalic projection, also have a retinal projection

to the visual cortex via the lateral geniculate nucleus of the thalamus. Consequently, the optic tectum in "lower" animals (avian, amphibian, ichthyoid) performs many of the visual functions which are shared by the visual cortex and the superior colliculus in mammals.

The mammalian superior colliculus is a laminated structure consisting of alternating cellular and fibrous layers. From dorsal to ventral, they are as follows:

- 1) stratum zonale
- 2) stratum griseum superficiale
- 3) stratum opticum
- 4) stratum griseum intermediale
- 5) stratum album intermediale
- 6) stratum griseum profundum
- 7) stratum album profundum

These strata concentrically surround the periaqueductal gray matter. Unlike fish, birds and amphibians, which have a lateral ventricle, mammals do not have any delineating anatomical feature which separates the tegmentum from the superior colliculus⁴⁹. Since tectum means "roof" and is inappropriate in mammals, the term colliculus or "mound" is used.

Visual Inputs:

The retinal projection to the superior colliculus in the cat contains both crossed and uncrossed fibers, which enter the stratum opticum via the lateral brachium⁶⁸. For animals like the cat, the fibers central to the optic chiasm form a considerable binocular projection to the superior colliculus and the lateral geniculate nucleus. Thus, retinal axons from both eyes reach both sides of the central nervous system and provide binocular information to the

superior colliculus and, via the lateral geniculate nucleus, to the visual cortex. On the other hand, rodents like the hamster probably have an almost completely crossed optic pathway similar to that of the rat⁹². In the rat and cat the retinal nerves terminate throughout the contralateral stratum griseum superficiale^{36,39,59}. Hoffmann⁴¹ has found in the cat that some retinal fibers project exclusively from the retina to the superior colliculus, some project only to the lateral geniculate nucleus, and some fibers branch out to both. Fukuda and Stone²⁶, however, modify this by showing that W-cells (of the area centralis) project predominantly to the superior colliculus, X-cells (of the area centralis) project predominantly to the lateral geniculate nucleus, and Y-cells (primarily of the retina's periphery) project to both the midbrain and forebrain.

VISUAL INPUTS TO THE SUPERIOR COLLICULUS

Source	Termination
Contralateral retina	Stratum griseum superficiale
Ipsilateral retina	Stratum griseum superficiale
Ipsilateral visual cortex	All laminae of the superior colliculus (cat)
	Stratum griseum superficiale (rat)
Superior colliculus:	
Stratum opticum	Stratum opticum
Stratum griseum intermediale	Stratum griseum intermediale
Stratum griseum profundum	Stratum griseum profundum

CHART A

The visual corticotectal pathway in the cat is ipsilateral and enters the stratum opticum primarily via the lateral brachium, and

to a lesser extent, the medial brachium^{27,57}. These terminations are found throughout the superior colliculus^{11,57}, the central gray matter and subjacent tegmentum⁵⁷. In the rat⁵⁹ the visual cortico-tectal fibers terminate primarily in the bottom half of the stratum griseum superficiale. Additionally, the superior colliculus communicates with the opposite superior colliculus^{20,74}. Only stratum opticum and the deep gray laminae project to the opposite side, and they do so in a point-to-point, reciprocal manner and only in the rostral half of the superior colliculus (see Chart A).

The superior colliculus, therefore, receives visual information from the retina directly and indirectly after the information has been processed in the visual cortex. The result of such an arrangement is only now being investigated (see below, *PHYSIOLOGY*).

Nonvisual Inputs (Chart B):

Auditory input arrives in the superior colliculus from the auditory cortex^{24,27,57} and inferior colliculus^{73,81}. Lesions of the auditory cortex produced terminal degeneration in all layers below stratum opticum^{27,57}. Lesions of the inferior colliculus caused terminal degeneration ipsilaterally and contralaterally throughout the deeper layers of the superior colliculus in the cat⁸¹ and the monkey⁷³. This is consistent with the physiology of the superior colliculus (see below).

Somatic input to the superior colliculus enters by several different routes. The somatic cortex projects to the deeper layers of the ipsilateral superior colliculus by ascending dorsally from the cerebral peduncle and entering ventrolaterally^{27,57,96}. Nauta and

NONVISUAL INPUTS TO THE SUPERIOR COLLICULUS

Modality	Source	Termination
Acoustic	Auditory cortex	Strata intermediale Strata profundae
	Inferior colliculus	Strata intermediale Strata profundae
Somatic	Somatic cortex	Strata intermediale Strata profundae
	Trigeminal nucleus	Strata intermediale Strata profundae
	Spinothalamic pathway (Spinotectal tract)	Strata intermediale Strata profundae
Other	Mesencephalic reticular formation (n. cuneiformis)	Stratum griseum intermediale and profundum
	Periaqueductal gray	Stratum griseum intermediale and profundum
	Frontal eye fields	Stratum zonale Stratum opticum Strata intermediale Strata profundae
	Occipital eye fields	Stratum zonale Stratum opticum Strata intermediale Strata profundae
	Motor cortex (Precentral gyrus)	Stratum griseum superficiale Strata intermediale Strata profundae
	Limbic cortex	Strata intermediale Strata profundae
	Prefrontal association cortex	Strata intermediale Strata profundae

CHART B

Kuypers⁷⁵ showed that lesions of the trigeminal nucleus produced terminal degenerations bilaterally in the deep layers of the superior colliculus. The contribution of the nucleus caudalis of the

trigeminal system may provide the basis for the single unit activity in the superior colliculus in response to noxious stimuli from the face and head^{77,108} (see below).

Somatic input from the limbs and trunk is provided by the spinothalamic pathway, which includes the spinotectal projection. In the rat⁶, the spinotectal tract originates from the whole length of the spinal cord and distributes to the caudal half of the contralateral superior colliculus. These fiber terminals were found only in stratum album intermediale and strata profundum, whereas in the monkey they were found throughout all the deeper layers below stratum opticum^{53,66}. Another recently identified connection to the superior colliculus is the nucleus cuneiformis of the mesencephalic reticular formation. Edwards and Olmos¹⁹ used autoradiographic tracing methods to show that this nucleus projects primarily to stratum griseum intermediale and stratum griseum profundum with some fibers located in the superficial laminae of the superior colliculus. There are some projections from the nucleus cuneiformis which cross in the commissure of the superior colliculus and terminate only in the deeper layers of the opposite superior colliculus. In addition, the periaqueductal gray and cerebellum also project to the deep layers^{5,37}.

The frontal and occipital eye fields, motor cortex areas concerned with conjugate eye deviations project to the superior colliculus. Both project to the strata intermediale and profundae, as evidenced by terminal degeneration there after cortical lesions^{8,12,57}. More recently it has been shown that the frontal

eye fields also project to stratum zonale and stratum opticum⁵⁶. In addition, the precentral gyrus of the motor cortex and the limbic cortex project fibers to the intermediate and deeper laminae of the superior colliculus^{57,94}. The motor cortex has also been shown to project to the bottom of stratum griseum superficiale⁹⁴.

Until recently, the frontal eye fields were thought to be the only frontal areas of the cortex to project to the superior colliculus. It now has been shown autoradiographically that the prefrontal association cortex projects to the intermediate and deep strata as well³¹.

The importance of somesthetic input to the superior colliculus is apparent from the "orientation" role assigned to the superior colliculus. However, the other collicular inputs (n. cuneiformis, periaqueductal gray, motor eye fields, and motor, limbic and association cortex areas) have not been thoroughly investigated and their roles are speculative.

Efferent Projections (Chart C):

The superior colliculus has numerous efferent projections responsible for motor reactions. Consequently the eyes, head, pinnae, and limbs move via activation of the deep layers of the superior colliculus.

Edwards²⁰ showed that there are descending crossed and uncrossed projections from the superior colliculus to the central gray matter. These fibers reach the nucleus of Darkschewitsch and the interstitial nucleus of Cajal, and a dense area overlying the oculomotor nucleus. This last area corresponds to the nucleus of the medial

longitudinal fasciculus, which projects to and from the abducens nucleus and thus may form part of the communication net for superior colliculus-oculomotor controls^{20,60}. Others have also found that the superior colliculus projects to the nuclei of Darkschewitsch and Cajal, which are accessory nuclei of oculomotor function. The axons to these nuclei originate from the deeper laminae of the superior colliculus, and form a decussating group of fibers which are often called the "predorsal bundle". Destruction of the predorsal bundle causes a bilateral degeneration in the accessory nuclei³, and contributes to the terminal degeneration found medially in the reticular formation^{3,11,38,75}, in the inferior olivary complex^{25,38}, and in the dorsal part of the ventral horn of the spinal cord as far caudally as C-6³. This degeneration in Rexed laminae 6 through 8 was also seen by Nyberg-Hansen⁷⁶ and Petras⁸⁰, and provides evidence for a "tectospinal" tract. So far, though, no superior colliculus axons have been found to terminate upon α motoneurons and Edwards¹⁸ indicates in the cat that there is not a projection from the superior colliculus significant enough to be called a "tectospinal" tract.

A second descending bundle from the superior colliculus is the ipsilateral projection to the mesencephalic reticular formation. These superior colliculus fibers were found to be scattered and few in number³. The third descending bundle, on the other hand, is the largest and projects from the deep laminae of the superior colliculus ipsilaterally to the dorsolateral pontine nucleus^{3,11,74}. Here the terminal degeneration was found to be significant, especially in the dorsomedial part of the nucleus. Additionally, some degeneration in

this bundle occurred in the contralateral pontine nucleus, penetrated the ipsilateral magnocellular region of the medial geniculate nucleus in the thalamus³, and ended in the contralateral motor facial nucleus and parabigeminal nucleus³⁸.

EFFERENT PROJECTIONS FROM THE SUPERIOR COLLICULUS

Sites of Termination

N. Darkschewitsch	N. Cajal
N. Medial Longitudinal Fasciculus	Reticular Formation
Inferior Olivary Complex	Thalamus
Spinal Cord (Rexed laminae 6-7-8)	Motor Facial Nucleus
Dorsolateral Pontine Nucleus	Parabigeminal Nucleus
Suprageniculate Nucleus	Pretectum
Pulvinar	Substantia Nigra
"H" Fields of Forel	Zona Incerta

CHART C

Ascending tectofugal fibers project to the pretectum^{3,38,74}, the suprageniculate nucleus^{3,11,35,63,74}, the pulvinar^{3,35,38,63}, the nuclei of the caudal thalamus^{3,35,38,52,74}, the ventral region of the lateral geniculate body^{3,38,74}, and the magnocellular portion of the medial geniculate body³. Additionally, tectofugal fibers in the cat distribute to the substantia nigra¹¹ and zona incerta and "H" fields of Forel⁷⁴.

The importance of such extensive projections from the superior colliculus has not yet been elucidated. Certainly much of the output of the superior colliculus has to do with efficient elicitation of eye movements, as has already been shown. Generally it is thought that all forms of sensory stimulation in some way reach the superior colliculus and is integrated for localization and

appropriate muscular response to or away from the stimulus. Consequently, the animal survives its encounters with the environment.

PHYSIOLOGY

Visual Cells-- Receptive Field Properties

If an animal has monocular vision like the mouse¹⁶, rat⁹², and hamster¹¹³, almost all of the fibers project to the contralateral superior colliculus after crossing in the optic chiasm. This partially accounts for the few binocular cells found in the colliculus of these animals. In animals like the cat¹⁰⁷ and monkey¹⁴ the ipsilateral corticotectal pathway is primarily responsible for the number of binocular cells in the superior colliculus. In addition, the ipsilateral retinal projection to the superior colliculus is more extensive than in rodents. The result in either case is a representation, or map, of visual space existing within the superficial layers of the superior colliculus. In rodents the visual map is of the contralateral eye. In the cat and monkey almost a complete visual field from both eyes is represented in each superior colliculus.

The map is composed of receptive fields of the visual cells in the superior colliculus. A receptive field of a visual cell is a region within which a light stimulus influences the cell. The receptive field of each visual cell in the superior colliculus is organized according to direct or indirect retinal inputs (see above, ANATOMY).

The topographic map has some common features in all mammals. The medial half of the superior colliculus receives visual

information from the superior part of the visual field and the lateral half of the superior colliculus receives visual information from the inferior part of the visual field. As electrode penetrations are made medial to lateral in the superior colliculus, receptive fields are located from superior to inferior in the visual field. Likewise, the nasal (anterior) visual fields reach the rostral parts of the superior colliculus and the temporal (posterior) visual fields reach the caudal parts of the superior colliculus.

The borders of the receptive fields overlap. As a visual stimulus moves in the visual field, thousands of collicular cells are excited or inhibited depending upon the manner with which each cell perceives the stimulus as it moves within the cell's receptive field. Thus, the stimulus' location on the map is delineated. This may provide the basis for an animal's ability to locate objects in visual space. Therefore, it is of considerable interest to document the stimulus characteristics which evoke responses in superior colliculus cells.

Superior colliculus visual cells respond to flashing lights with responses at light onset, offset ("ON","OFF") or at both. However, movement evokes a more sustained and vigorous response and is therefore "preferred" over stationary stimuli^{97,107}. Although stimulus shape is not critical in evoking optimal responses from superior colliculus cells^{14,107}, the size of the stimulus may be. In both the cat¹⁰⁷ and monkey^{14,114} some cells gave optimal responses which were evoked by stimuli considerably smaller than the receptive field. In general, however, the primary criterion was that the

stimulus not overlap the receptive field borders and encroach upon the suppressive region known to border upon the receptive field^{14,65,101,114}. In addition to stimulus size, other parameters such as velocity, direction of movement, rate of stimulus presentation, and the degree of attention the animal pays to the stimulus are all very influential on a collicular cell's response.

Although the optimum velocity of stimulus movement varies from cell to cell within the superior colliculus, in general it has been found that preferred velocities range from 0.5 up to 50°/sec^{14,101,107,109}, with 10°/sec and 50°/sec most often found to be optimal. In one study velocity was shown to change the responses to the directions of stimulus movement, resulting in a different preferred direction of movement¹⁰¹.

Direction of movement has been found to be critical in some visual cortical cells^{46,112}, and this same characteristic is true of some collicular cells. There is a difference, however, between directional selectivity in cortical cells and superior colliculus cells. Cortical cells respond least to stimulus movement which is perpendicular to the "preferred", or optimal direction. On the other hand, directionally selective cells of the superior colliculus respond poorly or not at all in the "null" direction which is 180° (or opposite) to the preferred direction. The proportion of collicular cells which are directionally selective varies from species to species (see Chart D). This raises doubt as to the behavioral importance of directional selectivity. Directional selectivity is a property of individual neurons which supposedly facilitates eye movements in order to acquire and maintain fixation on a moving

stimulus. It is also one of the properties which can be influenced by the visual cortex. For instance, in the cat it has been shown that the incidence of directional selectivity in superior colliculus cells drops from greater than 50% to below 10% after cortical ablation^{72,79,116}. Obviously the information of the visual cortex is used to modify the information in the superior colliculus insofar as directional selectivity is concerned. Yet, the functional importance of directional selectivity in superior colliculus cells remains obscure and it varies considerably among species.

PROPORTION OF SUPERIOR COLLICULUS CELLS
DEMONSTRATING DIRECTIONAL SELECTIVITY

Species	Per Cent
Monkey ²⁸	10
Cat ¹⁰⁷	75
Hamster ⁸³	58
Rat ⁴⁷	0

CHART D

Iterative rate is the interval between the presentation of successive stimuli. A response decrement is observed when stimuli are presented at a rate too fast to allow for sufficient recovery^{14,44,76,117}. This response decrement, called "fatigue", can be lessened if the iterative rate is long enough to allow the cell to "recover" from the previous stimulus.

Response fatigue is related to another response decrement that is observed behaviorally: "habituation". Wurtz and Goldberg²⁹ have shown a similar neurophysiological phenomenon in which decreased

responses of a cell occur when a monkey stops attending to a stimulus (the receptive field target) located in the receptive field of the cell being studied. They observed that

1. the superior colliculus cell's discharge is enhanced if attention is directed toward the receptive field target during a saccade;
2. "habituation" does not occur on successive saccades as long as attention is directed toward the receptive field target;
3. "habituation" does occur when attention wanes.

They concluded from these observations that the superior colliculus is important in the shifting of visual attention. It therefore seems reasonable to suppose that the rate of stimulus presentation and behavioral attention are physiologically related.

Nonvisual Cells

Superior colliculus neurons in the deeper laminae have been found to respond to acoustic stimuli and to electrical stimulation of the inferior colliculus. Syka and Straschill¹¹¹ have shown that stimulation of the inferior colliculus causes cells in the stratum griseum intermediale and stratum griseum profundum to respond with short latencies (< 5 msec), which are probably monosynaptically connected, and with longer latencies (5-200 msec), which are multisynaptically connected. These acoustic cells prefer complex sounds^{16,33,113}, such as rustling, hissing, clicking, crackling, handclaps, etc., all of which encompass broad-band sounds of many frequencies. Pure tones are usually ineffective. One study in the mouse¹⁶ shows that acoustic cells were often anatomically grouped in clusters and many times had multimodal input, i.e., responded to both acoustic and somatic stimuli. Since not all sounds evoke a response from these neurons, it is probable that these cells are

primarily involved in orientation and attentive roles rather than in the discrimination of frequency.

Tactile representation, though not visual representation, has been shown to exist in the deeper laminae of the superior colliculus as early as the first few days after birth¹⁰³. Somatic units in adult animals respond to electrical stimulation of the skin¹⁰², tapping and squeezing of the skin, displacement of body hair and vibrissae, and manipulation of subcutaneous tissues^{16,102,105,113}. Most of these cells were activated by cutaneous, low threshold mechanoreceptive stimuli^{102,105}.

Somatic cells have been shown to be organized in a topographic map similar to that of the superficial visual cells^{16,104,105,113}. Thus, somatic cells in the same penetration usually have overlapping receptive fields on the same part of the body^{105,113}, and electrode penetrations made rostral to caudal in the superior colliculus find somatic cells with receptive fields which are located, respectively, from head to tail on the body. This somatotopic organization is consistent with the anatomy of somesthetic projections to the superior colliculus (see above) and provides the physiological basis for an animal's ability to orient to tactile stimuli.

Another system of inputs to the superior colliculus has been demonstrated physiologically. Cooper *et. al.*¹³ and Fillenz²¹, respectively found multiunit (goat) and single unit (cat) discharges caused by stretching the extraocular muscles. In addition it has been shown that collicular cells can be driven by electrical stimulation of extraocular and neck muscle afferents¹ and fore- and hindlimb

afferents², thus demonstrating proprioceptive input to the superior colliculus. Extraocular muscle control does, in fact, depend in part upon superior colliculus input to the abducens nucleus³⁴. The monosynaptic, and to a larger extent, disynaptic connections to this oculomotor control center demonstrates the importance of feedback (via visual afferents) on orienting and following movements (oculomotor response) which is considered a function of the superior colliculus. Any orientation response, whether visual or nonvisual, is a complicated system of movements altered in the very next instant by what changes are perceived by the animal with regard to its immediate environmental surroundings and its own body position. Even though the visual orientation role has been most elegantly demonstrated in the hamster, little is known about the physiology of the hamster superior colliculus. For this reason the following experiments were conducted.

METHODS

Fifty-four adult golden hamsters which weighed 85-170 grams were used in these experiments. All of the animals were anesthetized with urethane (1.3 mg/kg i.p.). Supplemental doses of urethane (0.25 mg/kg i.p.) were used as required in order to maintain the level of anesthesia. Atropine sulfate (4.0 mg/kg i.p.) was given to reduce secretory fluids in the respiratory tract which could interfere with respiration, and additionally to ensure pupillary dilation. Body temperature was kept at 36-38°C by a circulating hot water pad. In some early experiments eight animals were paralyzed with Flaxedil (20.0 mg i.m.). During these experiments the animals were

artificially respired with 40% oxygen and 60% nitrous oxide. It was usually difficult to maintain artificial respiration for long periods of time; thus, this technique was no longer used after the unparalyzed condition showed that eye movements were either absent or minimal.

Each animal's head was immobilized by mounting it in a modified stereotaxic head-holder using a horizontal bar which was anchored to the skull with two screws. A bridge of dental acrylic extended from the screws to the horizontal bar. The bar was positioned caudal to the pinnae and attached to a stereotaxic apparatus by standard ear bars. This structure provided the animal with a visual field that was unobstructed from most angles, and also allowed access to the body and limbs for presentation of somatic stimuli. Each hamster's eyes were covered with clear contact lenses to prevent corneal drying. The eyelids were held open with traction sutures. A translucent plexiglass hemisphere was positioned 28 cm in front of the animal and centered on the animal's nose. The plexiglass hemisphere provided a surface upon which visual stimuli could be presented and receptive fields mapped. Receptive field location in visual space was calculated in degrees of laterality measured from the nose. Permanent records were kept of the size, location and organization of each receptive field, which were then compared to receptive fields in the same penetration and other penetrations.

A slow speed drill was used to open an area approximately 16 mm^2 in the cranium, exposing the sagittal sinus and both cerebral hemispheres. Effort was made to preserve the sinus and cortex. All electrode penetrations were made through the dura with fine tungsten

electrodes whose tips were electrolytically etched to 1-4 μm and whose shafts were insulated with isonel varnish. Impedances of the electrodes were measured at 60 Hz and ranged from 6.0 to over 10.0 $\text{M}\Omega$. Electrode penetrations into the superior colliculus were vertical and placed so that cells were sampled from throughout the structure. This procedure required that the electrode puncture the sagittal sinus in order to reach the medial and caudal portions of the superior colliculus. These penetrations, as with those which entered the cortex, produced no bleeding except after the electrode was removed. The bleeding that occurred then was easily controlled using gel foam.

Unit discharges were amplified and presented over a loudspeaker and oscillographically displayed. Selected unit responses were photographed from taped recordings made of each cell, and impulse counts were registered on an Ortec 770 counter after passing them through an Ortec single channel analyzer. Only well-isolated single units with a 2:1 signal-to-noise ratio or greater were included for documentation, although some multiunit recordings were made at the surface of the superior colliculus. Unit waveshape and duration were documented for all isolated cells, as was the travel distance of the electrode during the time that the cell was isolated. Usually this distance exceeded 100 μm . Unit waveshapes were always biphasic, even when poorly isolated, and were indicative of cell rather than axonal recordings⁴⁵.

A variety of stimuli was presented while searching for and during isolation of a collicular cell. Visual stimuli consisted of

various sizes of moving and stationary pulsed light ($7.6-9.4 \text{ cd/m}^2$) on a dark background (0.1 cd/m^2) and dark spots or bars (0.2 cd/m^2) on a light background (50 cd/m^2). Initially a hand-held Keeler pantoscope projecting a spot or bar of light was used to search in the visual field for multiunit and single unit response. This stimulus was also used to map the receptive field of all cells responsive to visual stimuli, either by moving it from the periphery towards the area of maximum response, or by flashing it ON and OFF. During this procedure qualitative judgements were made concerning the size, velocity, and direction of the optimal stimulus. Quantitative evaluation of the cell's response to various stimuli was accomplished by presenting the stimuli under the electronic control of a galvanometer-driven mirror system. This system provided accurate repetition of spots or bars of light of various sizes, and at precise velocities, distances of travel, directions of movement and iterative rates. Auditory stimuli were usually complex sounds such as hand-claps, clicks, and hisses, and whistles. Somatic stimuli consisted of manual movement or compression of the skin, muscles, and deep tissue, and the use of airstreams, von Frey hairs, and camel's-hair brushes to move body hair and vibrissae. Nociceptive stimuli were produced by pinching the skin with a serrated forceps, pin-prick, and an ember held 2-4 mm above the skin. At the conclusion of a successful electrode penetration, small electrolytic lesions ($70\mu\text{A}$ @ 20 sec) were placed at strategic locations in order to aid in localizing the recorded cells in the brain.

At the conclusion of an experiment the animal was sacrificed with urethane and perfused through the heart with saline and 10% formalin. The brain was removed, and frozen sections were cut, mounted, and stained with cresyl violet for histological reconstruction of the electrode penetrations.

RESULTS

A total of 313 cells were studied in the hamster midbrain and 210 of them were histologically identified to be in the superior colliculus. The other units were found in the periaqueductal gray matter, the subjacent tegmentum, and pretectum. After a cell was isolated its receptive field borders were delineated. This was followed by a series of quantitative tests to be completed on each cell in which the number of impulses evoked by various stimuli was used as the criterion for judging the effectiveness of those stimuli. Conducting the full series of tests on each cell was not always possible. However, many cells were observed for 3-5 hours and quantitative data was accumulated for each of the various stimulus parameters discussed below. The numbers and statistics for these parameters is presented under each heading.

Laminar Organization and Modality Segregation

Cells in the upper layers of the superior colliculus (stratum opticum and above) were found to respond exclusively to visual stimuli. However, intermediate and deeper layer cells formed a population which responded to somatic, acoustic, noxious, or visual stimuli. Some cells responded to more than one sensory modality (multimodal) and 18 could not be activated by any of the stimuli

presented. Cells responding to visual stimuli decreased with increasing depth in the superior colliculus whereas acoustic and especially somatic- or noxious-responding cells became more abundant until the subjacent tegmentum was reached (see Fig 1). The population then consisted of a greater ratio (31/57) of unresponsive cells. Based on these experiments the central gray, which forms the other bordering structure subjacent to the superior colliculus, was populated with a greater proportion (10/19) of noxious-responding cells than the superior colliculus. No segregation between neural structures could be made based strictly upon physiologic properties, i.e., the cell responses were enough alike so that the superior colliculus could not be differentiated from the subjacent tegmentum or periaqueductal gray. Only after histological reconstruction could cells in the superior colliculus be accurately distinguished.

Visual Receptive Fields

After the electrode passed through the dura, it was lowered approximately 2.5 mm below the surface of the cortex, at which point a continuously moving visual stimulus was passed over the visual field until dense multiunit response developed from a quiet background. The normal procedure for isolating collicular cells was a slow, electrode descent (1-5 micron steps). During the slow, step-wise descent visual, somatic, acoustic and noxious stimuli were presented. Even using this procedure, it was difficult to isolate cells at the very top of the colliculus.

The difficulty in isolating cells in the most superficial layer of the superior colliculus has also been noted in a study of the

mouse¹⁶. The multiunit visual hash, which is so prevalent in the most superficial lamina of the superior colliculus in the hamster and mouse and possibly due to cell and axon density, made it very easy to define the area of the visual field represented in that region of the superior colliculus. It was noted that the visual topography of the superior colliculus was basically the same as for other mammalian species (see above, PHYSIOLOGY).

Mapping a visual receptive field required two procedures. Initially a small ($< 3^0$) spot or rectangle of light was moved inward from the periphery of the visual field at various velocities. The borders of the receptive field were delineated as points where vigorous discharges were elicited. At the same time, qualitative observations were made regarding the best direction and velocity range over which the cell responded. Once this "movement receptive field" was defined, the receptive field was mapped again in 80 cells using a stationary pulsed light source flashed within and around the movement receptive field. This second response area, referred to as the "stationary receptive field", was sometimes superimposed on the movement receptive field, but in some cells was distinctly different.

The movement receptive field was usually oval in shape and was oriented most often with the longer axis in the horizontal plane. For all of the visual receptive fields a 1.15:1 mean ratio existed for horizontal to vertical axes, even though as much as a 2:1 ratio was common for individual receptive fields. Although the movement and stationary receptive fields usually had common centers, the borders of the latter did sometimes extend beyond the borders of the movement receptive fields (see Fig 2).

Visual cells in the superior colliculus preferred moving stimuli to stationary pulsed light. Once the optimal velocity and direction was found, the cell could be reliably driven. Exceptions to this were found, for example a few cells preferred stationary stimuli and would not fire to a moving stimulus no matter how it was presented.

Most of the cells were tested for a response to a stationary pulsed light which equalled 5-26% of the receptive field diameter and was flashed repeatedly within and around the movement receptive field. Discharges were elicited by cells at both light onset ("ON") and offset ("OFF") (n=44). Cells responding only to "ON" (n=20) or "OFF" (n=10) were also encountered.

The receptive fields of visual cells in the superior colliculus were not arranged in a fashion typical of retinal, lateral geniculate nucleus, or cortical visual cells. Rather than a side-by-side or center-surround segregation of "ON" and "OFF" responses, a less discrete organization was found. In all cells the center of the receptive field responded the same with both large or small pulsating lights. Then, as identical stimuli were progressively moved toward the periphery, the response began to wane.

In "ON-OFF" cells, the response was more variable. Even though the probability of an "ON" or "OFF" was unpredictable throughout the receptive field, unresponsive subregions were always in the periphery. In 14 of these cells, one or more of the peripheral regions became responsive to either "ON" or "OFF" only (see Fig 3). In most of the "ON-OFF" cells, either the "ON" or the "OFF" would attenuate to the repetitive pulses of light throughout the stationary receptive

field. Additionally, if the interpulse interval was too short (< 1 sec), the cell would discharge only to the "preferred" pulse, i.e., either "ON" or "OFF", or would not fire at all.

Response Attenuation of Visual Cells

Successive, identical, moving stimuli produced fewer discharges (Fig 4) in 70% of the cells ($n=47$) studied for their response to repeating stimuli. A vigorous response could be reinstated after a 20-30 second interval between stimuli (the interstimulus interval). In order to study and evaluate the stimulus parameters discussed below, an interstimulus interval of 10-15 seconds was chosen. This minimized response attenuation and also allowed sufficient time for acquiring an adequate number of trials for each phase of the test protocol.

Effect of Stimulus Size on Visual Response

While mapping the receptive fields of the visual cells it was apparent that the stimulus need not equal the size of the receptive field in order to evoke a strong response. In fact, stimuli smaller than the receptive field evoked very strong responses. Various sizes of moving light stimuli were passed through the center of the receptive field at an optimum velocity. During the study of twenty-three cells, the stimuli were presented from one or two directions. The first direction selected was the optimum direction of movement that was determined qualitatively during receptive field mapping or during testing for directional preference. A cell responding equally for all directions received the stimuli in the horizontal axis. The mean discharge rates were then compared. Ten repetitions of each

movement in every direction tested were presented at 10 or 15 second intervals. Smaller stimuli were preferred by most of the cells tested (see Fig 5). In fact, all but three of the cells preferred stimuli that were 50% or less of the receptive field diameter. Discharge frequencies did increase as stimulus size increased. However, this spatial summation only occurred at the smaller stimulus sizes from one to 35 percent of the receptive field diameter (see Figs 6,7). Once the optimum width was reached, any increase in stimulus size produced either no change in the discharge rate in half the cells, or caused a progressively reduced response (spatial inhibition, see Fig 6), as occurred in the other 50% of the cells. Apparently an interaction between spatial summation and inhibition determines the discharge frequency of a cell to a given stimulus.

The size-response relationship also interacts with another receptive field characteristic: the cell's preference for a given direction of stimulus movement. A cell without directional preference evokes almost the same number of impulses in response to a stimulus presented from all eight directions (4 axes separated by 45°). The spatial summation for stimulus sizes of 1-35% of the receptive field diameter was the same for opposing directions (example, see Fig 7) when a cell was not directionally selective. However, if one direction was selectively preferred by the cell, then the relationship between stimulus width and discharge rate became opposite for the two opposing directions of movement (see Fig 8). In this last example, an increasing discharge occurred in the preferred direction, but in the "null", or least preferred direction a decreased discharge occurred.

Velocity Preferences of Visual Cells

During mapping of a cell's movement receptive field, it was noticed that the velocity of the stimulus had to be within narrow limits to produce an optimal response. Very high velocities of greater than $200^{\circ}/\text{sec}$ almost always failed to elicit strong responses and in many cases no response could be elicited at all, whereas very slow velocities less than $50^{\circ}/\text{sec}$ usually produced strong responses. This variability was studied quantitatively with electronically controlled stimuli. The velocity range employed was $2\text{--}485^{\circ}/\text{sec}$. Ten trials at 10 or 15 second intervals were performed at each of the predetermined velocities in the preferred direction. When all directions were equally effective, stimuli were presented in the horizontal axis. Initially, a small, rectangular light stimulus approximating the optimum size was moved through the center of the receptive field at a velocity near the qualitatively determined optimum. Velocities above and below the optimum were then presented to determine the range of velocities to which the cells ($n=45$) would respond.

Collicular cells generally preferred slower velocities ($< 50^{\circ}/\text{sec}$), with 50% of them failing to discharge at velocities in excess of $150^{\circ}/\text{sec}$. The most frequently occurring optimum velocity for both superficial and deep layers of the superior colliculus was $10^{\circ}/\text{sec}$ (see Fig 9). The optimum velocity was apparent for each cell, since variance above or below it produced a significant response decrement (see Fig 10). In cells with slower preferred velocities, variance from the optimum velocity was observed to be even more

critical. Even though the variance was only a matter of a few degrees per second, the resultant effect was more extreme. This was noted qualitatively during the study of each cell, however it was confirmed for all the cells once the combined data was normalized and plotted semilogarithmically. Figure 11 suggests that a percent variance on either side of the optimum velocity (100%) will produce similar response decrements.

Directional Preferences of Visual Cells

It had been noticed from initial attempts to activate a cell that some directions elicited stronger responses than others, and in 88 cells responses to different directions of stimulus movement were tested. Stimuli of less than 35% of the receptive field diameter were presented at optimal velocities. The light stimulus was moved in four axes (8 directions separated by 45°). The number of discharges per traverse for 10 trials at 10 or 15 second intervals was documented for each of the eight directions. The duration of time that the stimulus was moving within the receptive field was calculated, and mean impulses per second were compared for the eight directions.

The criterion for classifying a cell as directionally "assymetrical" was that the response differences between two opposing directions exceed one standard error of the mean or greater. The opposing directions of movement were then called the "preferred" direction and the "null" direction and were separated by 180° or, in several instances, 135° . A majority (65%) of the cells tested showed this preferred-null relationship. Reversing the contrast between the

stimulus and background in several of these cells did not reverse the directional preference.

If the number of discharges evoked by two opposing directions of movement was 2:1 or greater, then the cell was classified as directionally "selective". Using this criterion, 59% of the cells were so classified. Collicular cells preferred stimulus movement towards the upper nasal quadrant of visual space (see Fig 12).

The degree to which a cell was selectively tuned to a direction varied from one cell to the next. For example, one cell preferring vertical movements showed a gradual but progressive decrease in its impulse frequency when the direction of movement was altered on either side by 45° , 90° and 135° . The extreme was found in two cells whose preferred and null directions were perpendicular and not opposite. These cells were similar to directionally selective cortical cells.

Since size and velocity were potent influences on a cell's response, interactions between these parameters and directional preference occurred. Often, the number of discharges for opposing directions became progressively similar as the velocity deviated from the optimum (see Fig 10). Thus, directional preference did not manifest itself if a cell was tested at extreme velocities away from optimum. A similar effect occurred when the optimum stimulus size was exceeded. In one cell a loss of directional preference was noted when the stimulus exceeded the optimum size even though it was still smaller than the diameter of the receptive field.

Nonvisual Representation in the Superior Colliculus

The majority (82%) of the somatic cells isolated in and around the superior colliculus (n=106) were activated by gentle stimulation of body hair or skin. Subcutaneous tissues were also manipulated, but very few (18%) of the superior colliculus cells responded. The responses to the tactile stimuli were always transient even though the stimuli were maintained, and they had discharge properties typical of low threshold mechanoreceptors.

The receptive fields of the somatic cells in the superior colliculus were organized in a somatotopic plan similar to other species. Although this plan was not documented in great detail, it was noticed that the head and forelimbs were represented rostrally in the superior colliculus and the hindlimbs were represented caudally. The sizes of these receptive fields ranged from a few square millimeters on the face to more than half the contralateral body surface.

Two subpopulations of the somatic cells found in the hamster midbrain responded to noxious stimuli. An ember was used to produce noxious heat, raising the skin temperatures of the nares, tail and glabrous skin of the paws to 45-50° C. Pinches were produced by a serrated forceps. Pin-pricks were also used. Those midbrain cells which fired to both innocuous and noxious stimuli (n=28) were designated "nonspecific nociceptive cells". These cells were optimally driven by brief but forceful (noxious) stimulations of the body extremities, the nares, pinnae, tail and body skin. The "nociceptive receptive field" delineated by these noxious stimulations always encompassed the receptive field delineated by the innocuous

stimulations. The latter fields were confined to small regions of the body whereas nociceptive receptive fields were almost always bilateral and extended over most of the body surface. The most effective zones for noxious stimulation were the tail, pinnae and paws. Stimulating the trunk usually produced little or no response in these cells. The response to noxious inputs, in contrast to the response to light tactile manipulations, was long and sustained when the stimulation was maintained and lasted for as long as two minutes after the noxious input was terminated (see Fig 13).

The "nonspecific nociceptive cells" were activated not only by gentle somatic stimuli, but also by moving and stationary pulsed light stimuli (n=3) and acoustic stimuli (n=1). Two cells responded to "trimodal" inputs of visual, tactile, and noxious origin.

A second subpopulation of somatic cells responded exclusively to forceful (noxious) levels of stimulation (n=37). Their responses were similar to the "nonspecific nociceptive cells" except that innocuous stimuli were ineffective in driving them. For this reason they were designated "specific nociceptive cells." Together the specific and nonspecific nociceptive cells made up a significant portion of the nonvisual representation in the lower laminae of the superior colliculus, and also in the surrounding tissue (see Fig 14).

The nociceptive response of these cells, both specific and non-specific, could be attenuated or completely abolished without affecting their non-noxious response properties by administering the morphine-like drug, etorphine (0.001-0.1 mg/kg). This narcotic

ameliorates responses to pain, and was observed in these experiments to leave responses to non-noxious stimuli intact (see Fig 15).

The analgesic effects of etorphine were reversed by the administration of the narcotic antagonist, naloxone (1 mg/kg). Following the intraperitoneal injection of this drug, the nociceptive response was reinstated, usually within several minutes. These pharmacological data provided further evidence for designating these cells as nociceptive.

Acoustic cells (n=11) were encountered very infrequently in the hamster midbrain. These cells were only responsive to complex sounds; whistling and tonal bars were ineffective. Thus, hissing, handclaps, and fingersnaps produced brisk, transient responses which, if presented on the ipsilateral side of the head, were poor or nonexistent. Sounds presented contralaterally elicited more impulses.

DISCUSSION

Visual Receptive Fields

In the upper layers of the hamster superior colliculus the cells were only activated by visual stimuli moving within small receptive fields which were organized in a visuotopic fashion. The receptive fields of the visual cells became larger in the lower layers in the superior colliculus. This corresponds to the presence of direct retinal projections (small receptive fields) to upper laminae and widespread corticotectal connections (large receptive fields) to the deeper laminae^{33,64,79}.

Regional segregation of responses to stationary light ("ON" and "OFF") within a receptive field, a characteristic of the geniculostriate system, was not present in the hamster collicular cells. The receptive fields, however, were not homogeneous in the hamster colliculus, but were similar to those of the monkey¹¹⁴. Highly responsive and poorly responsive subregions existed in the receptive fields of both upper and lower laminar cells. This receptive field nonhomogeneity was also noticed when visual stimuli of different sizes were compared for their response effectiveness. The response of a cell usually increased as the stimulus width increased. However, once an optimal stimulus size was reached, response declined with further increases in stimulus width. This occurred even though the stimulus was smaller than the receptive field. What appears to be the excitatory receptive field borders apparently encompasses both excitatory and inhibitory spatial subregions. This receptive field pattern has been noted in the cat^{17,42,61} and monkey¹¹⁴, and for both species the effectiveness of a given stimulus will be determined, in part, by the interaction of excitatory and inhibitory processes which may have different spatial and temporal characteristics.

Velocity Selectivity

Slowly moving targets (10^0 /sec or less), regardless of the direction of movement or stimulus size, were the most effective in eliciting the highest response for the majority of collicular cells. Tiao and Blakemore¹¹³ have also noted the effectiveness of slowly moving stimuli and have suggested that these cells may be involved

in stabilizing eye position relative to the head, since the hamster makes head, rather than eye, movements. The coordination of eye and head movements is important in all visually active animals, and one may reasonably expect low velocity cells to perform the same function in all species which have them, whether the role of these cells is in stabilizing eye position or in facilitating the correction of small tracking errors. Yet, in contrast to the hamster, the cat¹⁰¹ and the monkey¹⁴ (both of which have collicular cells which prefer slowly moving stimuli) make frequent eye movements. Thus the argument for a "stabilizing" role is weak. It appears that very few of the visual receptive field characteristics of superior colliculus cells are significantly different in these three species.

Directional Selectivity

With the exception of the rat⁴⁷ the one receptive field property of superior colliculus cells which has been observed in all species studied thus far is an optimum direction of stimulus movement. Although noted by others^{83,110,113}, estimates of the percentage of superior colliculus visual cells having directional selectivity vary, sometimes remarkably. Differences in stimulus properties may have contributed significantly to these discrepancies. In this study directional selectivity was not found to be immutable: its presence was dependent upon stimulus size and velocity, and was most pronounced when stimulus size and velocity were at their respective optima. Directional selectivity could be minimized or obliterated by significant changes in stimulus parameters. Such changes may possibly have led to an underestimation of the incidence during other studies of this receptive field property.

Laminar Organization

Below stratum opticum visual cells were encountered, albeit less frequently. Somatic, acoustic and multimodal cells became prominent features of the intermediate and deeper laminae of the superior colliculus, and also the upper subjacent tegmentum and periaqueductal grey. Thus, stratification of modalities in the superior colliculus was displayed. The upper layers were exclusively visual; the lower layers were multimodal.

Somatic Representation

A general somatotopic plan was noted and found to be in register with the overlapping visuotopic map. Thus, the anterior superior colliculus represented the face and central visual space, whereas the posterior superior colliculus represented the caudal aspects of the body and peripheral visual space. This topography is described in greater detail for the hamster by Tiao and Blakemore¹¹³ and Finlay *et. al.*²², for the mouse by Drager and Hubel¹⁶, and for the cat by Stein *et. al.*¹⁰⁵.

The majority of the superior colliculus somatic cells were responsive to gentle cutaneous stimuli and had receptive field sizes which corresponded to peripheral innervation density. These cells have also been described in the cat¹⁰⁵ as having low threshold mechanoreceptive properties. Additionally, cells requiring sub-cutaneous stimulation have been found in the cat¹⁰⁵ but not cells with high threshold properties^{33,105}. Similar findings have been documented here, except that cells which required or were optimally activated by noxious stimuli were also found. These nociceptive

cells were histologically located in the intermediate and deeper layers of the superior colliculus, and the subjacent tegmentum, periaqueductal gray and pretectum.

It seems unlikely that this nociceptive representation is unique to the hamster. It is presumably a characteristic of all mammals. Electrical stimulation of the superior colliculus has been shown to produce painful sensations in man⁸² and behavior indicative of pain in cat⁹⁵. These observations are consistent with the presence of nociceptive collicular cells in these species. Previous failure to locate nociceptive cells in the cat midbrain^{16,33} may have resulted from the use of nitrous oxide, an analgesic which depresses neuronal responses to noxious stimuli^{15,54}.

The specific role of the superior colliculus in a pain experience is speculative. Indeed, central processing of pain apparently entails many aspects which presently remain elusive, but which involve at least two components: motivational/affective and sensory discriminative. Melzack and Casey⁶⁹ believe the motivational/affective component of pain is subserved by paleospinothalamic pathways to the reticular formation and the mesencephalon and the sensory discriminative component primarily by neospinothalamic pathways to the ventrobasal complex of the thalamus. The superior colliculus, located in the mesencephalon, would therefore fall within the motivational/affective aspect of this theory. Additionally, the superior colliculus nociceptive cells have large receptive fields which make it highly unlikely that they would signal precise, spatial information. Consequently, these cells may

only alert the animal to the presence (and maybe the laterality) of a noxious stimulus. This expectation is consistent with lesion experiments in cats^{97,99,100}, which showed maladaptive responses to noxious stimuli after ablation of the superior colliculus.

Similarity To Other Species

Species similarities in the organization and receptive field properties of collicular cells are striking. Stratification of modalities is essentially the same^{14,16,33,44,62,102,105} in the rodent, lagomorph, carnivore, and primate, as is the somatotopic register^{16,105,112}. The behavioral consequences after lesioning the superior colliculus are similar in many species^{32,33,48,79,98}. In fact, the within-species differences between the physiology of the visual cortex and superior colliculus are far greater than the differences between superior colliculus physiology in different species. This is a consequence of the segregation of function found in the mammalian visual system, although the tree shrew may be an exception^{50,93,115}.

Interspecies differences exist in directional selectivity, a receptive field characteristic observed for nearly all species thus far studied. Each species prefers a certain direction of movement. The involvement of the visual cortex in this trait is also species specific. In the cat, directional selectivity is highly dependent upon the intact visual cortex, and the direction most frequently preferred is nasal-temporal along the horizontal axis¹⁰⁷. In the rabbit, the presence or absence of the visual cortex is inconsequential and the preferred direction is temporal-nasal along the

horizontal axis⁶². In the ground squirrel⁷⁰ the visual cortex is also uninvolved, but the preferred directions are randomly distributed throughout all axes. In the mouse¹⁶ the preferred direction is inferior-superior with a slight nasal component. The present study shows that directional selectivity in the hamster superior colliculus is a combination of that found in the rabbit and mouse, with preferred directions oriented primarily within 90° across the upper nasal quadrant of visual space.

Directional selectivity has been assumed to be a necessary property for orienting behavior. Yet, there is still no evidence to suggest that the orienting or attentive capabilities of a specie are directly or indirectly related to a direction of movement most often found to be optimum for superior colliculus cells. Nor is the incidence of directional selectivity related to the ability of an animal to orient to and follow environmental targets. After lesions of area 17 in the visual cortex of the cat, orienting and attentive responses are unchanged⁷⁹ even though the incidence of directionally selective cells is low. The incidence of directionally selective cells in the monkey is naturally low, yet attentive and orienting behavior is excellent^{14,28}. The intact rat shows appropriate orienting behavior, but has been reported to have no cells with directional selectivity in its superior colliculus⁴⁷ and shows attentive and orienting deficits when the superior colliculus is lesioned^{32,98}. Other subtle, but critical, species differences can be expected to be found in the future. At present, however, it appears that a variety of animals have been provided with the same basic neural

system, one that appears to adapt to different environmental settings where attentive and orienting behavior to very different stimuli are necessary for survival.

FIGURE LEGENDS

Figure 1

Cell distribution by sensory modality in the hamster midbrain. Coronal sections are approximately 375 microns apart, displayed from rostral to caudal. Laminae are numbered 1-4, consecutively representing stratum griseum superficiale, stratum opticum, strata intermediale, and strata profundum. The upper laminae (stratum opticum and above) are strictly made up of visual cells $\square$. The lower laminae contain visual, somatic $\blacksquare$ (innocuous-responding and noxious-responding), acoustic Δ , and multimodal o cells.

Figure 2

A comparison of the difference in sizes between movement and stationary receptive fields (RFs). Moving and stationary stimuli demarcated the border of each cell's receptive field (n=80). When these maps were compared, the majority of the time (68%) they coincided (within a 3% calculated error). A significant number (32%) of the stationary receptive fields did exceed the borders of the movement receptive fields.

Figure 3

The stationary receptive field of a superficial layer cell. A stationary light (3° in size) pulsed throughout the receptive field produced primarily "ON" and "OFF" responses in its center. This cell was classified "ON-OFF" ($\pm$), even though its peripheral regions evoked either "ON" (+) or "OFF" (-) to the same stimulus. o = no response.

Figure 4

Response attenuation to repetitive stimuli of a cell located in stratum griseum intermediale. Using an interstimulus interval of one second, a small light bar was repeatedly passed through the center of the receptive field. Increasing the interstimulus interval to 20 seconds allowed sufficient rest for the cell to regain responsiveness to within 78% of its initial discharge.

Figure 5

Comparison of the stimulus widths which evoked the highest discharge frequencies (optimum response) of the cells tested ($n=23$). Collicular cells seldom preferred stimuli which filled the receptive field (RF), but rather gave brisk responses to very small stimuli (10% or less of the receptive field diameter).

Figure 6

Comparison of the effect of various stimulus widths on the discharge frequency of an intermediate layer cell. Stimulus widths from 0.6° (3% of the receptive field diameter) to 20° (100% of the receptive field diameter) were moved through the receptive field (RF) horizontally in a nasal-temporal direction. Stimulus length was maintained at 3.5° . The mean response for 10 trials at each stimulus width is plotted to show the discharge frequency in impulses per second above spontaneous rate (S.R.). Vertical lines are the standard errors of the mean. Discharge frequency increased as the stimulus size was increased (spatial summation) up to 30% of the receptive field diameter. Progressively larger stimuli produced a declining response, even at sizes smaller than the receptive field (spatial inhibition).

Figure 7

The size-response relationship of a superficial layer cell which was not directionally selective. Each point represents the mean response above spontaneous rate (S.R.) of ten trials. Vertical lines represent standard errors of the mean. Arrows indicate the direction of movement. In both directions, frequency response increased dramatically as stimulus size increased from 8% to 29% of the receptive field (RF) diameter. Beyond that size the increase in response was not significant.

Figure 8

The size-response relationship of a superficial layer cell which was directionally selective. Each point represents the mean increase or decrease in frequency response from the spontaneous rate (S.R.). Vertical lines represent standard errors of the mean for 10 repetitions. Arrows indicate the direction of movement through the receptive field (RF) in the horizontal plane: (o) is in the temporal to nasal, or "preferred" direction; (●) is in the nasal to temporal, or "null" direction. As the stimulus size increased, response changes became increasingly divergent. The "preferred" direction evoked more discharges and the "null" direction evoked fewer discharges.

Figure 9

Comparison of the percentage of upper and lower layer cells and their preferred velocities. An optimal-sized stimulus in the preferred direction was presented at from $2^{\circ}/\text{sec}$ to $485^{\circ}/\text{sec}$. The preferred velocities (those evoking the highest discharges) were

then categorized by 10^0 increments. Slow velocities of 10^0 /sec or less were preferred most often by both upper and lower layer cells, even though a greater number of the cells below stratum opticum (S.O.) preferred high velocities.

Figure 10

Response changes of an intermediate layer, directionally selective cell as a function of stimulus velocity. Each point represents the mean response above spontaneous rate (S.R.) of ten presentations at that velocity. Vertical lines represent standard errors of the mean. Arrows show the "preferred" (●) and "null" (○) directions. A velocity of 40^0 /sec was optimum for this cell. The response difference between the two directions is less when the stimulus is presented very fast or very slow.

Figure 11

A comparison of optimum velocities versus optimum responses for the population of cells studied ($n=45$). Both frequency responses and discharge rates were normalized and graphed semilogarithmically as percentages. Thus optimum velocity (100%) evokes the optimum response (100%), and variations from the optimum velocity cause a response decrement. This chart suggests that constant changes (as a function of percent) in velocity throughout the whole velocity range evoke similar response changes (as a function of percent).

Figure 12

A plot of the preferred directions of 52 collicular cells. This polar coordinate map shows that the direction of movement most preferred in the hamster superior colliculus is towards the upper nasal quadrant of visual space.

Figure 13

Sustained response of a deep layer cell stimulated with a noxious pinch of the tail. Each point represents the frequency response in impulses per second for the previous two seconds. Typical of all nociceptors, however stimulated (pinch or heat), were the "wind-up" discharges and long train of impulses which outlasted the period of stimulation (in this case, three seconds).

Figure 14

Distribution of nociceptive-responding cells in the midbrain of the hamster. These cells were histologically located throughout the whole rostro-caudal length of the colliculus. Coronal sections are displayed from rostral to caudal, approximately 375 microns apart. Laminae are numbered 1-4, consecutively representing *stratum griseum superficiale*, *stratum opticum*, *strata intermediale*, and *strata profundum*. The nonspecific nociceptive (o) and specific nociceptive (●) cells were found only in the laminae below *stratum opticum* and in the periaqueductal gray (Pag) and the tegmentum (Teg).

Figure 15

A "nonspecific nociceptive cell" located in *stratum griseum intermediale*. This cell, in addition to responding to noxious inputs, also discharged in response to moving and stationary pulsed light. The visual receptive field was mapped using a moving light bar, and the discharges shown in the oscillograms occurred when the contralateral forepaw was heated to 45-50° C (A). (B). The cell reacted to a stationary pulsed light by ceasing its spontaneous activity at light onset (upward trace) and by giving a vigorous

burst at light offset (downward trace). This visual response was not affected by etorphine (see B). The cell's nociceptive response (C) is compared to its response after administration of etorphine (D). When the attenuation produced by etorphine was reversed by naloxone, a narcotic antagonist, the cell again responded to the noxious heat (E). Traces above the oscillograms indicate the onset of the noxious stimulus (upward) and offset (downward). The responses of this cell during each of these exercises are plotted (F) versus time as impulses per second above spontaneous activity*.



Figure 1

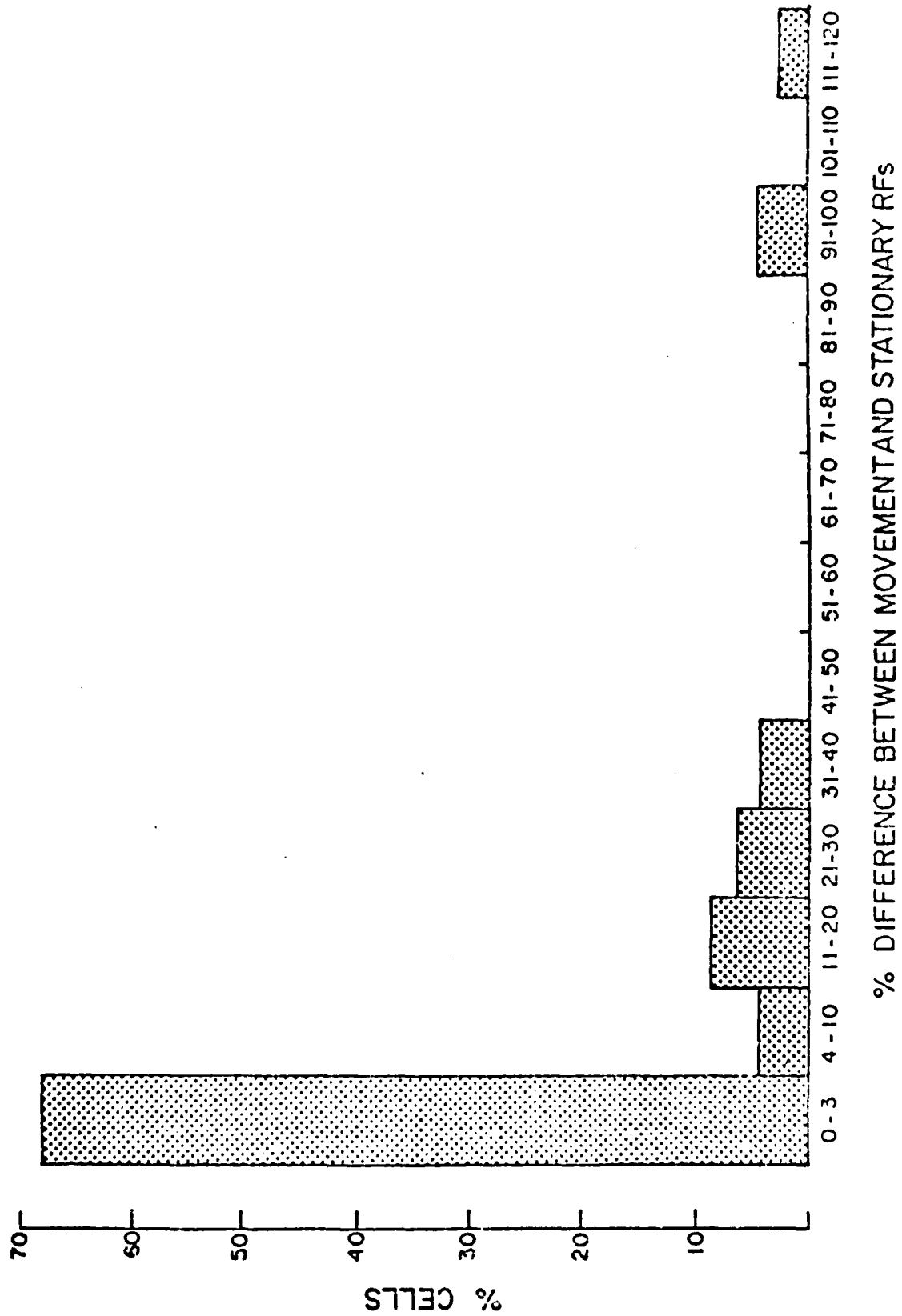


Figure 2

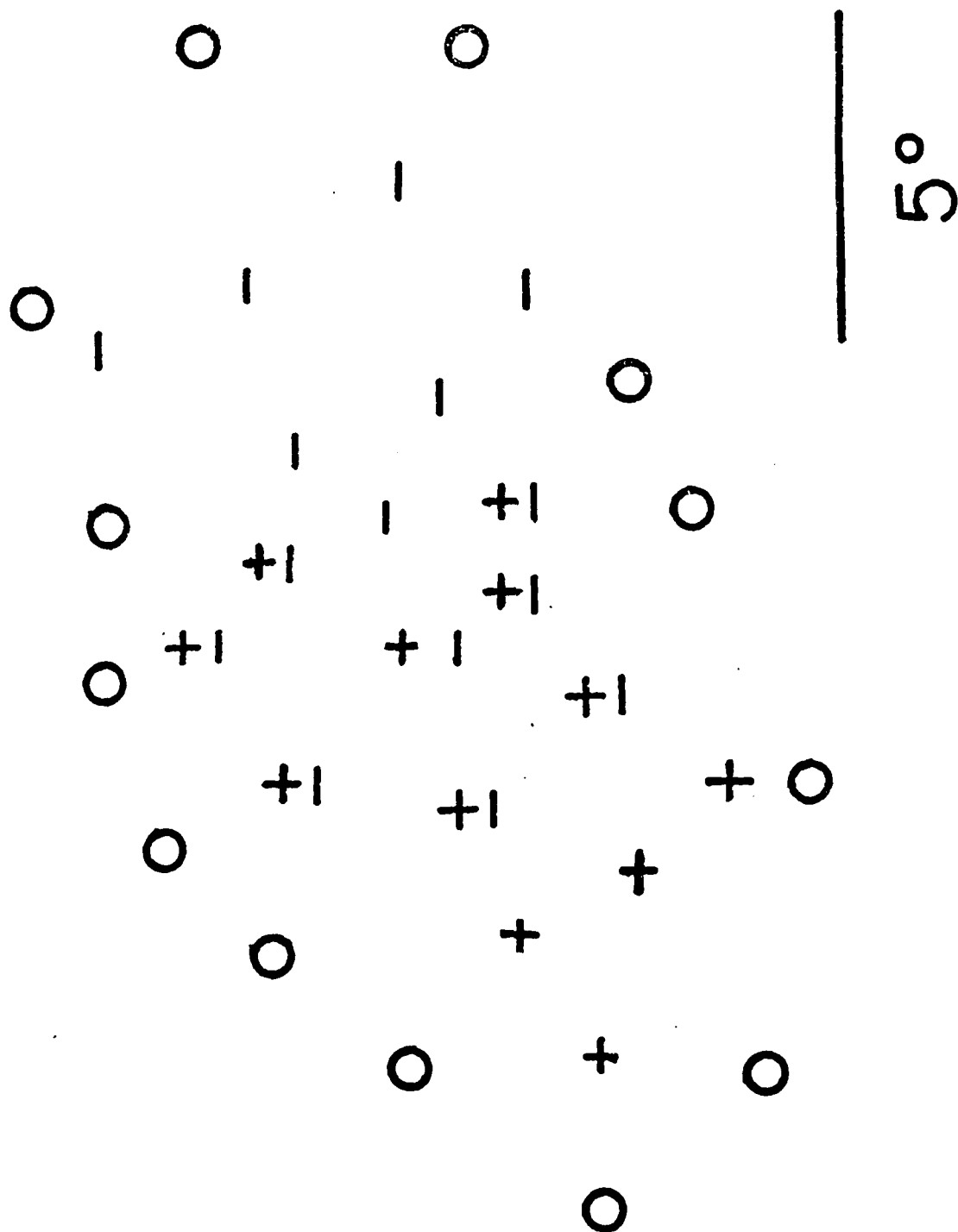


Figure 3

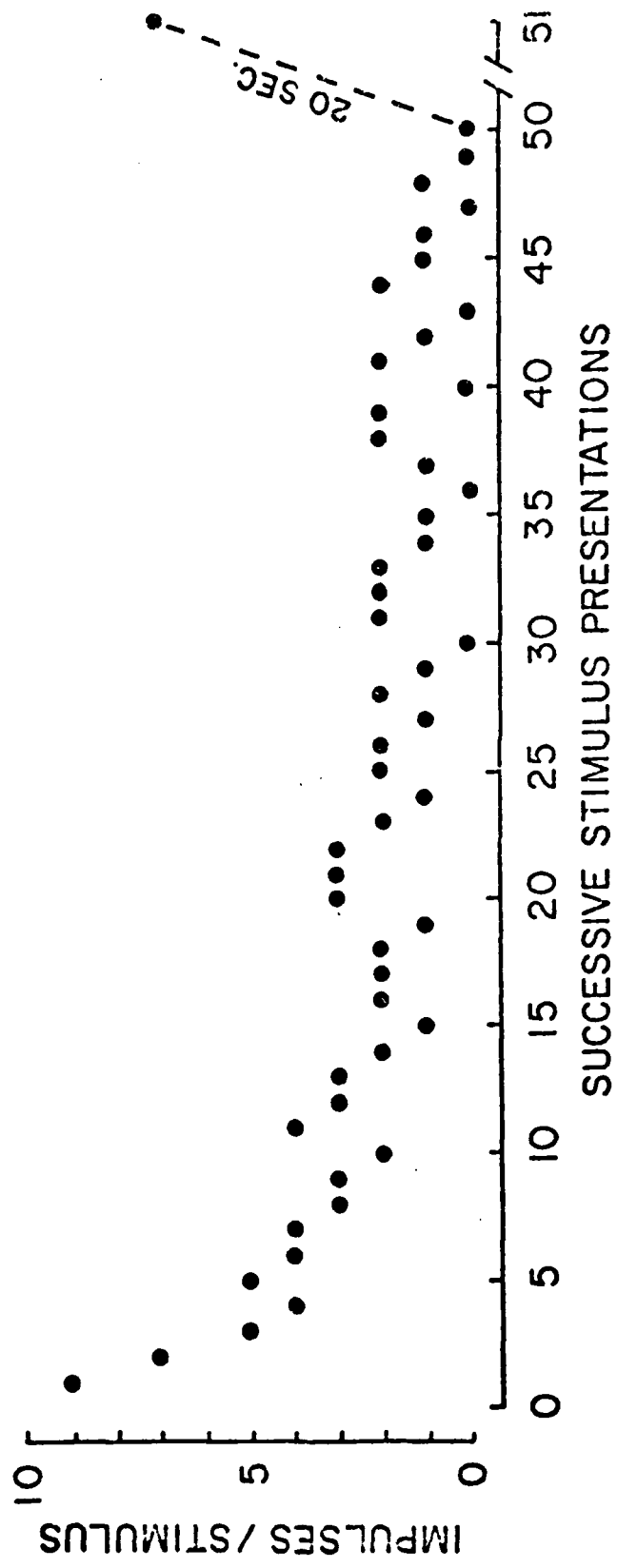


Figure 4

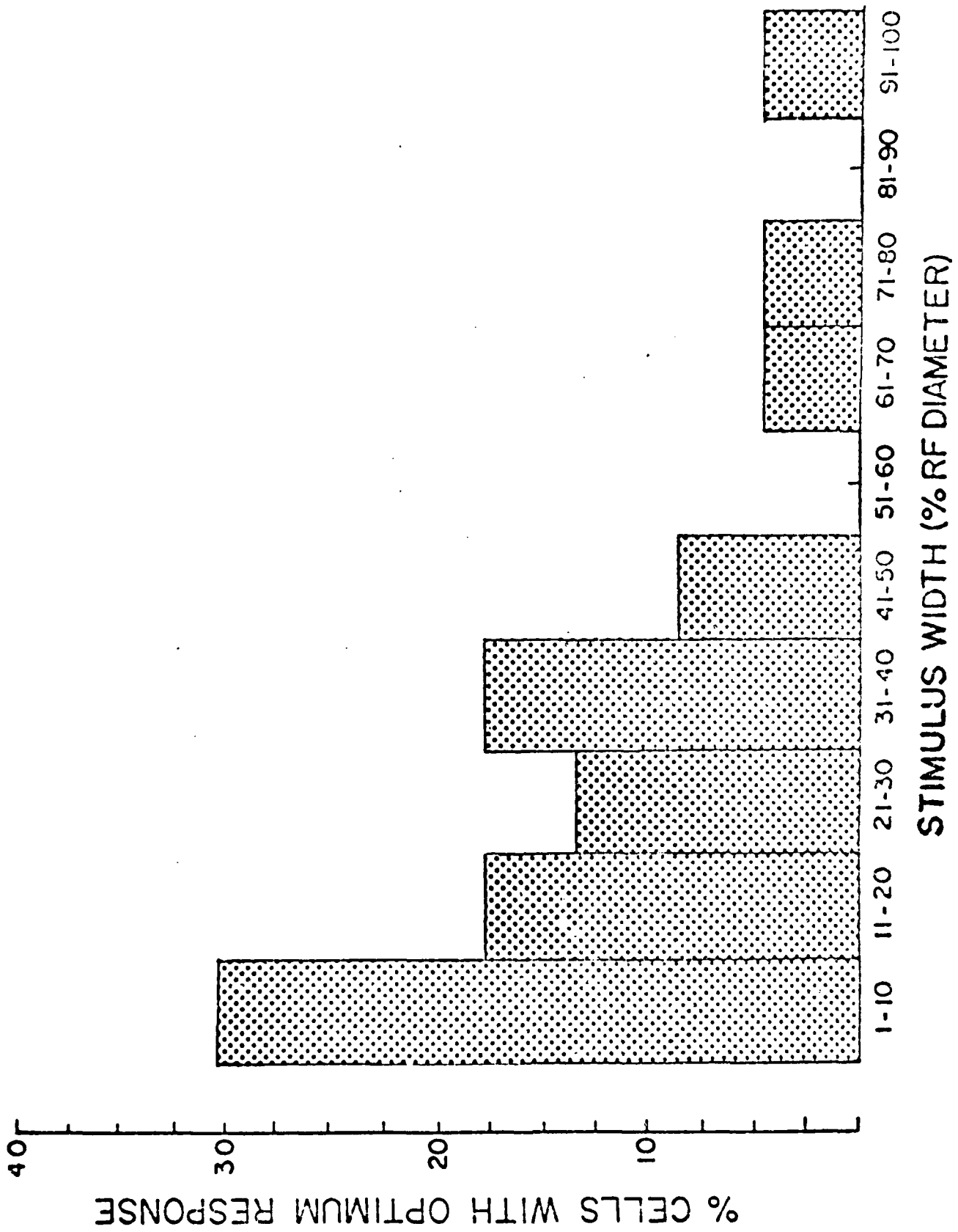


Figure 5

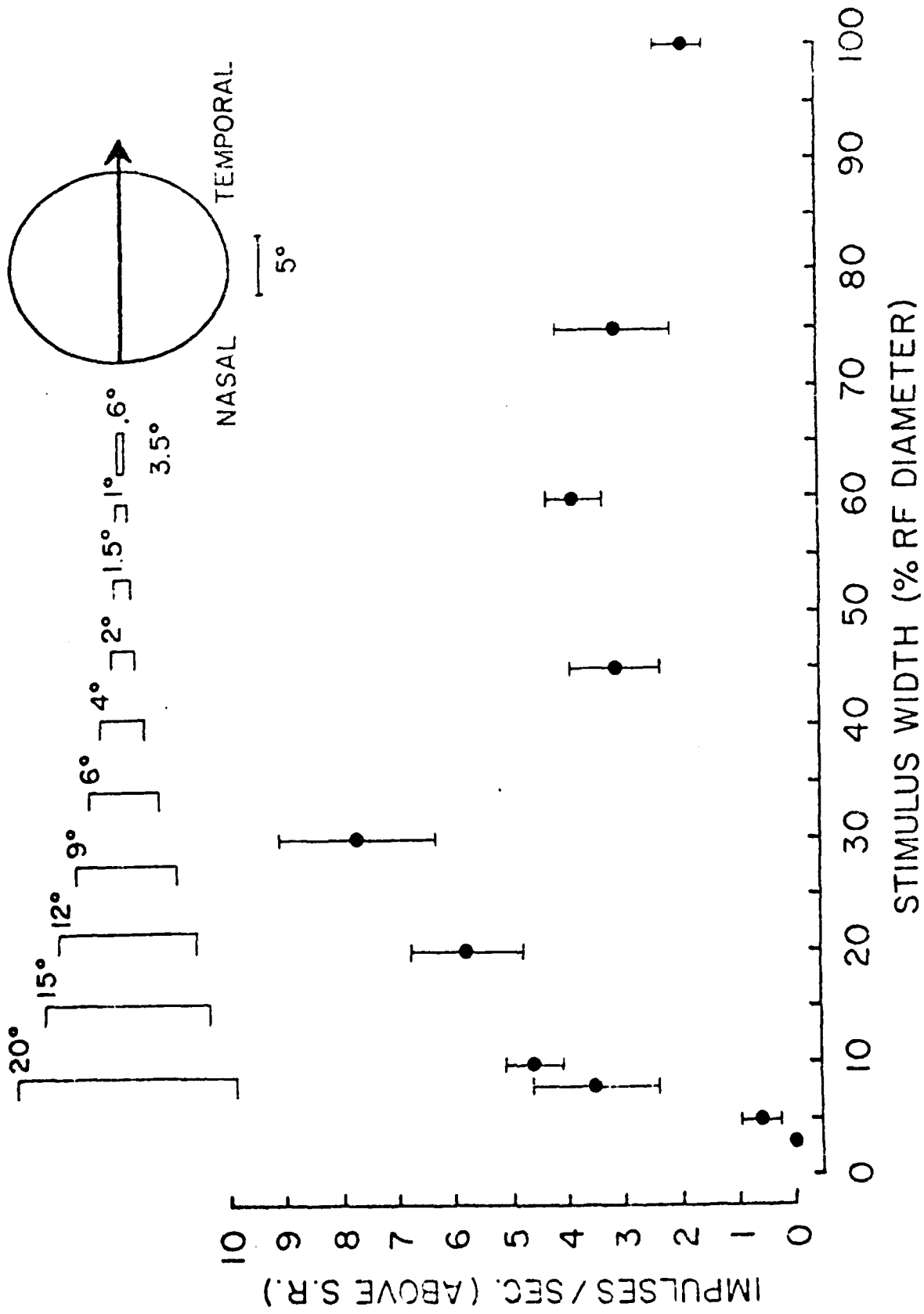


Figure 6

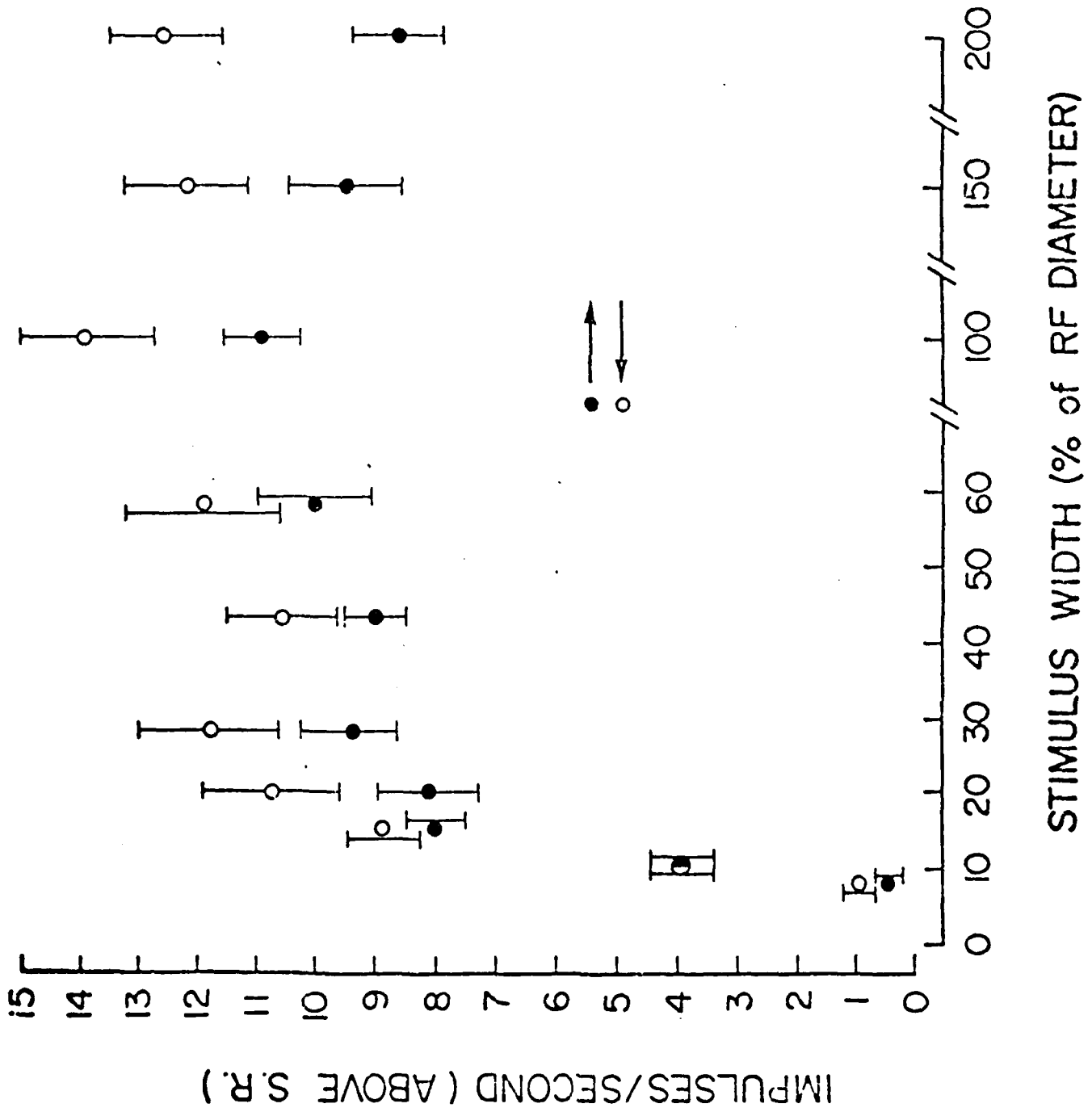


Figure 7

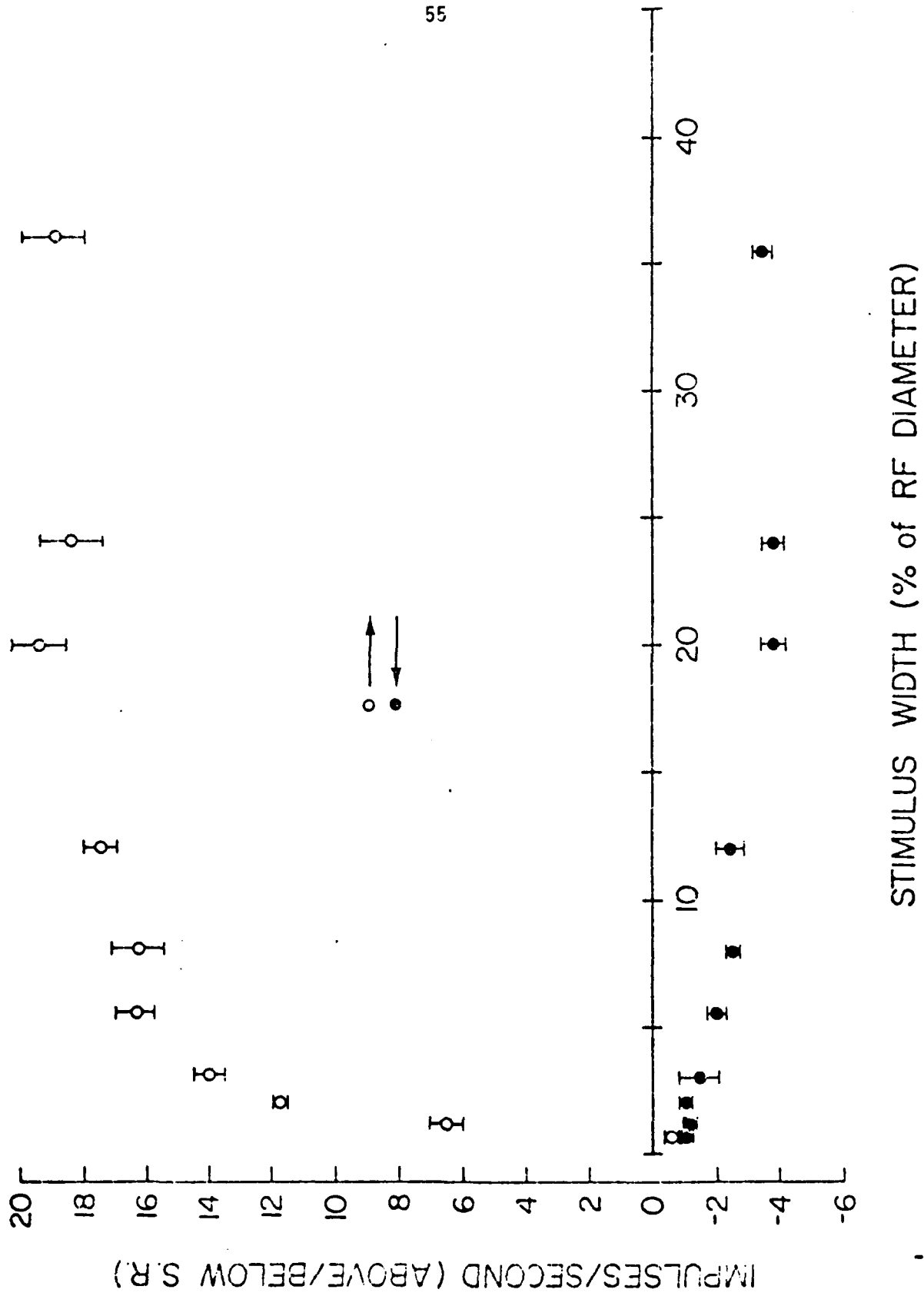


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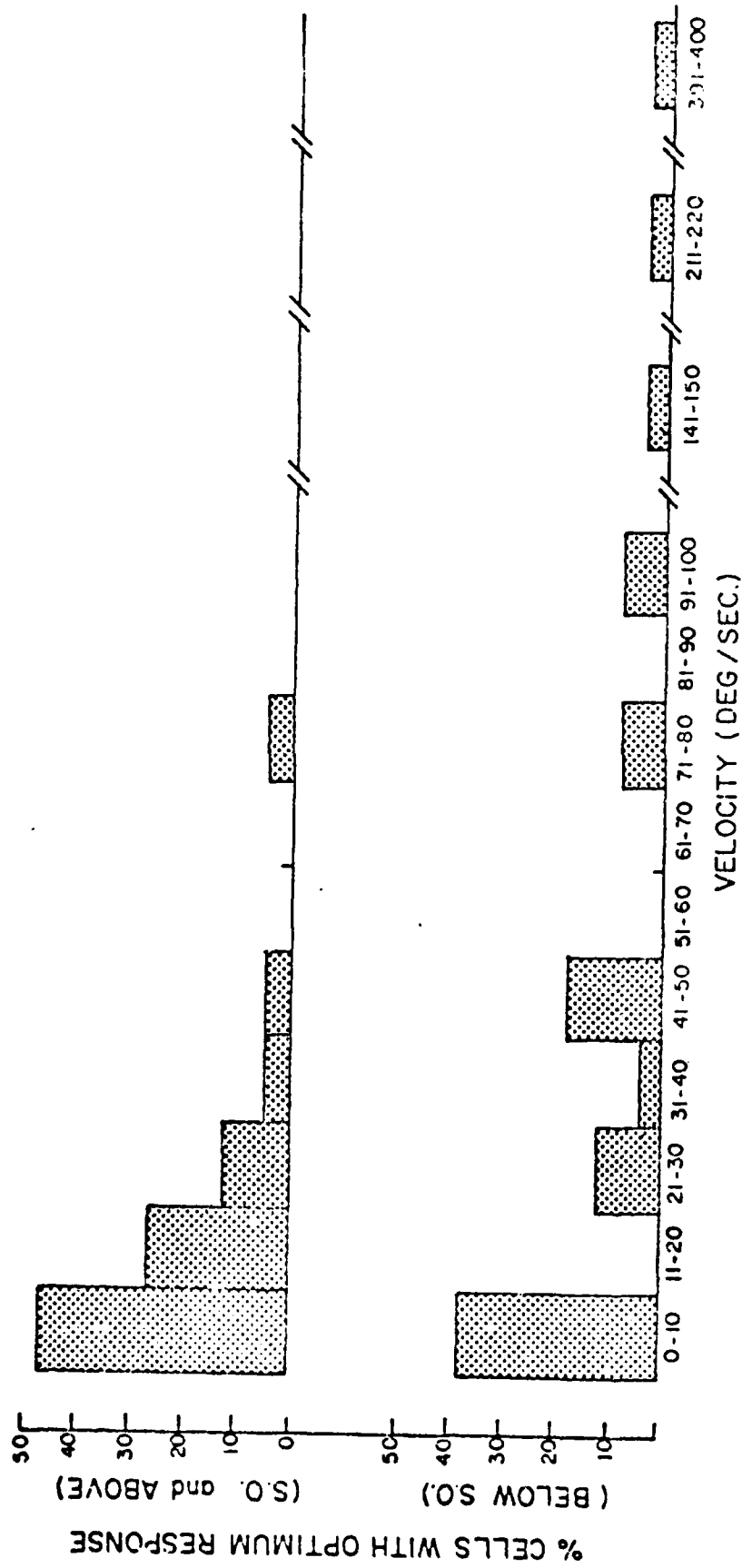


Figure 9

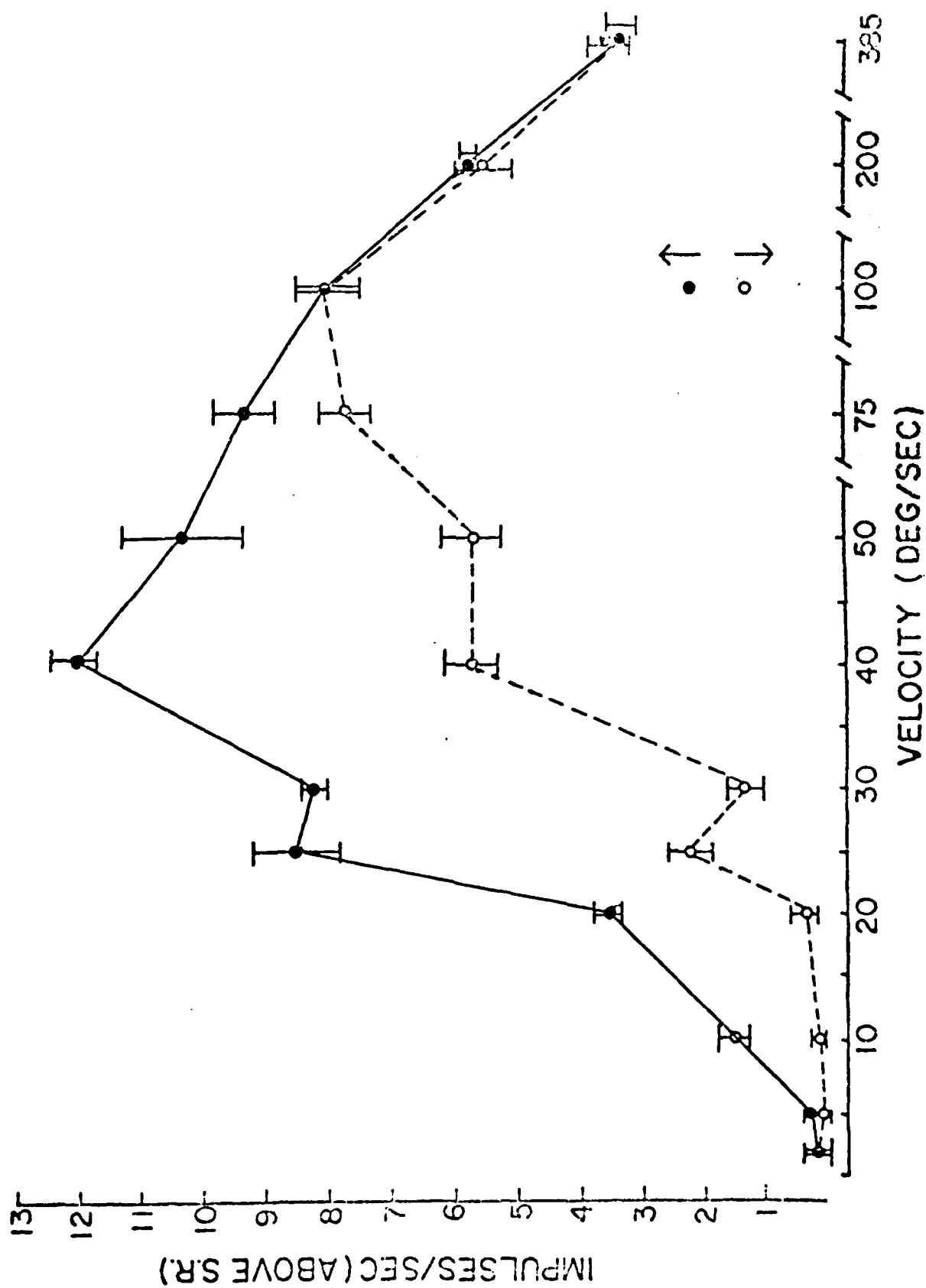


Figure 10

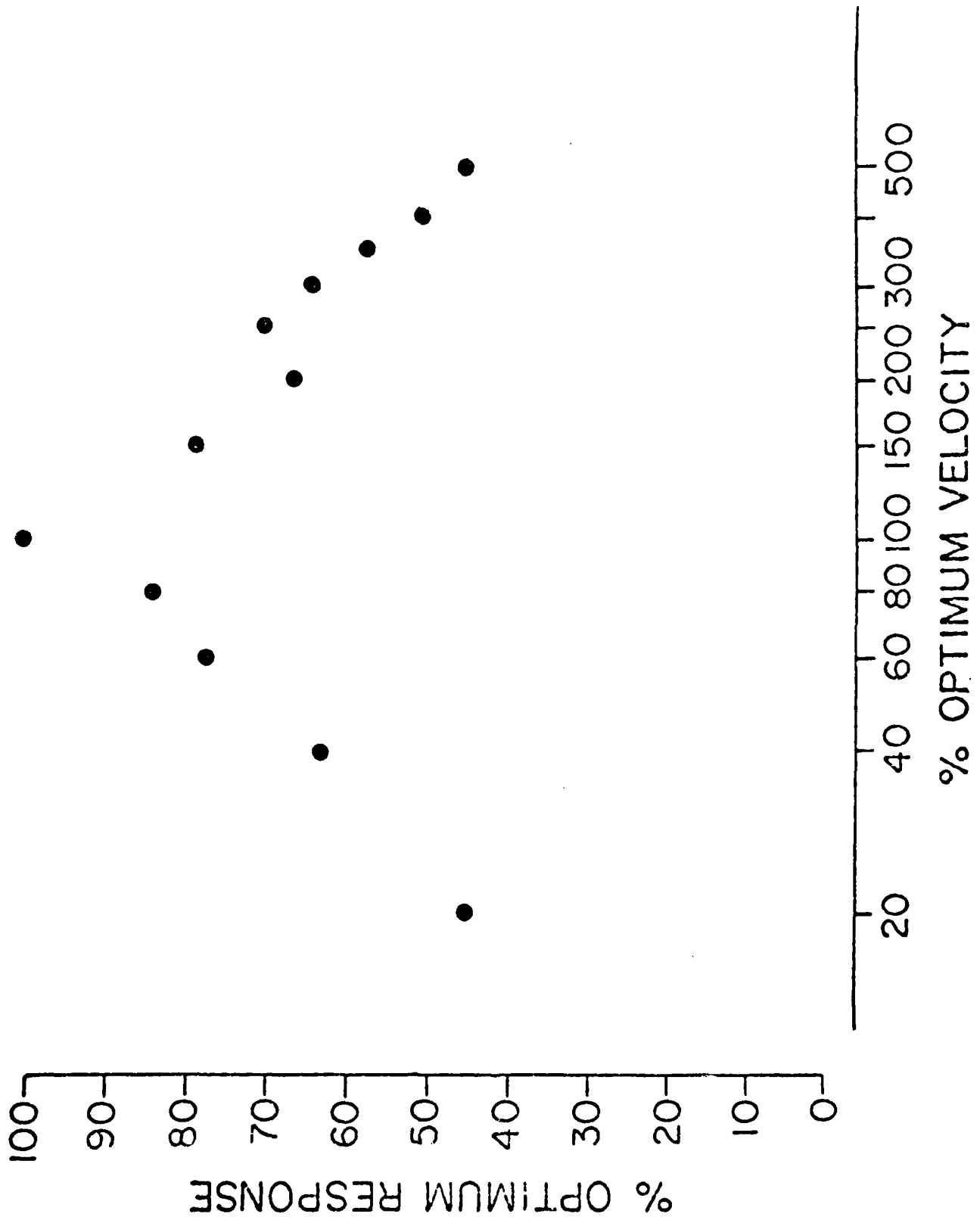


Figure 11

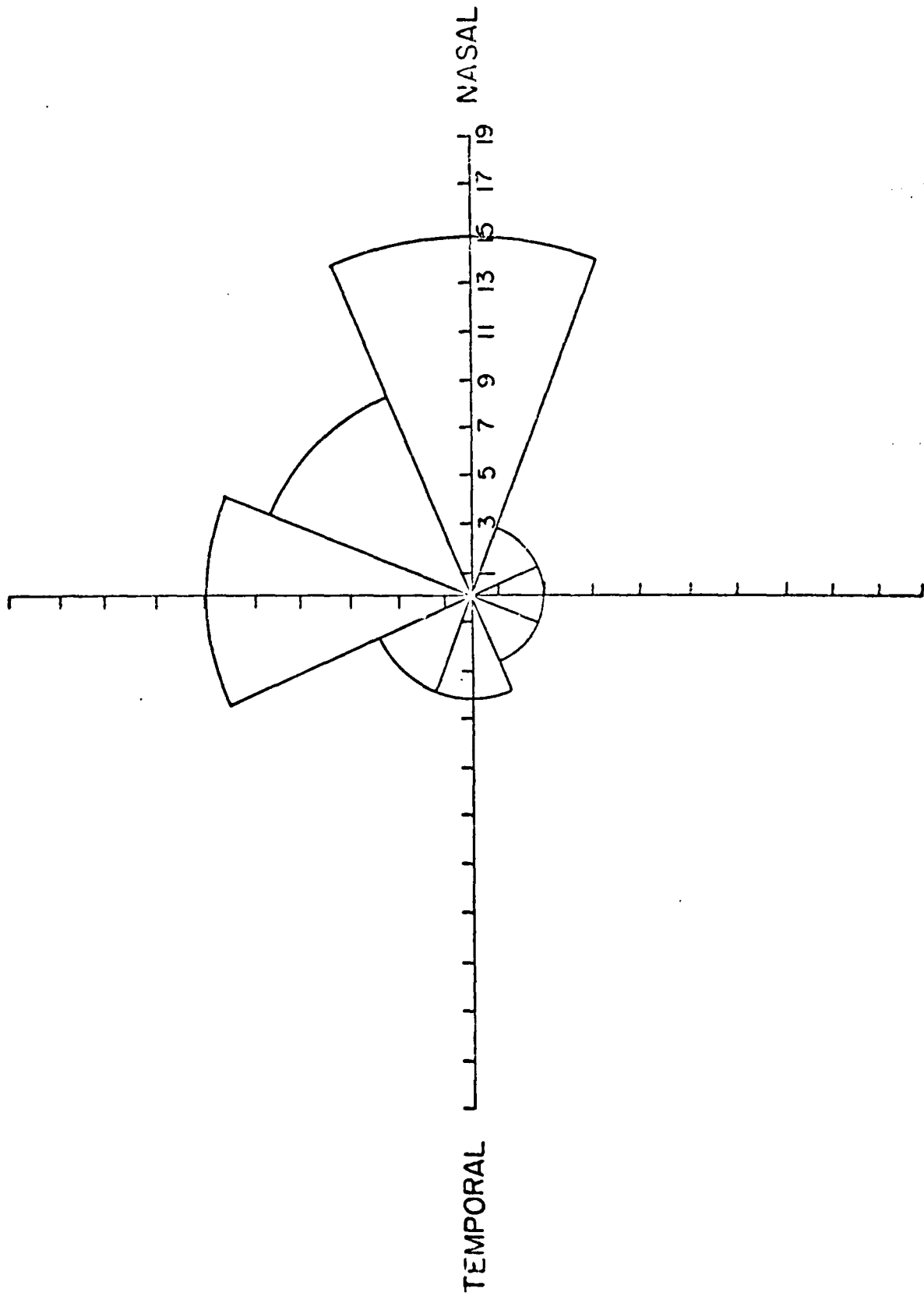


Figure 12

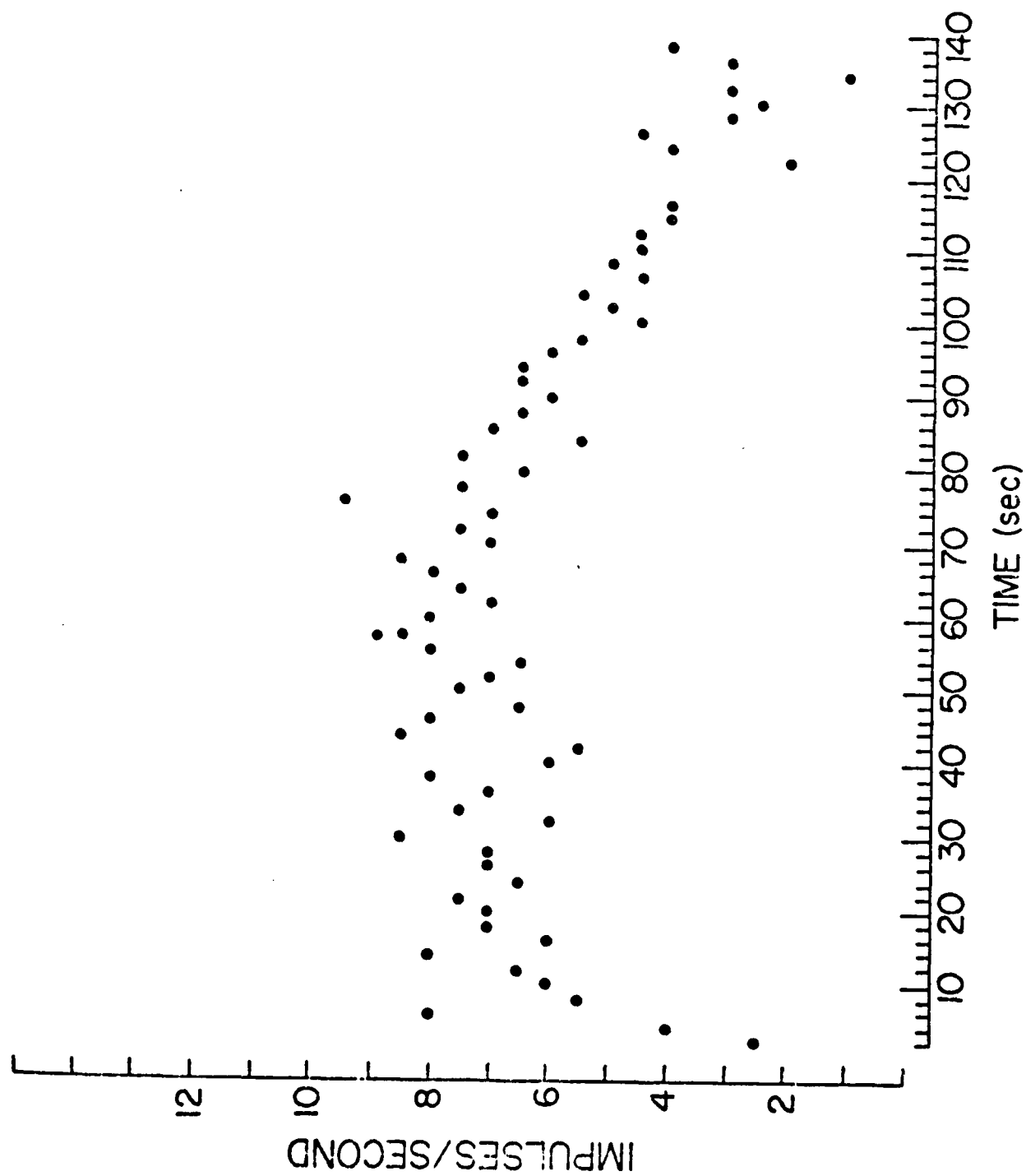


Figure 13

Pinch

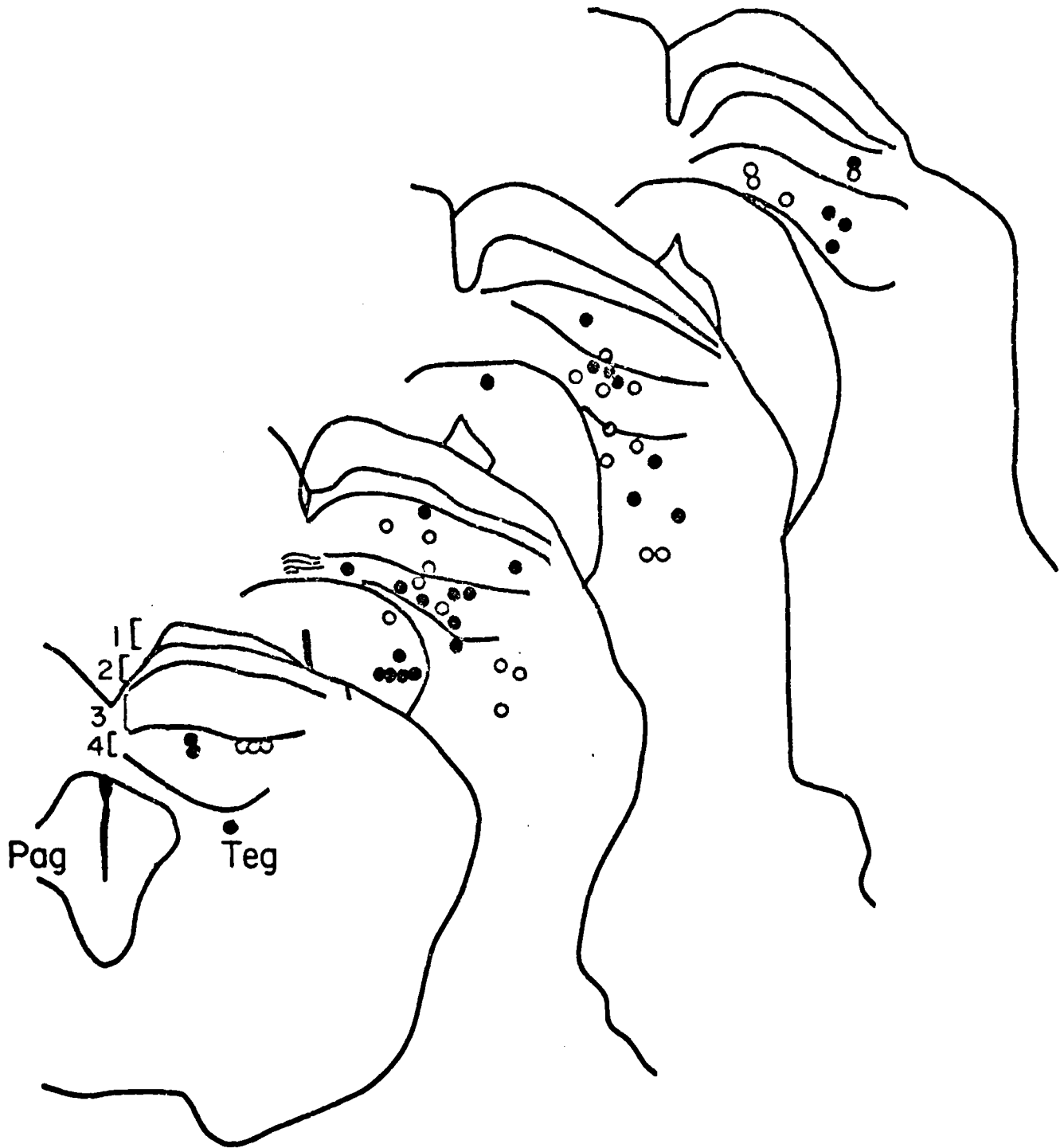
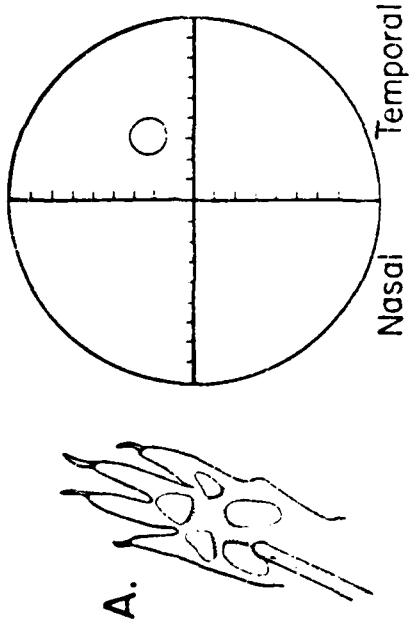
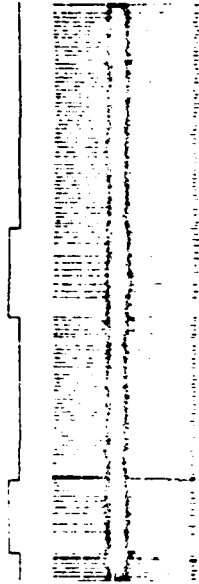


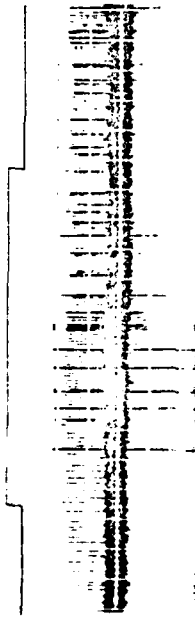
Figure 14



B. VISUAL



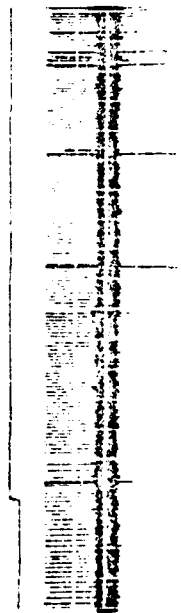
C. NOXIOUS



D. NOXIOUS / ETORPHINE



E. NOXIOUS / NALOXONE



2 sec.

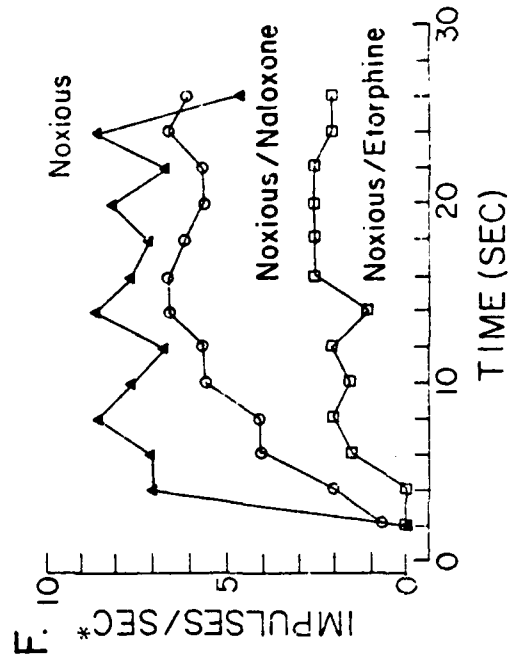


Figure 15

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