NEURAL REPRESENTATION OF SIMPLE VISUAL STIMULI

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By

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SCOPE AND CONTENTS: Activity of individual cells in the visual cortex of the cat was observed during patterned stimulation of the retina. Orientation and illumination of a simple light-dark stimulus were varied. Cells gave the same response to different stimuli, suggesting that 'place' theories of pattern recognition, theories based solely on 'which' cells are responding, are inadequate. It is suggested that stimuli are represented by the relative activity across several neurons.

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INTRODUCTION

The aim of the present study is to examine the neural representation of simple visual stimuli. An understanding of how visual information is represented in the nervous system would help in explaining the mechanisms of some of the perceptual phenomena which depend on visual input.

Most modern theories of pattern recognition postulate stimulus analyzing mechanisms which detect specific features in the visual array. These analyzers extract information about size, contrast, movement, and position of simple contours. The outputs of the analyzers may be successively combined, forming a hierarchical process in which the outputs of one level of analyzers converge on the analyzers of the next level. Higher level analyzers would represent more complex patterns. Presumably the types of analyzers are limited, but the ways in which they can be interconnected are not (Sutherland, 1968; Norman, 1969; Wickelgren, 1969).

Clearly the neural make-up of these analyzers is most important. It defines the features abstracted and thus describes the visual world to the brain: the brain does not see the world as it is, but as it is re-

presented by the neural input.

Current explanations of the neural bases of pattern recognition (Sutherland, 1968; Thompson, 1969; and Wickelgren, 1969) rely heavily on the work of Lettvin, Maturana, Pitts & McCulloch (1961) and Hubel and Wiesel (1959, 1962, 1965). These works emphasize the very specific stimulus preferences of individual neurons. Moreover, preferred stimuli may be highly organized perceptual units. There are neurons in the optic tectum of the frog which respond selectively to small, black, moving objects (Lettvin, et al, 1961). The stimulus requirements of these neurons fit very well the description of a common fly cruising past the nose of a frog at a distance of about ten inches. These neurons have (appropriately ?) been called bug detectors and assigned the major function of providing the frog's brain with the information that there is a morsel of food within striking distance. Thus the activity of an individual neuron might indicate when a member of a particular class of stimuli is present in the environment. These neurons not only satisfy many of the requirements of a pattern recognition mechanism but, further, seem to perform the actual pattern recognition function itself.

The cat, more versatile than the frog, can make a large variety of very fine discriminations and has a sophisticated general purpose visual system. In the

primary visual cortex (area 17 of Talbot & Marshall) of the cat a neuron will respond to a straight line or edge having a particular orientation and movement at a particular position in the visual field. Hubel and Wiesel (1965) suggest that such neurons are the basic elements of the pattern recognition system. Higher in the nervous system (areas 18 and 19) a neuron responds only to a figure composed of two line segments having certain orientations and specific movement and position (Hubel and Wiesel, 1965). The numerous projections of the neurons in area 17 suggest that a given neuron might be involved in the representation of several different complex stimuli, each of which contains the basic feature to which it responds selectively.

The findings of Lettvin and his colleagues and Hubel and Wiesel have been interpreted as supporting a strictly anatomical basis of pattern recognition (Hubel and Wiesel, 1965; Sutherland, 1968; Thompson, 1969; and Wickelgren, 1969). Such "place" theories imply that stimulus identification corresponds in a one-to-one way with locus of activity. Both Thompson and Wickelgren claim that even very complex stimuli and concepts are represented by individual neurons. Thompson (1969) has found neurons which respond to the seventh stimulus in a repeated series of stimuli regardless of whether the stimulus is visual or auditory and over a wide range of

inter-stimulus intervals. He suggests that these neurons code the abstract concept of the number seven and other neurons might represent general classes of objects such as dogs or automobiles.

In a recognition system based solely on locus of activity, or so-called detector neurons, the acuity of the neural system depends on the acuity of the detectors. Thus, those afferent connections which determine the orientation preference of a cortical neuron also determine the orientation range over which the neuron will respond. If only locus of activity is considered, as is done in a place theory, then a given neuron represents not simply its preferred orientation, but all those orientations to which it responds. Campbell, et al (1968) find that neurons in the cat's cortex respond over a range of <u>at least</u> thirty degrees orientation. Such neurons would hardly account for fine discriminations. Humans can discriminate orientation changes of three degrees (Andrews, 1969) and rabbits can discriminate changes of about ten degrees (Van Hof & Wiersma, 1967). It seems likely that the cat's ability to discriminate orientation changes would fall somewhere in between these values.

The notion that pattern recognition is based on some type of feature analysis is supported by several kinds of behavioral evidence: backward masking, cross-adaptation, stabilized images and after images (see re-

view by Weisstein, 1969). In feature analysis, complex stimuli are broken down by the nervous system into a number of basic stimulus elements. The analyzers are cells in the brain which respond only to certain features of visual stimuli but not to others. Using human observers Gilinsky & Doherty (1969) found that a masking stimulus was most effective when presented at the same orientation and retinal locus as the test stimulus and progressively less effective as the orientation difference between the masking and test stimulus increased. The masking effect reached zero when the orientation difference was 45 degrees. Gilinsky and Doherty suggest that the effect is mediated by neurons which are sensitive to the orientation of contours similar to the neurons found by Hubel and Wiesel in the cat cortex.

A stabilized retinal image of a simple line disappears and reappears completely as a unit while the lines comprising a more complex figure disappear and reappear independently of each other (Pritchard, Heron and Hebb, 1960). "Each separate element of the more complex figure, however, disappears and regenerates as a unit" (Heckenmueller, 1965). These findings are consistent with the notion that there are independent feature analyzers to represent basic stimulus elements.

The present study investigates the preferential response of neurons in the cat's visual cortex to particular stimuli. The activity of these neurons is influenced differentially by several different aspects of a visual stimulus such as orientation (Hubel & Wiesel, 1959, 1962), position (Hubel & Wiesel, 1959; Burns, Heron & Pritchard, 1962), intensity (Jung, 1961), and movement (Hubel & Wiesel, 1962).

For those aspects of the stimulus (dimensions) which have been studied systematically, regular relationships have been found between different values of a dimension and the average number of spikes elicited from a neuron. For most dimensions of the stimulus, the relationship is an inverted U function. For example, a given neuron will respond most strongly to a stimulus at a particular position in the visual field. At positions progressively further away from this position weaker and weaker responses are evoked (Hubel & Wiesel, 1959; Burns, Heron & Pritchard, 1962). Similarly an orientation of the stimulus can be found which elicits the strongest response and progressively weaker responses are obtained when the stimulus is rotated away from this orientation (Hubel & Wiesel, 1959; Campbell, Clelland, Cooper & Enroth-Cugell, 1968). The stimuli which evoke maximal responses are straight edges, lines or simple combinations of these

(Hubel and Wiesel, 1962). A simple light-dark edge is the most basic. Apparently the stimulus preferences of individual neurons are sufficiently distributed so that there are neurons for every orientation at all positions in the visual field (Hubel and Wiesel, 1962; Burns, et al, 1962). The point of interest about stimulus dimensions having an inverted U relationship to firing rate is that different cells respond maximally to different values on these dimensions i.e. cells do not all prefer the same stimulus value.

The relationship between stimulus intensity and response of a single neuron seems to be quite different from an inverted U function. Both the total level of illumination and the relative intensity (contrast) may effect the activity of a cell. Using diffuse flashes of light Jung (1961) found that one group of neurons (presumed to be cortical neurons) respond most strongly to the brightest flash, dimmer flashes yielding weaker responses; the activity varying approximately with the logarithm of stimulus intensity. Baumgartner and Hakas (1962) report similar results using patterned light (see Jung, 1961). But Hubel (1960) argues that cortical neurons respond weakly, if at all, to diffuse light flashes and that those neurons recorded from the cortex which do give a response to diffuse flashes are geniculate cells whose axons terminate in the cortex. Spinnelli and Bar-

rett (1969) claim that cortical neurons are relatively unaffected by changes in the total level of illumination of a patterned stimulus. Despite these different findings it is clear that the mutually antagonistic regions of their receptive fields make cortical units especially sensitive to relative intensity in different parts of their fields (Hubel, 1963). If the response of a cortical unit is based on a summation of the effects from excitatory and inhibitory regions and within each region intensity has a monotonic effect i.e. increasing the intensity of the light falling on an excitatory region increases the response and increasing the intensity of the light falling on an inhibitory region decreases the response (Hubel and Wiesel, 1959; Poggio, et al, 1970), then the highest contrast should produce the strongest response.

The intensity-frequency principle, demonstrated for a great variety of sensory nerves, states that the rate of firing of a fiber will increase with the stimulus intensity up to a limit imposed by the refractory period (Adrian, 1928). If the principle holds for cortical neurons, they would all prefer high intensity stimuli. There is little data on this issue, but what there is suggests that cortical cells are either unaffected by intensity or increase firing rate with intensity. There is no evidence of neurons which respond maximally to stimuli at various intermediate contrasts or illumination - those

most often encountered in normal surroundings. This is markedly different from stimulus orientation which is represented by various neurons preferring different orientations.

The effects of changing orientation and intensity might be seen in a single neuron. We would like to know if the response changes are qualitatively (temporal pattern of firing) or quantitatively (number of spikes) different for the two stimulus aspects. If such differences exist they would constitute a possible basis on which the nervous system discriminates stimulus changes along one of these dimensions as different from changes along the other. If no such differences exist in a single neuron then other forms of stimulus coding must provide the information necessary for such a discrimination to be made.

Perkel & Bullock (1968) have described a number of (candidate) neural codes which may be in use. There is one or more candidate codes based on each of the following questions: Which cell is active? How much is the cell firing? There are also multicell candidate codes which include all the combinations of these questions applied to more than one cell. We can choose among the possible codes by observing the effects of various manipulations of the stimulus. If a stimulus change produces an effect as measured by a code then that code remains as a candidate. If the stimulus change produces

no change as measured by a code, and if the stimulus change is shown to be capable of controlling behavior, then that code is eliminated as a candidate for carrying information about that stimulus change in the particular neural units investigated. There are further restrictions imposed on the candidate codes by the variable response of individual neurons to repeated presentations of a stimulus. A code specifying a different neuron to represent each stimulus would be rejected on the basis of insufficiency if a neuron responded infrequently to the stimulus it was supposed to represent. Additional evidence enabling us to choose among candidate codes comes from reports of lesion experiments and stimulus generalization experiments found in the literature.

If orientation changes affect a neuron's response and illumination changes also affect the response, then there may be a 'trade-off' between these effects: various combinations of orientation and illumination might produce the same response. There is a well known trade-off between illumination and stimulus area in optic nerve fibers of the frog (Hartline, 1940), corresponding to the perceptual trade-off observed in humans (Ricco's Law, see Osgood, 1954). But there is no perceptual trade-off between illumination and orientation. The different combinations of illumination and orientation which might yield the same neural response are clearly distinguishable perceptually.

This implies that not only are stimuli not identified by which neuron is active, but neither are they identified by adding the information of how strongly the neuron is firing.

For a number of other sensory systems it has been suggested that individual neurons are not specific enough in their stimulus requirements to represent stimuli distinctively (Milner, 1958; Melzack & Wall, 1962; Erickson, 1968). Melzack and Wall point out that individual receptors in the skin respond to a broad spectrum ofcutaneous stimuli. They conclude that stimuli must be represented by the activity across several afferent fibers. Analogous observations and interpretations have been made for the gustatory system (Erickson, 1968).

Presuming the intensity-frequency principle to be generally applicable both Milner and Erickson suggest that the firing rate of an individual neuron is an ambiguous indicator of stimulus values in many modalities. Here again it is suggested that stimuli are represented by the activity across several neurons.

The purpose of the present study is to test the ability of the place theory in describing the neural representation of a simple visual stimulus. The results are expected to show that the same quantitative response is obtained for different stimuli - stimuli which are readily discriminated behaviorally. The findings will be used to

evaluate some of the candidate neural codes for representing stimuli. It is expected that the results will indicate that particular combinations of neurons are necessary to unequivocally identify a particular stimulus.

If simple stimuli such as edges are the basic elements of pattern recognition then a clear understanding of how they are represented in the brain might aid in elucidating the neural mechanisms subserving pattern recognition.

METHODS

Biological Preparation

Cats were initially anesthetized with ethyl chloride and ether or with halothane and an endotracheal tube coated with five percent Xylocaine ointment was inserted. An opaque contact lens was placed on the right eye. The left eye was irrigated with one percent atropine sulphate in physiological saline to dilate the pupil and a transparent contact lens slipped over the cornea. An artificial pupil of four millimeters diameter was placed in front of the contact lens. The contact lens prevented the cornea from drying and held the nictitating membrane away from the field of vision. The right saphenous vein was catheterized to allow for intravenous administration of drugs.

After a midline scalp incision the skin and fascia were retracted. Two small holes, two millimeters in diameter, were drilled through the skull at least seventeen millimeters posterior of bregma and just to the right of the midline. Thus the two holes were directly above the lateral and postlateral gyri. The holes were filled with bone wax. The scalp incision was irrigated with two percent Xylocaine and general anesthesia discontinued.

Cats were then paralyzed with intravenous gallamine (Flaxedil) 40 mg/hr. and artificially respirated (Gross, Schiller, Wells and Gerstein, 1967). The expired air was monitored by a Harvard CO_2 analyzer and CO_2 content was maintained at 2.8 - 3.2 percent. Temperature was maintained at 37°C. Four cats were anesthetized with nitrous oxide during the experiment.

Recording System

Neuronal activity was monitored by a microelectrode in line with a Grass DP9-B preamplifier which was equipped with band pass filters. Activity was recorded on one channel of a Tandberg stereo tape recorder (Model 64). The stimulus events were simultaneously recorded on the second channel. Visual and auditory displays were available to the experimenter on a Tektronix 502A oscilloscope and a gated loudspeaker, respectively (Fig. 1).

Neurons were isolated by using glass coated, gold plated tungsten microelectrodes with tip resistances ranging from 0.5 to 7.0 megohms and tip size of about 3 microns, made by Hamilton Research Instruments Ltd. The microelectrodes were 25 mm. long and the upper 15 mm. were uninsulated.

The electrode tip was inserted into the bone wax in one of the holes in the skull. A hollow glass

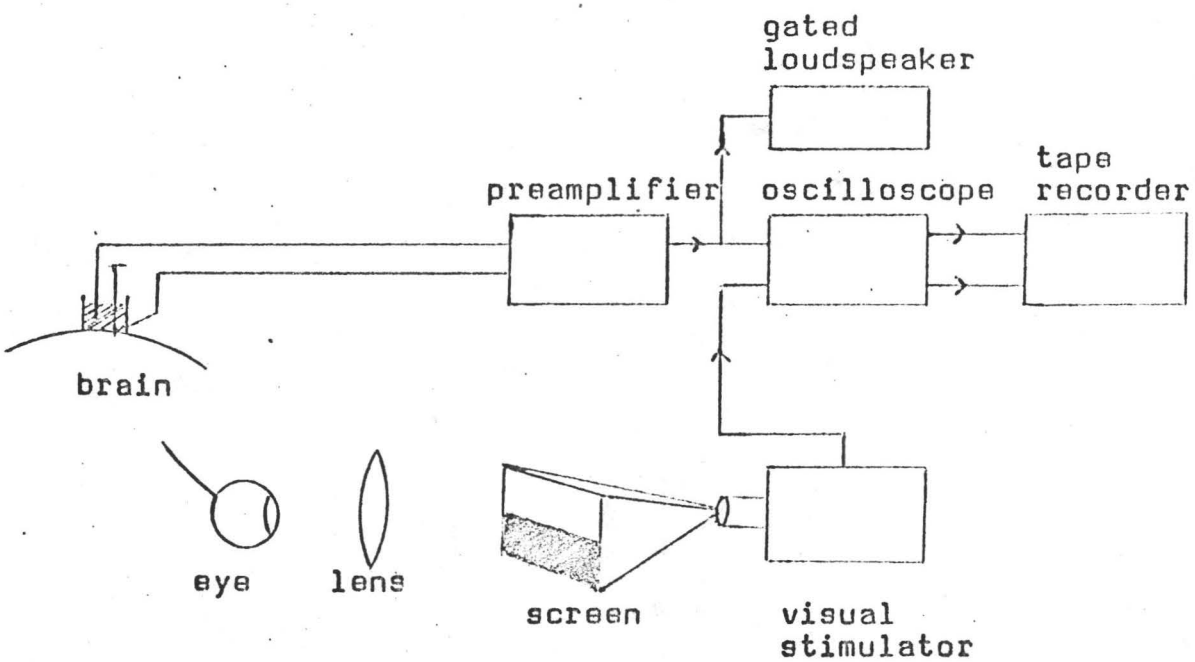


Fig. 1. Diagram of recording setup.

cylinder (2 cm. long X 1 cm. diameter) was placed on the skull concentric to the electrode (Fig. 2). Melted paraffin was poured into the cylinder to a height of about 15 mm. When the paraffin hardened the remainder of the cylinder was filled with physiological saline. (The upper portion of the microelectrode was uninsulated and thus exposed to the saline.) A lead wire dipped into the saline in the cylinder gave access to any electrical activity picked up by the microelectrode. The clamp which held the cat's head in place was used as the indifferent electrode. The paraffin block allowed the microelectrode to be driven along its axis by a hydraulic microdrive but held the microelectrode firmly in place when a neuron was located. The use of a closed skull recording system kept pulsations of the cortex due to heart beat and respiration to a minimum (Burns and Robson, 1960; Mountcastle, Davies & Berman, 1957). In addition, the paraffin served to dampen any high frequency vibrations.

Optical Stimulation

Collimated light from a 500 watt tungsten source was directed onto a 35 mm. slide of a light rectangle on a darker background. The light passed through a projection lens and was reflected by a mirror and through a dove prism onto a back projection screen. The resulting image was a

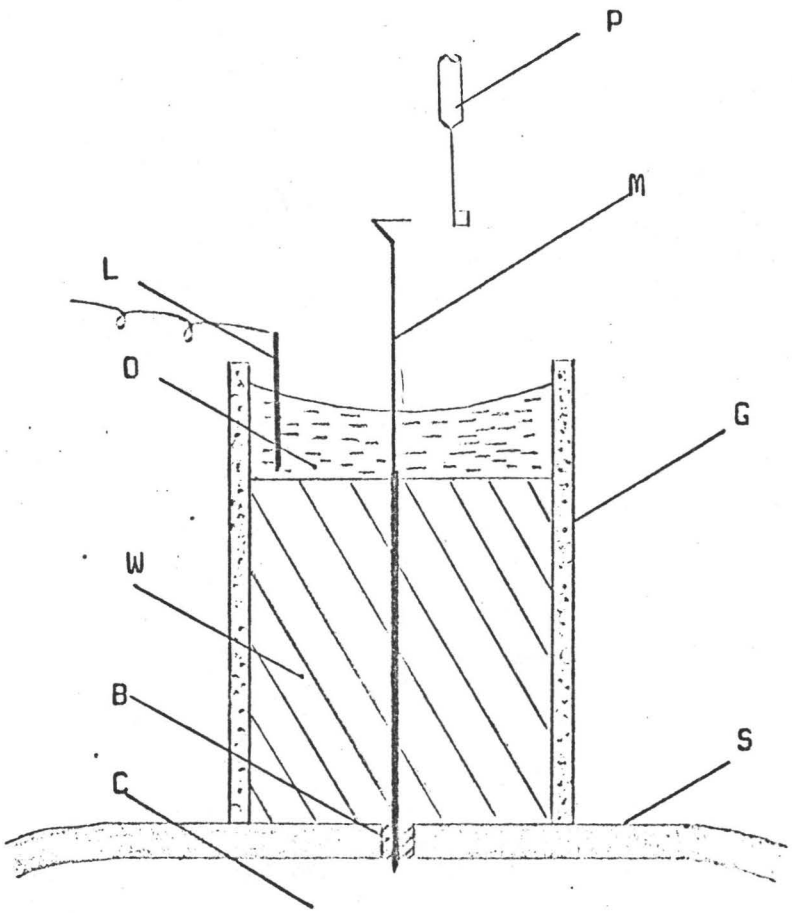


Fig. 2. Wax system which supports microelectrode.
P: push-rod from hydraulic drive
M: microelectrode
G: glass cylinder
S: skull
L: lead wire to amplifier
D: saline
W: wax
B: bone wax
C: cortex

light rectangle on a darker background. The long and short sides of the rectangle subtended visual angles of 60 and 40 degrees respectively at the cat's retina. The effective stimulus was the light-dark border at one of the long sides of the rectangle since cortical receptive fields are known to be much smaller than this figure (Hubel and Wiesel, 1962; Jones, 1970). The mirror, mounted on the coil of a galvanometer, moved in response to signals from a square wave generator. Thus the image on the screen was oscillated at 3 cycles per second and 0.5 degrees arc amplitude, imitating physiological nystagmus. The slide in the projector could be translated in two perpendicular planes by micromanipulators and the projected beam rotated by the dove prism. In this way the light-dark border could be projected in any desired position and orientation. Intensity of the projected beam was varied by means of Wratten neutral-density filters over a range of two and one-half log units. The filters changed the intensity of both the rectangle and the background simultaneously.

In a second set of experiments in which the effects of relative intensity were of primary interest a pair of polarizing filters were used. An image of the edge of one filter was focused on the screen. Since the light passing through the two filters depends on the relative orientation of their polarizing planes rotation of the second filter, held parallel to the first, varied

the relative intensity across the edge. In this way relative intensity (contrast) was reduced in steps from 91 to 33 percent:

$$\text{contrast} = \frac{\text{brightness 1} - \text{brightness 2}}{\text{brightness 1}} \times 100$$

Average luminance increased slightly, from .23 to .57 foot lamberts, as contrast decreased.

The cat was placed about 40 cm. from the screen. The light-dark border on the screen was focused onto the cat's retina by an ancillary lens, accomodation having been paralyzed. To check the focus, the image of the border on the retina was observed directly with a beam splitter held between the ancillary lens and the cat's eye. Minor adjustments were made as they were necessary.

Procedure

After the surgical preparation was completed and the optics adjusted, the microelectrode was mounted in the wax holder. The microelectrode was then pushed through the dura and slowly advanced through the cortex while the light-dark border was oscillated at many different positions and orientations in the visual field. When a neuron was detected the microelectrode was stopped in place and the orientation and position located that gave the maximum response on the audiomonitor.

The border was then oscillated repetitively at various orientations surrounding that estimated to be most effective. The number of different orientations depended on the apparent selectivity of the response and the length of time the neuron was held. This procedure yielded data on the orientational selectivity of a neuron's response.

At each orientation four to seven luminance levels were tested in a decreasing series. Each combination of orientation and luminance was tested for thirty seconds, during which ninety stimulus cycles occurred.

The effect of decreasing the contrast across the border (the relative intensity of the light and dark areas) was examined in six neurons.

As time would permit, samples were obtained of neuronal activity during steady, diffuse illumination at two luminance levels. Several neurons were also tested with flashing diffuse light to assess the response to this form of stimulation.

Data was stored on magnetic tape for future analysis.

RESULTS

Recordings of extracellular discharges were obtained from 56 individual neurons in 31 cats. An effective stimulus was found for each of these neurons. Three other neurons were isolated but no effective stimulus was found despite a prolonged search of the visual field with several stimulus patterns. Experiments were carried out only on neurons which clearly responded to a stimulus. In addition, a large number of neurons were rejected because their discharges could not be isolated from the discharges of neighboring neurons. The 56 selected neurons were thoroughly examined with regard to the effects of changes in stimulus orientation and intensity. Several neurons (38) also provided information about the effects of different levels of diffuse illumination.

The neuron sample was located in the lateral and postlateral gyri within two millimeters of the midline and between 17 and 21 millimeters posterior of bregma. Neurons in this portion of the cortex have receptive fields in or near the area centralis of the retina (Hubel & Wiesel, 1962; Jones, 1970). Such a sample is presumed to be involved in pattern recognition functions because of its sensitivity

to the various aspects of visual form (Hubel & Wiesel, 1965) and because destruction of this area abolishes pattern recognition (Kluver, 1942).

Orientation

In the preliminary search the receptive field of the neuron was located and the stimulus orientation which produced the strongest response was determined. The effects of orientation changes in the frontal plane were determined. Three major blood vessels on the retina provided an estimate of the orientation of the eye in the paralyzed state and were used as a reference. Selective orientation effects were exhibited by all responding neurons. Figure 3 shows the effects of changes in stimulus orientation on the responses of six different units: (a) and (b) are very selective units, (c) through (f) are units displaying rather broad orientation effects. Similar responses for other units are illustrated in the Appendix. Units displaying very broad orientation effects were tested on only one side of the response peak. The firing rate at the preferred stimulus orientation varied from cell to cell ranging from 58.6 to 3.7 spikes per second. At stimulus orientations progressively further away from the preferred orientation the firing rate gradually decreased, approaching the spontaneous rate. The decline of firing rate with orientation changes varied considerably

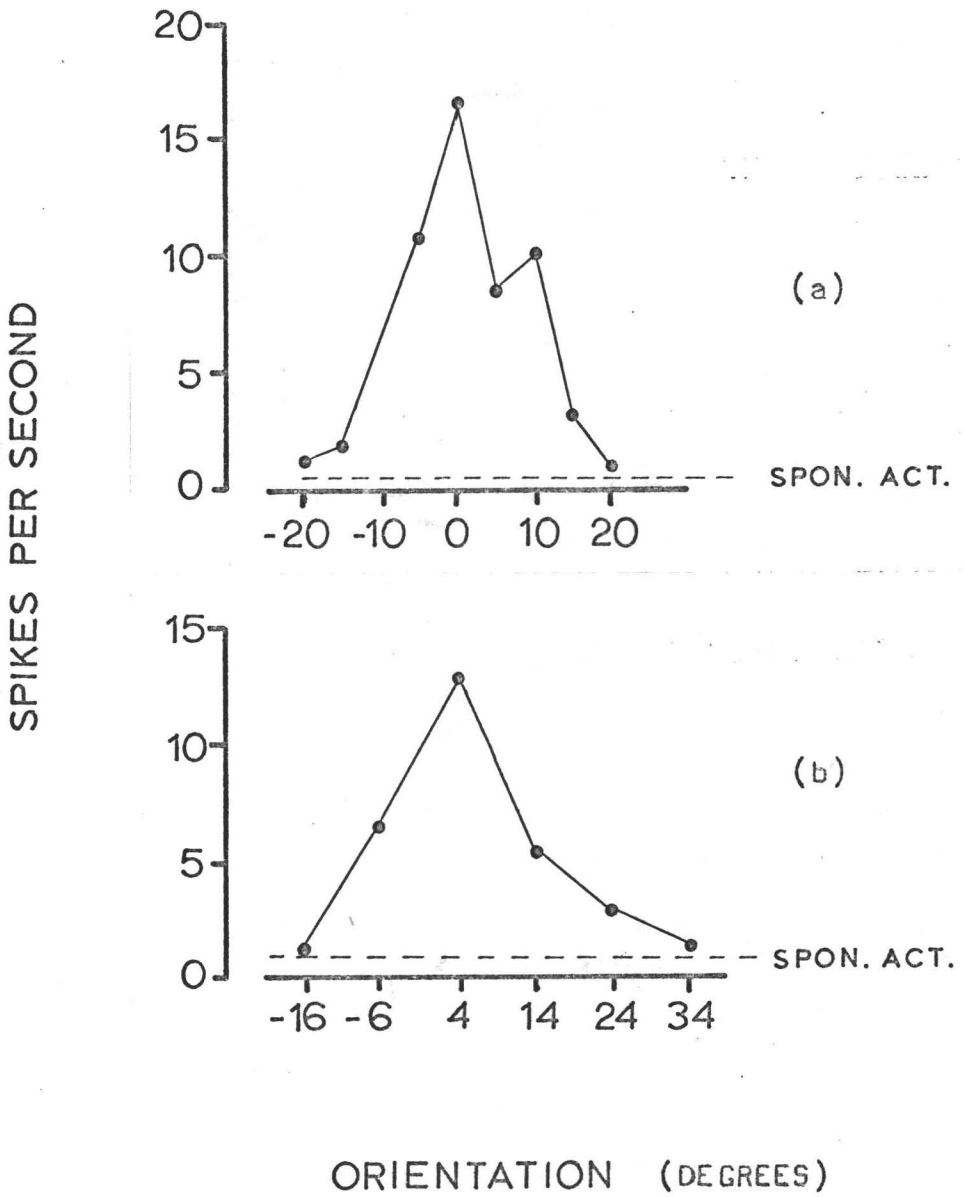
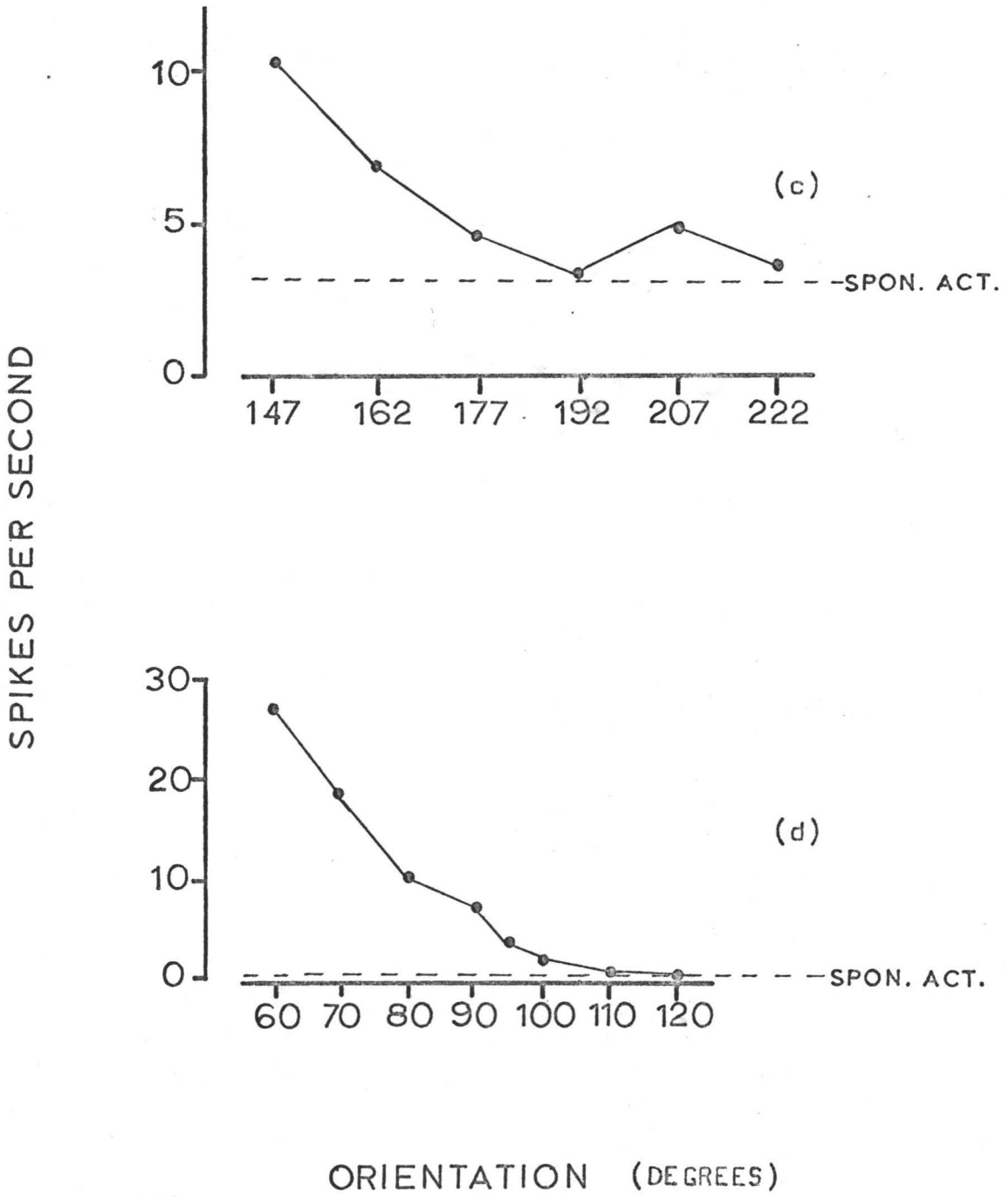
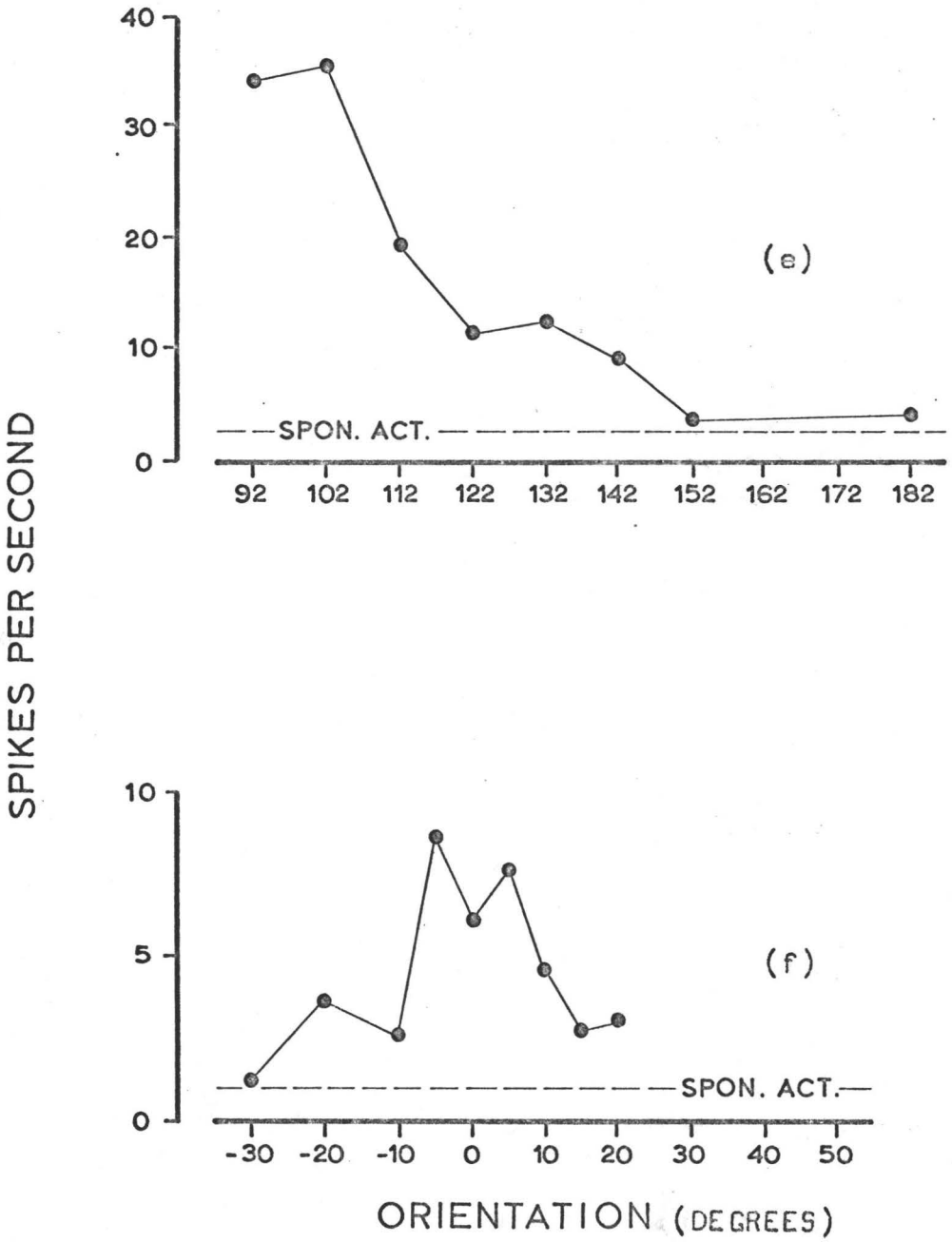


Fig. 3 The effects of stimulus orientation on firing rate: six cells are shown, including the two (3a & 3b) having the greatest sensitivity for orientation changes. Horizontal = 0 degrees. Average luminance: 3.26 Ft.L.


10
5
0
(c)
SPON. ACT.
147
162
177
192
207
222
30
20
10
0
(d)
SPON. ACT.
60
70
80
90
100
110
120
SPIKES PER SECOND
ORIENTATION (DEGREES)


SPIKES PER SECOND
40
30
20
10
0
(e)
SPON. ACT.
92
102
112
122
132
142
152
162
172
182
10
5
0
(f)
SPON. ACT.
-30
-20
-10
0
10
20
30
40
50
ORIENTATION (DEGREES)

between cells. The most selective unit reached its spontaneous firing rate when the stimulus was oriented only twenty degrees away from the preferred orientation, while other units continued to respond at sixty degrees away.

For a few cells the firing rate at the least preferred orientations did not reach the spontaneous rate. The firing rates of a few other cells went below the spontaneous rate at some orientation away from the preferred orientation.

The distribution of preferred stimulus orientations for the present sample of cells shows a preponderance near the vertical and horizontal axes (Fig. 4). Nonetheless preferred stimulus orientations are widely distributed.

In summary, all responding neurons were sensitive to stimulus orientation, the most sensitive neurons continued to respond to a stimulus whose orientation varied over a range of at least twenty degrees. More neurons had orientation preferences near the vertical and horizontal axes than near the obliques.

Spontaneous Activity

Spontaneous activity was measured at two levels of steady, diffuse illumination: 6.00 Ft.L. and 0.01 Ft.L. These are the two extremes of the illumination used in the subsequent experiments with moving light-dark borders.

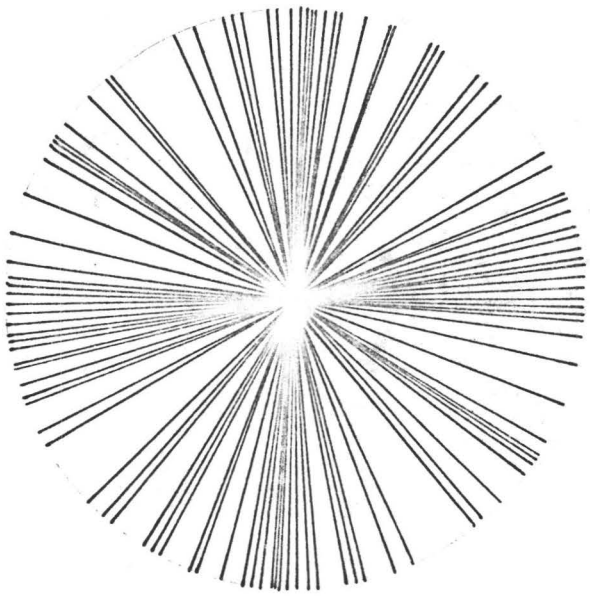


Fig. 4 DISTRIBUTION OF PREFERRED ORIENTATIONS.
(EACH DIAGONAL REPRESENTS ONE CELL)

Yet there was little difference in activity under these steady state conditions for most cells. Figure 5 compares the two spontaneous levels of activity. It appears that even large differences in diffuse illumination are not signalled by the firing rate of these neurons.

Intensity

The stimulus intensity was varied over a range of two and a half log units and the effect on each neuron's activity was studied. Average luminance of the oscillating light-dark stimulus was decreased in steps from 3.26 to 0.02 Ft.L. by means of neutral-density filters. The contrast at the border was 91 percent. Generally the firing rate increased as stimulus intensity increased. The effect varied from those cells which approximated a logarithmic relationship between firing rate and intensity (Fig. 6) to those which were relatively unaffected at higher intensities but decreased firing at low intensities (Fig. 7) and a few which showed little change in activity with stimulus intensity (Fig. 8). These are not categorical differences, but they indicate the range of effects obtained. The response of individual cells was often highly variable but general trends were usually apparent. None of the cells showed a consistent decrease in activity as stimulus intensity increased.

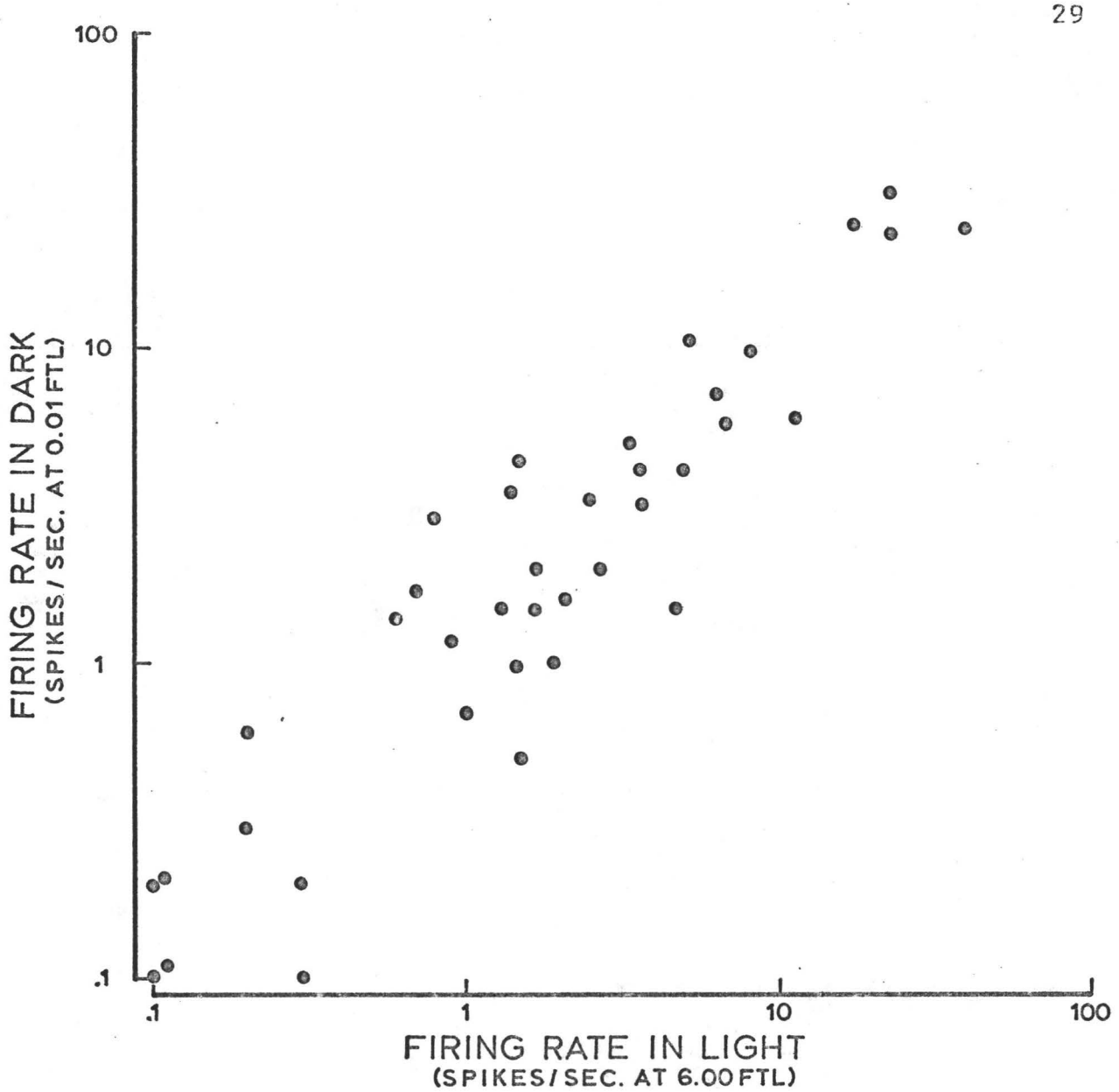


Fig. 5 Firing rate of 38 cells at two levels of steady, diffuse illumination: 6.00 Ft.L. and 0.01 Ft.L. Rate = spikes/sec. over a 30 second period.

Figs. 6 - 8 The effect of changes in average luminance on the response rate of a single neuron to an oscillating light-dark border. Intensity of luminance: 100 = 3.26 Ft.L. Each curve represents the effect of luminance on a neuron at its preferred stimulus orientation. Figures 6 through 8 illustrate the range of effects obtained from the various neurons. Figure 6 shows two neurons in which firing rate increases approximately as the logarithm of intensity. Figure 7: two neurons relatively unaffected at higher intensities. Figure 8: two neurons relatively unaffected by intensity changes.

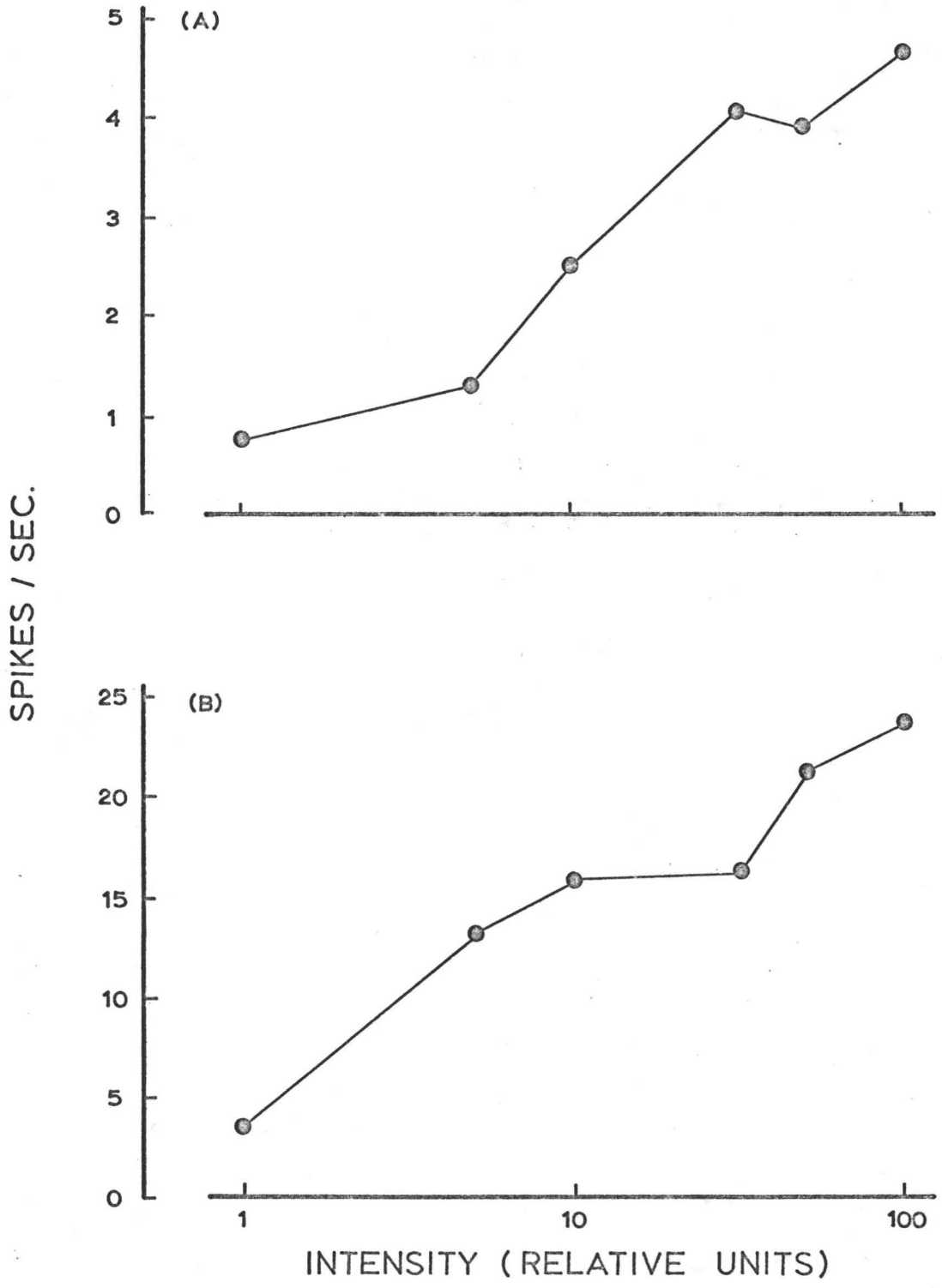

(A)
5
4
3
2
1
0
(B)
25
20
15
10
5
0
1
10
100
SPIKES / SEC.
INTENSITY (RELATIVE UNITS)

Fig. 6

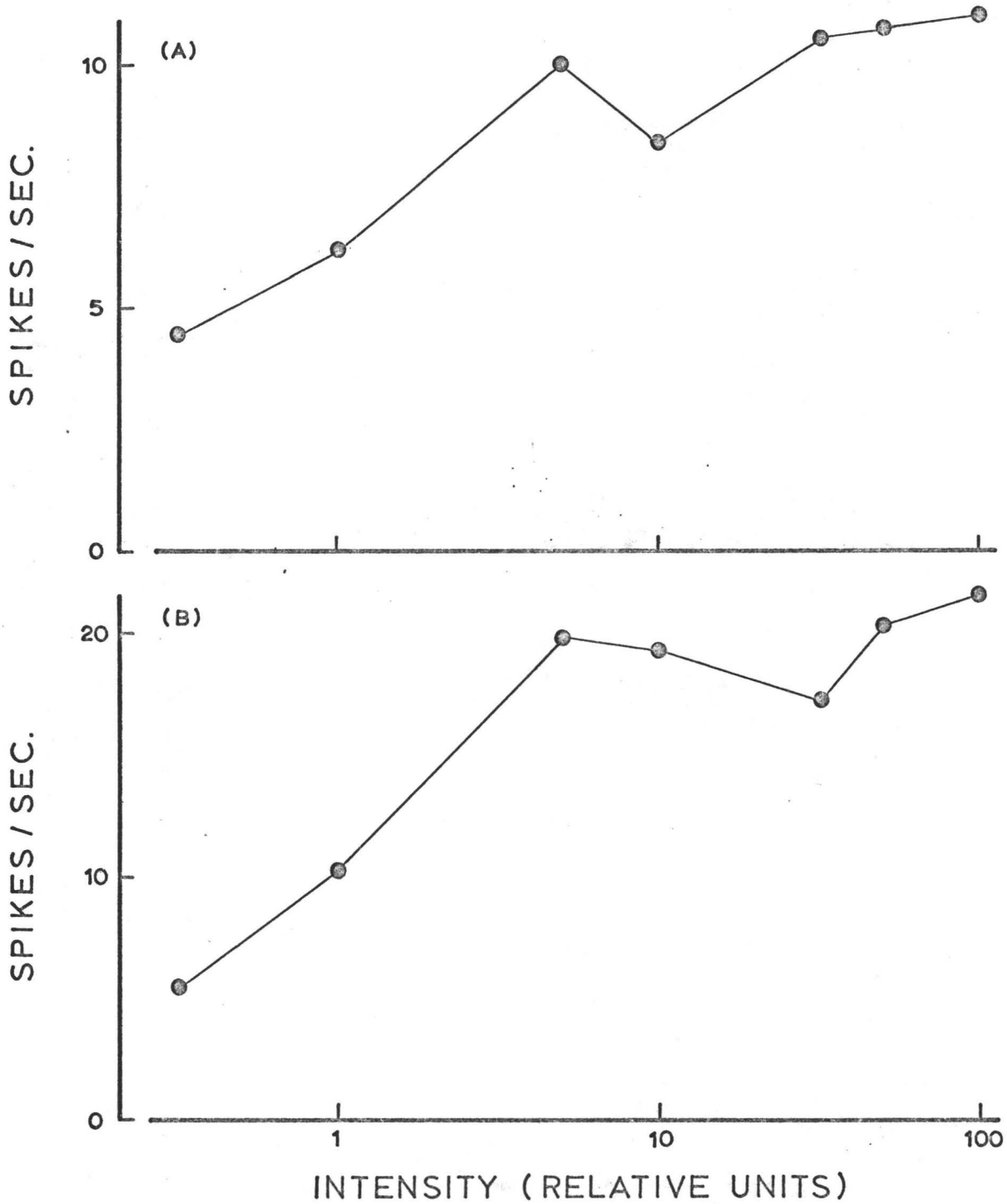

(A)
10
5
0
SPIKES / SEC.
(B)
20
10
0
SPIKES / SEC.
1
10
100
INTENSITY (RELATIVE UNITS)

Fig. 7

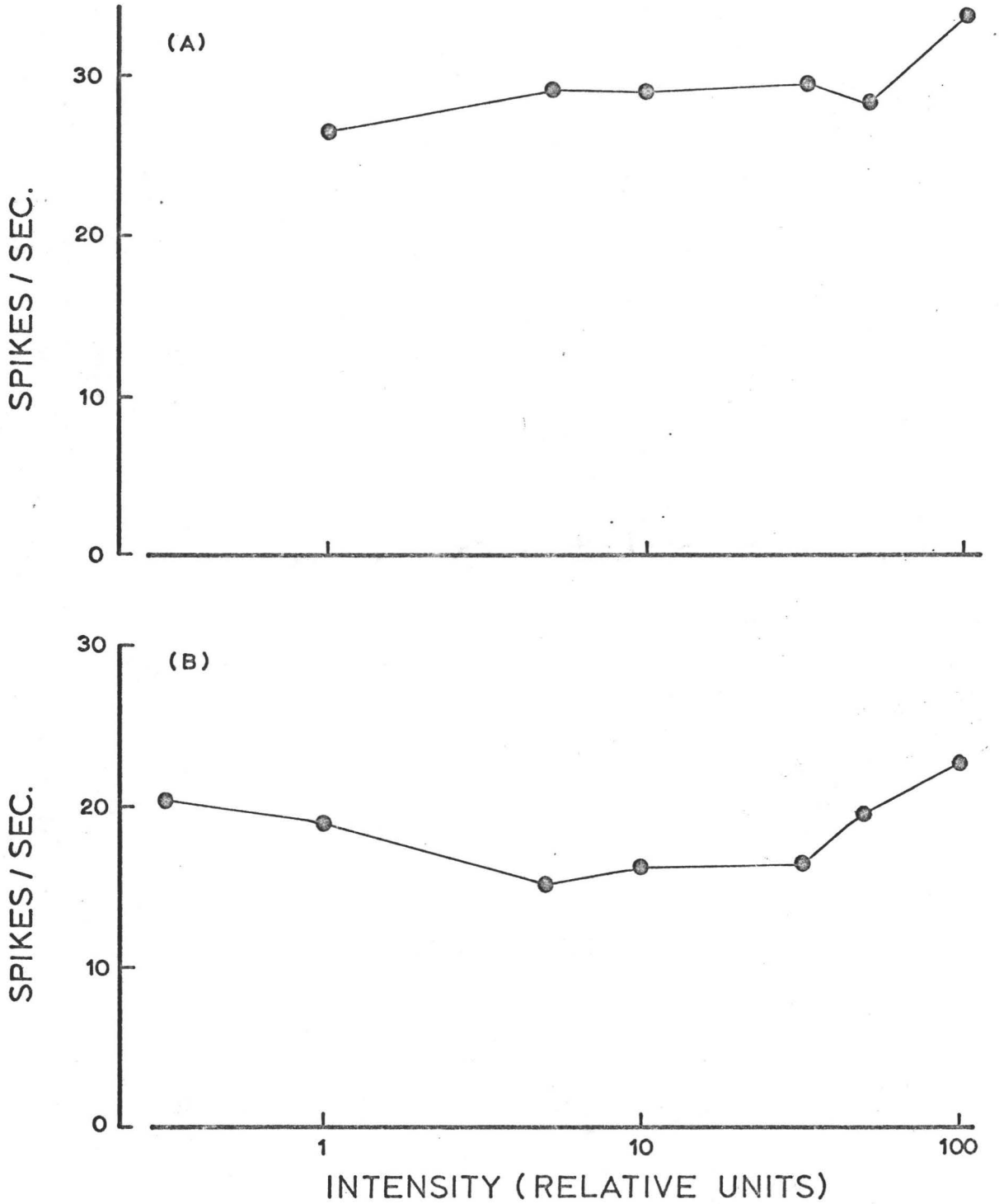

(A)
30
20
10
0
SPIKES / SEC.
(B)
30
20
10
0
SPIKES / SEC.
1
10
100
INTENSITY (RELATIVE UNITS)

Fig. 8

The large majority of the cells increased firing with intensity, but four of the 56 cells showed little or no systematic change in firing rate with intensity. For two of the four cells the firing rate during stimulation was higher than the spontaneous rate whereas the firing rate for the other two cells was about the same during stimulation and spontaneous activity. The latter two cells responded to stimulation with a redistribution of spikes relative to the time of stimulus movement. Rather than increase their overall rate of firing they increased firing during certain periods following the stimulus movement and decreased it at other times. These effects are illustrated in the post-stimulus histograms of cell discharges (Fig. 9).

Contrast

In addition to the primary experiment, a small number of cells (six) were examined with a light-dark border across which contrast was decreased from 91 to 33 percent while average luminance increased from .23 Ft.L. to .57 Ft.L. Luminance changes in this range were earlier shown to have strong effects. Since the previous experiments revealed a positive relationship between firing rate and average luminance, pitting the stimulus parameters against one another might reveal their relative effects i.e. low contrast levels correspond with high luminance .

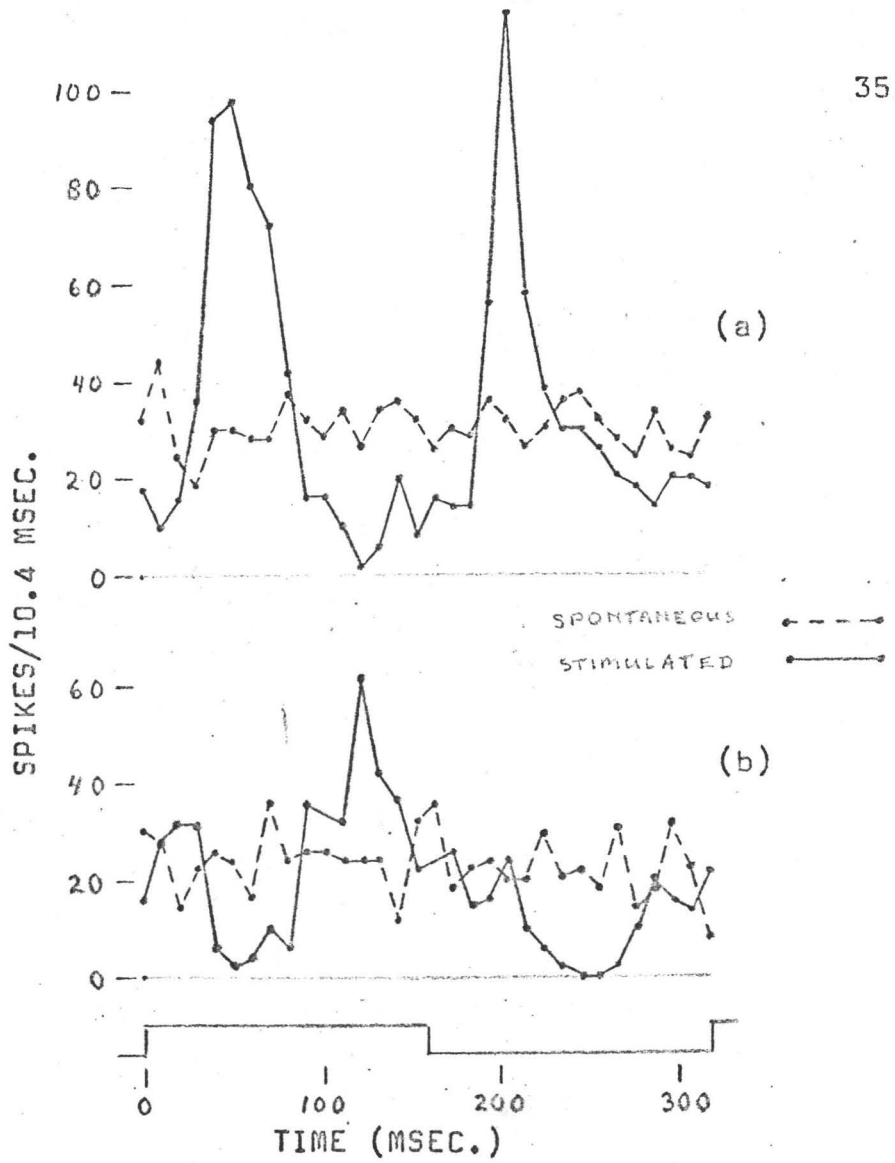


Fig. 9 Post-stimulus histograms comparing the activity of two cells with and without stimulation. Both cells show redistribution of discharges relative to the time of stimulus movement which is common to all of the cells studied. The cell in (a) also shows the typical increase in average firing rate during stimulation as compared to spontaneous activity. The other cell (b) fires at about the same average rate whether stimulated or unstimulated. Only one other cell did this. Interestingly, (b) shows a primary "off" response at about 40-80 milliseconds (Hubel & Wiesel, 1959).

The stimulus is a light-dark border (at the preferred orientation and maximum intensity) oscillating 3 times per second for 30 seconds. A stimulus marker without a stimulus is used to display spontaneous activity. The bottom line in the figure indicates the time of stimulus movement.

levels. Under these conditions neurons tended to decrease firing with decreased contrast suggesting a positive relationship between firing rate and contrast (Fig. 10). However, the contrast effect was not very strong, suggesting that the luminance change was having a reverse effect. Thus increases in luminance and contrast both tend to increase firing rate.

Figure 11 shows the response of a unit to simple luminance changes and also the response when luminance and contrast are opposed. The unit is relatively unaffected by luminance changes except for a sudden decrease in response at the lowest intensity (Fig. 11A). However, when contrast and luminance are opposed the unit increases in firing rate with increasing contrast indicating that contrast is having a stronger effect than luminance over these ranges (Fig. 11B).

Orientation-Intensity Relationship

The effects of stimulus intensity on a neuron's activity are gradually attenuated at less preferred stimulus orientations. For a single cell, a family of curves illustrates the intensity effects at different stimulus orientations (Fig. 12 and Appendix). Each point on the curves represents the cell's firing rate over a thirty second period during stimulation with an oscillating edge at the specified orientation and intensity. The curves

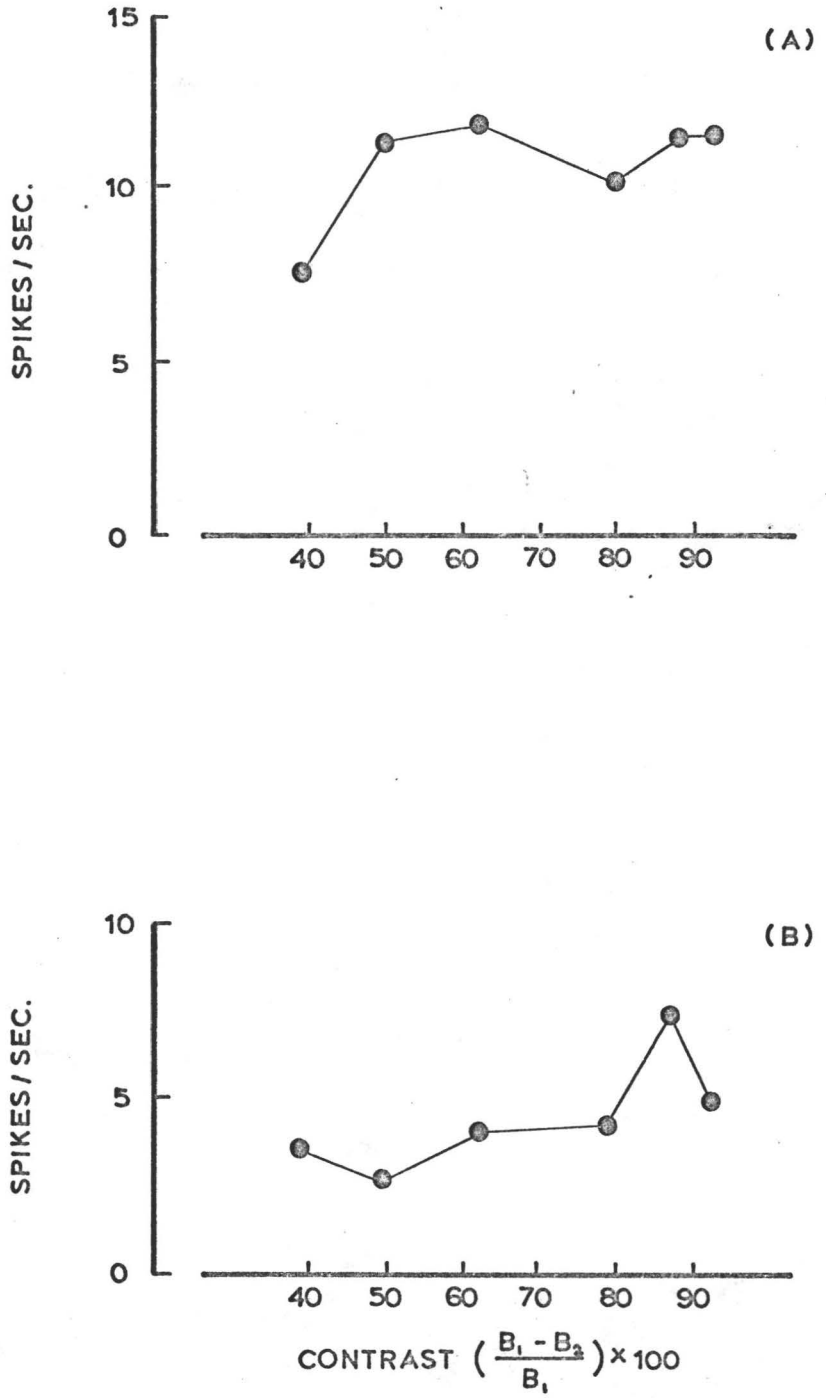


Fig. 10 The effect of contrast on firing rate. B_1 is the luminance of the brighter side of the stimulus. B_2 is the luminance of the darker side of the stimulus. (A) and (B) represent two dif-

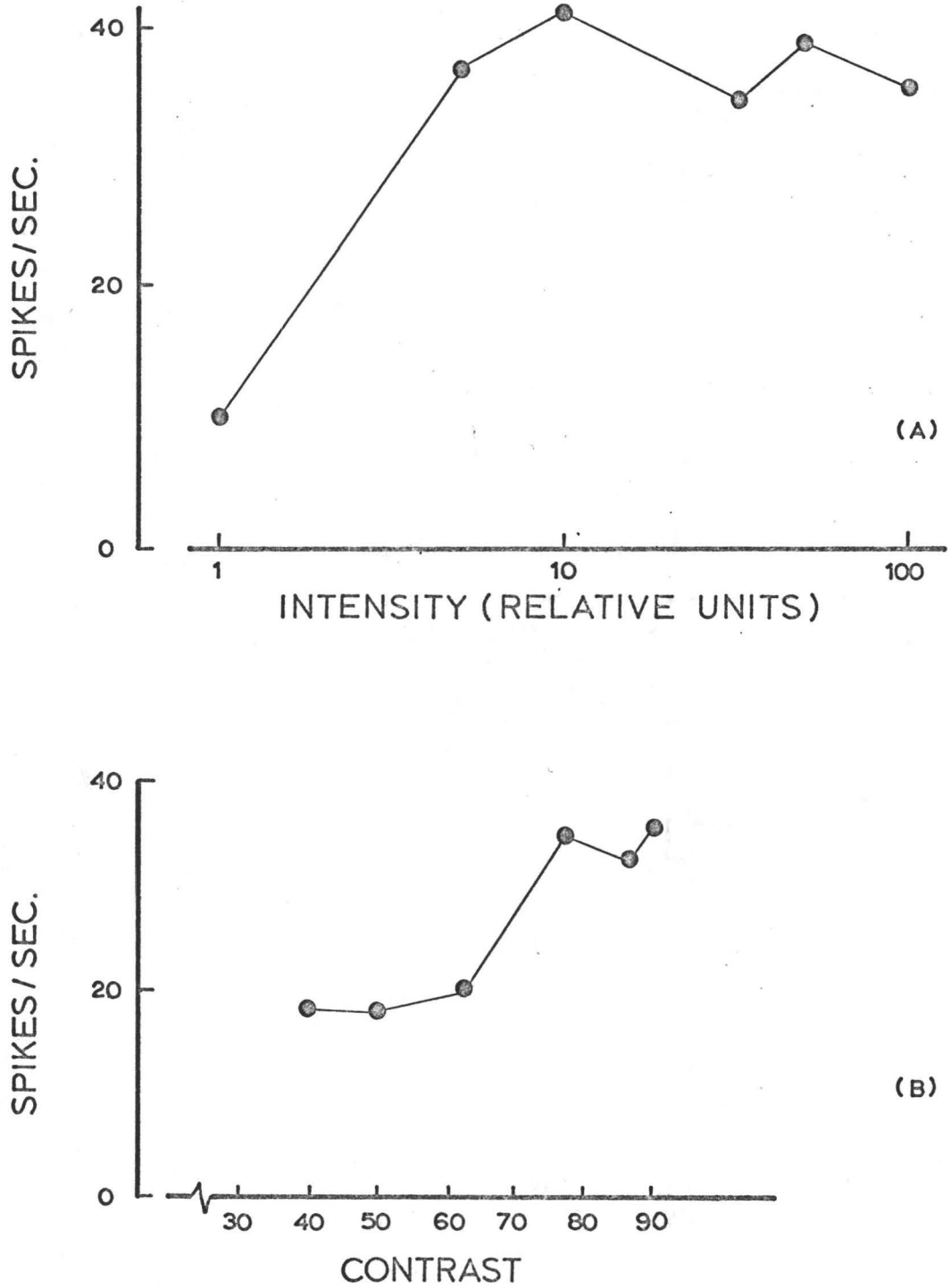


Fig. 11 The effect of (A) luminance changes and (B) contrast changes on the same neuron. Intensity of luminance: 100 = 3.26 ft.L.

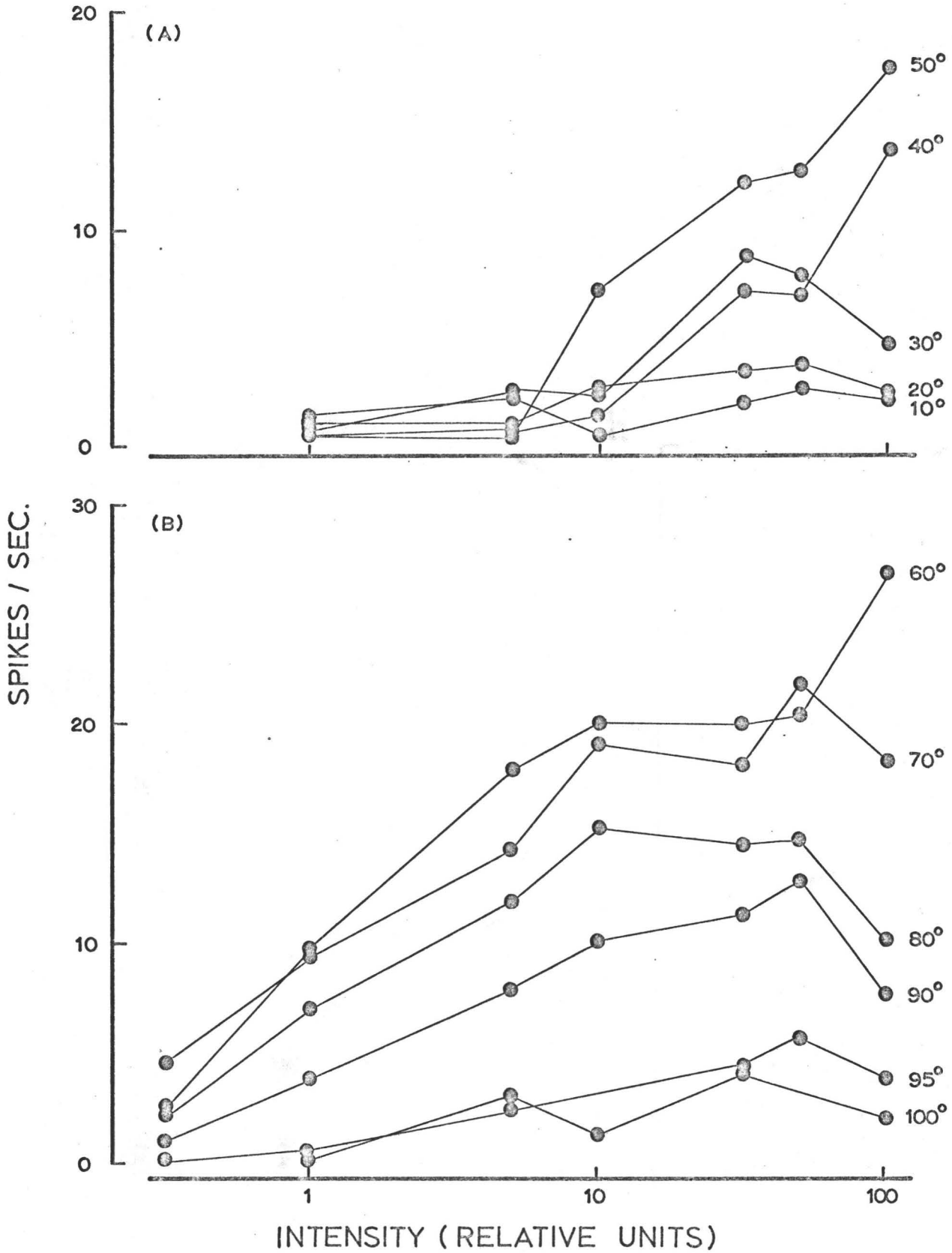
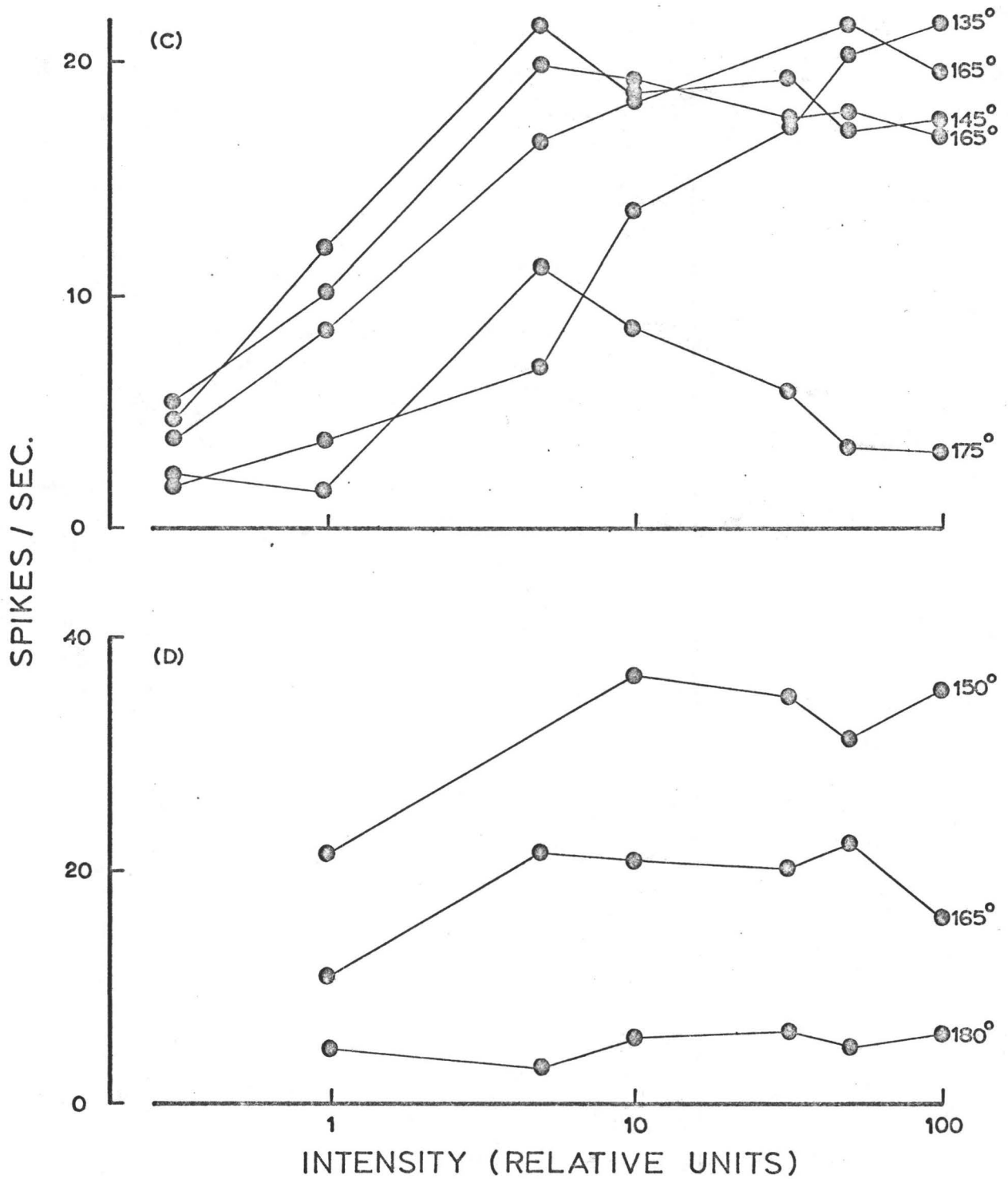


Fig. 12 Luminance effects at various stimulus orientations. (A) - (D) represent four different cells.


(C)
20
10
0
135°
165°
145°
165°
175°
(D)
40
20
0
150°
165°
180°
1
10
100
SPIKES / SEC.
INTENSITY (RELATIVE UNITS)

are not strictly monotonic but trends are apparent. It should be noted that the various cells achieve different maximum firing rates. Also, observe that different combinations of orientation and luminance produce the same firing rate. At the least effective orientation the effects of luminance are reduced or eliminated.

Figures 12A and 12B show two cells which are strongly affected by both orientation and luminance changes. The very low firing rate of the cell in figure 12A at the lower intensities suggests that this cell has a relatively high threshold for the stimuli employed. Figure 12C depicts a cell which is only slightly affected by intensity at the higher levels, but the firing rate drops off very rapidly at lower intensities. In a similar way the cell fires at a relatively high rate over a number of orientation changes (135 to 165 degrees) and then drops off suddenly (175 degrees). Figure 12D shows a cell which was little affected by intensity except at the lowest levels. However, the orientation effect was very strong, resulting in clearly separated curves which share the same firing rate at only one point. Only two cells were found which had this type of response. The significance of such response styles will be discussed later.

Families of curves for other units are illustrated in the Appendix.

Latency of Response

Reducing the average luminance of the stimulus had a marked effect on the latency of the response. A post stimulus time histogram shows when a cell fired relative to the time of movement of a repetitively oscillating stimulus. The mode in the histogram indicates at what time following the stimulus movement the cell fired most. The latency of the mode of the post stimulus time histogram increased with decreasing luminance (Fig. 13). This effect was remarkably consistent.

The latency of response of a single cell is not available as such to the nervous system because there is no stimulus marker in the brain. However the relative latency in different pathways is an important variable since it directly affects the temporal summation in convergent neurons.

Variability of Response to Identical Stimuli

The response of a unit to a particular stimulus varies considerably from one presentation to the next. This can be seen clearly in the responses to a repetitively oscillating light-dark border. Each cycle of movement constitutes a separate stimulus presentation. A cycle consists of a rapid 0.5 degree movement of the edge perpendicular to its axis, a stationary period of 167 msec., a rapid movement in the opposite direction returning the

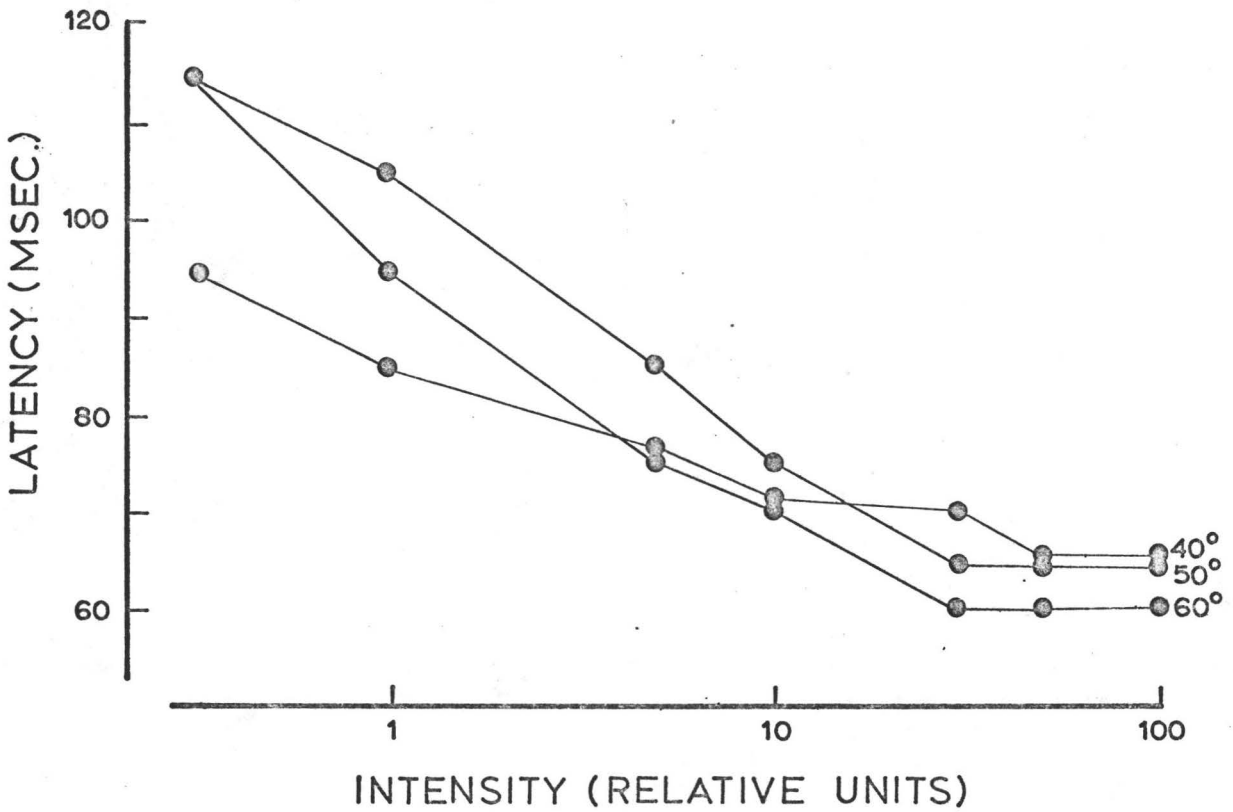


Fig. 13 The effect of luminance on the latency of the mode of the post stimulus histogram. Curves for one cell are presented. Stimulus values as in figure 6.

edge to its original position, and another stationary period of 167 msec. The unit may fail to respond on a large proportion of the stimulus presentations, yet interspersed with these are responses of varying numbers of spikes. Figure 14 shows a typical response pattern obtained during several stimulus cycles. Such a display gives an immediate impression of the strength of the response and yet maintains much of the detail of the original data. Although the occurrence of a response is intuitively obvious when compared with spontaneous activity, it is also clear that a rigorous definition of response to a single presentation would require a statistical statement of some sophistication in order to separate it from spontaneous activity, which often shows a tendency toward clustering (Smith & Smith, 1964). The distinction between spontaneous activity and response is further blurred because the brain does not know 'a priori' when the stimulus event occurred (Burns & Pritchard, 1964). It must be remembered that any definition of response put forward is generally meant to imply a neural mechanism capable of performing the necessary statistical operations.

In this section we are particularly interested in the pattern of the response, the temporal distribution of impulses from a single cell. The preceding results have dealt with the effects of various stimulus changes on a cell's firing rate. Firing rate is only one of a num-

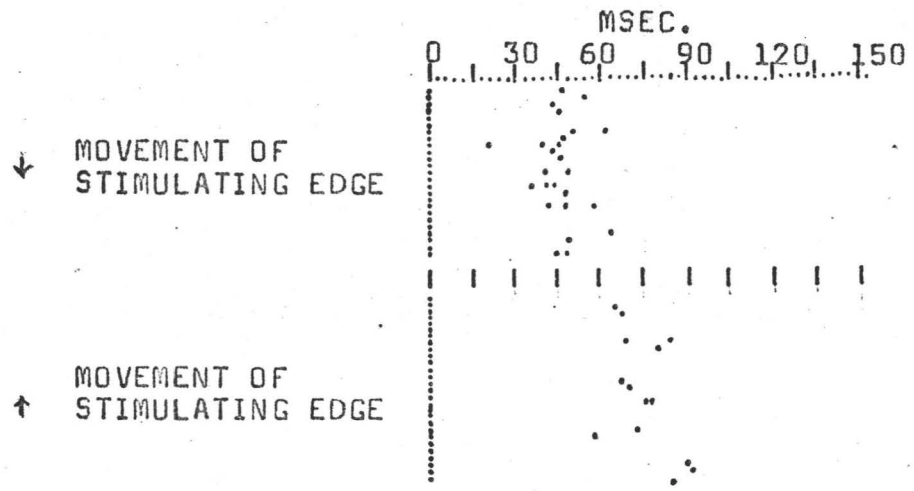


Fig. 14 Response to repeated movements of an edge. Each division on the abscissa represents 3 msec. Spots on the ordinate represent successive movements of the stimulus. The two directions of movement are separated on the ordinate. A spot on the display represents a spike discharge from the cell. The cell fires to movements in both directions but responds more frequently to downward movement. The responses to upward movements have a longer average latency. Note the variability in successive responses.

ber of candidate codes which may be used in the nervous system. Several different codes have been suggested which are based on details of the temporal pattern of response, such as alternating long and short interspike intervals (Perkel & Bulloch, 1968) and successive interspike intervals of the same duration (Burns & Pritchard, 1964). The following presentation is not meant to supercede these attempts, but rather to step back to look at the raw data. Figure 14 is little more than a spike train displayed in order to show when the stimulus events occurred. The point to be taken from these data is that the response is not an all-or-none event. The response is highly variable. It is for this reason that cortical cells are said to behave statistically (Burns, Heron & Pritchard, 1962) and to be unreliable (McCulloch, 1964).

The earlier statements about the effects of orientation and intensity must be taken as statistical statements. <u>On the average</u> a cell may fire more to high intensity stimuli than low intensity stimuli, but this does not show up in each and every stimulus presentation (Fig. 15). This is true for every cell in the present study.

The increase of average firing rate with increasing luminance is effected in two ways. Individual cells respond to a larger proportion of the presentations and produce more spikes when they respond. Put in another way - for some period of time following a stimulus move-

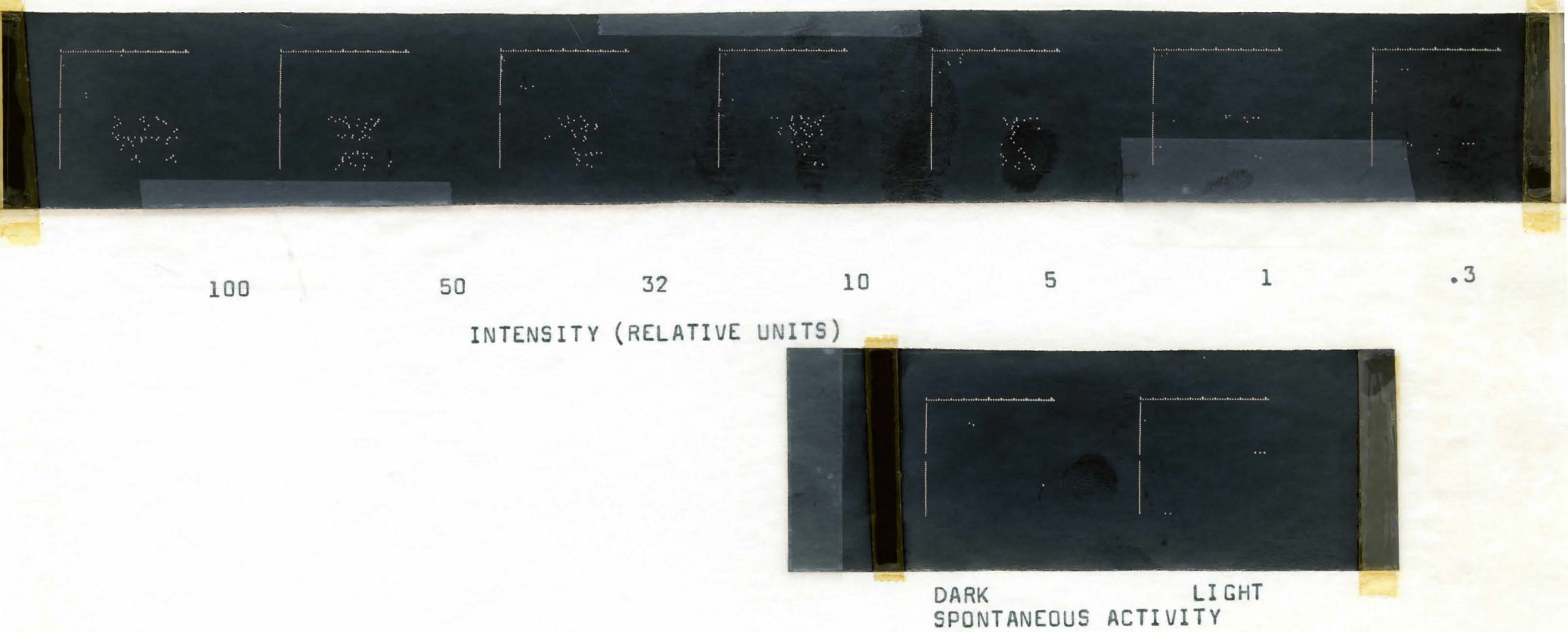


Fig. 15 The effects of stimulus intensity on response. Coordinates as in Figure 14, but the display is reduced in size to allow for comparison of different stimulus effects. The stimulus is located at the preferred orientation. A stimulus marker without a stimulus is used to display spontaneous activity.

ment the probability of a spike occurring increases with stimulus intensity. The point of the earlier statement is that one of the primary effects of a stimulus change such as intensity is to change the proportion of stimulus presentations which elicit a response. However, even when a stimulus elicits a strong response on the average, there are individual stimulus presentations to which no response occurs. This situation is seen in Figure 15. Even at the highest intensity (which elicited a very strong average response) three of 28 stimulus events were followed by no spikes at all. There are changes in the temporal distribution of spikes which show up to a varying extent in different cells. Stimulation tends to cluster firing at a particular time following stimulus movements. This tendency is usually enhanced by increases in luminance (Fig. 15). The latency also becomes more consistent.

Two important points are demonstrated in Figure 15: (1) during stimulation at low intensity and even during spontaneous activity, bursts of spikes occasionally occur even though the average firing rate in these conditions is quite low; (2) with a repeated stimulus the proportion of stimulus presentations which elicit a response is itself a variable with respect to intensity.

Response patterns for other units are illustrated in the Appendix.

Nine different criteria for a response are defined in Table I. The successes and failures of the various criteria when applied to the 56 cells in the present study are summarised in Table I.

TABLE I

Comparison of Different Criteria for a Response

Criterion for a Response	The number of cells responding to the stimulus according to this criterion	The number of cells not responding to the stimulus according to this criterion	The number of cells responding according to this criterion during spontaneous activity
1. The number of spikes within 30 sec. is greater than 0	56	0	56
2. The number of spikes during stimulation is greater than the number of spikes during spontaneous activity (30 sec.)	52	4	-
3. The firing during selected periods following a stimulus is higher or lower than expected during comparable periods of spontaneous activity as indicated in a poststimulus histogram (30 sec.)	56	0	-
4. Two or more successive interspike intervals of equal duration occur during the test period (8 sec.)	53	3	27

TABLE I

Continued

5. Two or more successive interspike intervals occur more often during stimulation than during a comparable period of spontaneous activity (8 sec.)	53	3	-
6. More spikes follow the first stimulus presentation than expected during a comparable period of spontaneous activity	51	5	-
7. Two or more successive interspike intervals of equal duration follow the first presentation of the stimulus	43	13	2
8. Two or more successive interspike intervals of equal duration follow each presentation of a stimulus (8 sec.)	0	56	0
9. One or more spikes follow each presentation of a stimulus (8 sec.)	17	39	4

DISCUSSION

Interpolation of the response curves for orientation and intensity indicates that for a given cell many different stimuli would produce the same response. This finding is incompatible with the notion of a trigger function in which a cell gives an all-or-none response to a particular stimulus (Wickelgren, 1969). The response of a cell does not unequivocally define the stimulus, rather it defines a set of stimuli which might be present. Large numbers of cells responding to these same stimuli in the same way would not help to identify which stimulus from the set is present, but would only identify the set more reliably.

It can be seen that in order to represent the stimulus distinctively and reliably using cells having the response characteristics described here it is necessary to compare the activity of cells which have converging sets. In fact cells which prefer different orientations have such sets. The results suggest that a stimulus is represented unequivocally by the pattern of activity across cells which prefer the stimulus and cells which prefer other stimuli. Thus several cells are involved in re-

presenting different stimuli on the basis of the relative amount of activity in each cell. Several factors lead to this conclusion.

The present data provide a number of requirements which must be met by any neural code put forward to represent these simple visual stimuli. The effects of orientation and intensity on firing rate indicate that firing rate of an individual cell is insufficient to identify the stimulus except in an unspecific way. The variable response to repetitive stimulation could be handled by a code involving the fine temporal patterning of impulses in a single cell only by throwing out huge amounts of information. For instance, codes based on long followed by short interspike intervals and codes based on repeated interspike intervals of the same duration require at least three spikes in response to a single stimulus presentation to make up the temporal pattern. The information provided by responses of one or two spikes would be lost. More complicated codes would tend to throw out even more of the responses.

A code dependent on the firing rate of many cells would overcome both problems. The variable response of individual cells to repetitive stimulation would be smoothed to a consistent response over many cells. The effects of orientation and intensity on firing rate would be handled by comparing the activity of those cells which prefer the stimulus with the activity of those cells which prefer other

stimuli but respond to the stimulus and the activity of those cells that do not respond to the stimulus. Such a multicell code easily overcomes the difficulty of separating spontaneous from stimulated activity. This can be quite difficult for individual cortical cells which often have high spontaneous rates composed of bursts of several impulses (Smith & Smith, 1964).

In such a multicell code there is no critical neuron and the stimulus identification is overdetermined. Consider that population of cells in the cortex which respond differentially to orientation of an edge at a particular location in the visual field. An edge presented at that location having an orientation of thirty five degrees at an intermediate stimulus intensity will cause cells having stimulus preferences near thirty five degrees to fire the most; firing rate decreasing as the stimulus preference varies from thirty five degrees. Cells having preferences more than say, fifty degrees away from the stimulus may not respond at all. If the stimulus intensity is increased the same cells will be firing the most, but at a higher rate, and in addition, more cells will be firing, perhaps up to stimulus preferences sixty degrees away from the stimulus. If, instead of intensity, orientation is changed then different cells will be firing most, but the number of cells responding will be generally unchanged.

Note that information is provided by both responding and non-responding cells, although those responding carry more information. To know the stimulus orientation we need only know which cells are firing most i.e. relative firing rate. To know stimulus intensity we need to know absolute firing rates of these cells. However, at every level in the visual system below the cortex there are cells carrying intensity information so this information is widely available (Barlow & Levick, 1969; Arden & Liu, 1960).

A multicell code based on the temporal pattern of impulses presumably could handle the orientation and intensity effects by having a particular spatio-temporal pattern for each stimulus, but fine temporal patterns of individual neurons would tend to be blurred during summation. Figures 14 and 15 show that a given cell has a variable latency of response to a stimulus. A multicell code based on temporal pattern would have to incorporate such variability. In addition, for a single cell the pattern of response varies from one presentation of a stimulus to the next. It is not at all clear how a multicell temporal code would handle such variability without dumping large amounts of information.

Furthermore, changes in firing rate are more effective at the post-synaptic membrane than changes in temporal pattern. However, due to the nature of summation of

post-synaptic potentials temporal pattern of input can affect the membrane independently of changes in firing rate. There are examples of cells which are sensitive to temporal pattern. Perkel & Bullock (1968) describe a pacemaker neuron in the cardiac ganglion of the lobster which responds differently to alternating long and short interspike intervals than to equal intervals, given the same mean rate. It is not clear that this sensitivity is functional.

As Perkel and Bullock (1968) point out, showing that information is available in the nervous system in a particular code does not necessarily indicate that this code is used by the nervous system. We are not yet in a position to demonstrate that a particular code is actually used in pattern recognition but there is behavioral evidence which indicates the type of codes which are most likely utilized. The phenomenon of stimulus generalization suggests that stimuli are not represented by unique stimulus detectors.

A pattern recognition system based on individual units which are stimulus detectors would predict no stimulus generalization. If a response was conditioned to occur in the presence of a particular stimulus we would expect it to occur only when that stimulus was present. However, the behavioral response occurs whenever <u>similar</u> stimuli are present, the strength of response depending on the similarity between conditioned and test stimuli. Such an effect

can be readily explained if a multicell code based on firing rate is used to represent the stimulus. The cells which prefer the stimulus used in conditioning fired most during training and thus developed the strongest attachment to the reinforced response. Neurons which do not prefer the conditioning stimulus but respond weakly to it develope an attachment to the reinforced response but at a weaker level. Thus generalization decrement occurs. Although such a scheme is highly speculative it is clear that the code which is indicated by the physiological evidence is compatible with the behavioral evidence.

Further limits are imposed on suggested neural representations by results from lesion experiments. Subtotal lesions of the striate cortex (area 17) leave animals relatively unimpaired in pattern discrimination, whereas total ablation eliminates pattern discrimination (Kluver, 1942; Wetzel, 1969). This cortical area is crucial for the function, but there is no critical neuron.

A number of general arguments can be brought against the approach suggested here and I would like to consider the two most salient. The first suggests that we simply haven't found the neurons which do have the very specific stimulus requirements expected of "detector" neurons. Considering the relatively small number of cells described in the present study in comparison with the total number of

cells in area 17 of the visual cortex, this is a valid criticism. However there is an established rationale supporting this approach as well as corroborating evidency from other studies. Certain visual patterns can be behaviorally discriminated and ablation of the visual cortex eliminates the ability to discriminate these patterns (Kluver, 1942). Thus tissue in this area is critical for pattern discrimination. Lesions outside of the visual system are relatively ineffective with regard to visual pattern recognition. Cells in the visual cortex respond differentially to visual patterns, being particularly sensitive to the orientation of straight lines and edges (Hubel & Wiesel, 1965). Perhaps the activity of cells in this area is the basis for the visual discriminations. The most compelling aspect of this rationale is the sensitivity of these cortical neurons to the parameters of visual stimuli.

Nonetheless, the possible existence of "detector" neurons cannot be disproved. The argument here is that neurons of the type described in the present study will not perform the detector function as described by a place theory. Furthermore, the cell in the present study showing the highest orientation sensitivity (Fig. 1a) compares closely with the most sensitive neurons found by Hubel & Wiesel (1962) and Campbell, Clelland, Cooper & Enroth-Cugell (1969).

A second argument against the present approach is that the stimuli used are trivial as compared to visual patterns which are meaningful to the cat i.e. mice, dogs, other cats. This would seem to be true except that overwhelming evidence is accumulating which suggests that pattern recognition is based on feature analysis - a breakdown of patterns into simple components (Weisstein, 1969). Further evidence comes from neurophysiological studies. The Hubel and Wiesel (1959, 1962, 1965) findings would not be considered important if it were not for the fact that neurons respond very strongly to the simple stimuli they employed. Unfortunately there has been very little consideration of response strength except within a limited experimental situation. Thus the experimenter describes which of the stimuli he used produced the largest response. There is no notion of how large a response he might have gotten if he had used all the possible stimuli. Such a measure would seem attainable, at least as an estimate, since we know some of the limits imposed on the firing rate of a neuron i.e. refractory periods. The measure would be particularly appropriate for those using firing rate as a response measure. It would overcome the severe limitations that time and imagination set on the stimuli used in an experiment and it would permit a comparison of response strength across different experiments. In argu-

ing the case for a detector cell it would have to be shown that the stimulus is very effective relative to what might be expected of the cell, not relative to the rest of a small sample of stimuli. At present, there is no independent criterion of a "good response" save that intuitively accepted by those in the area. Nonetheless it is clear that the simple stimuli presently employed are very effective in producing a response. Future studies of the response capability of neurons will presumably corroborate the effectiveness of simple stimulus elements.

A further point should be made concerning the duration over which a code would have its effect. We are searching for meaning in a sequence of interspike intervals somewhat as though trying to decipher Morse code or trying to understand speech in a foreign language. The question is where does one word end and the next word begin? Aside from knowing the meaning of the word we must know how to separate one word from the next.

In Morse code the end of a word is indicated by three short blank periods. In speech the rules are very complicated and often indeterminate. For the post-synaptic membrane the rule seems to be based on the duration of excitatory and inhibitory potentials. Transmission of an impulse at the synapse produces an excitatory or inhibitory potential at the post-synaptic membrane which lasts 80 - 100 milliseconds for neurons in the cortex (Eccles,

1964). However, the potentials have a short rise time and then decay exponentially with time. As a result maximum summation would occur over a time of about ten or twenty milliseconds. Perhaps this is the time over which changes in firing rate (or any other measure) would exert a major effect. This would seem to be the duration of a "word" in the neural language.

Given short duration for summation the relative latency in different fibers would be very important in synchronizing impulses across many fibers. Spike clusters that are separated by long inter-cluster intervals might relate to different aspects of the stimulus as suggested by Jung (1961).

The effects of varying orientations and intensity simultaneously show that different stimuli will produce the same response in a neuron. If the same response can be produced by stimuli that are obviously discriminable, then that neuron is not sufficient to discriminate between those stimuli. This situation obtains for several values of orientation and intensity. Furthermore this is a general situation due to the relationship between stimulus intensity and firing rate. On the basis of known relations between color, position, orientation and firing rate it can be argued that the same situation holds for many aspects of a visual stimulus. The behavior of neurons in other sensory systems indicates that the same situation

holds for some of the other modalities - somato-sensory and gustatory (Milner, 1958; Melzack & Wall, 1962; Mountcastle, 1967; Erickson, 1968; Uttal, 1969). For example, a fiber in the chorda tympani might respond most strongly to an NaCl solution applied to the tongue, but it will also respond to NH_4Cl and KCl. Moreover, the response to each of these solutions increases with concentration i.e. intensity (Erickson, 1968). Thus different stimuli would produce the same response.

There are two general properties which neurons in these sensory systems share and which leads to the suggestion that coding is similar in these systems (Milner, 1958; Erickson, 1968). First, cell firing is related to stimulus dimension by an inverted U function, or bell shaped curve. This is the stimulus preference exhibited by an individual cell. Second, response strength increases with stimulus intensity. The two properties lead inevitably to the situation that a given response might have been produced by any of several different stimuli. The only unequivocal representation of a stimulus in these modalities is the relative activity across several neurons. The argument deals specifically with firing rate, the most widely accepted neural code, although it may also apply to other codes.

There is an intuitive feeling for a single cell acting as a detector - perhaps it derives from Mueller's

classical theory of specific nerve energies in which the nature of the stimulus is indicated to the brain by means of which afferent fiber is active. There is no such feeling for the activity across several cells. A code based on the relative activity across a population of cells implies that the brain is more complex than expected and the implications for research strategy are considerable. The direction for research was clearly defined - find a cell and then find its preferred stimulus. Eventually such a procedure would turn up a cell for a white mouse (Burns & Smith, 1962), a cell for a piano (Attneave, 1961), and a cell for an automobile (Thompson, 1969). In fact, higher order detector neurons have been suggested as a replacement for the unscientific homunculus (Attneave, 1961).

Our concepts (derived largely from a familiarity with electrical wiring) seem inadequate for considering distributed information leading to either/or decisions, such as the recognition of a familiar face, without funneling to a single detector cell. Must all information lead to an on-and-off light switch? As Perkel and Bullock (1968) point out, a population of cells can readily perform such a decision making function whether by leading to a motor or glandular output, by resulting in a particular spatio-temporal distribution of activity in the population, or by some other means. Furthermore, since many synaptic inputs are usually required to produce an action

potential the efficacy of funneling several inputs into a single detector cell is not altogether clear in view of the fact that the detection or decision must be transmitted to other neurons involved in the behavioral response to the detection.

As mentioned earlier two cells were found which were relatively uninfluenced by intensity changes, yet they showed strong orientation effects. Cells of this type might be involved in form constancy i.e. the tendency to see forms as relatively unchanged under widely altered conditions of illumination. Other attributes one might expect of neurons involved in form constancy are insensitivity to stimulus location and size (Hubel & Wiesel, 1965).

However, sufficient emphasis must be made of the variability of response to identical stimuli. Even though the average firing rate of a cell may increase with an orientation or intensity change this increase does not show up in the firing of the cell following each and every stimulus presentation. Maffei (1968) suggests that the important information contained in a temporal average (average firing rate of a single cell to a repeated stimulus) is normally obtained by the brain in a spatial average (the average of several neighboring cells responding to a single stimulus presentation) since the brain is not usually presented

with repetitive stimuli and certainly doesn't require them.

The cells in the present study whose firing rates were relatively unaffected by intensity changes nonetheless showed a high variability in response to identical stimuli. A response to a single stimulus presentation is not necessarily representative of a cell's average response to that stimulus. As Arden and Soderberg (1961) found in lateral geniculate cells "... the variations in response to identical stimuli are often greater than can be produced by alteration of the stimulus parameters." We are thus led to the conclusion that stimuli are not represented distinctively by the firing of individual cells, but by the relative activity across many cells.

SUMMARY

1. Activity of single neurons in the cat's visual cortex was observed during patterned stimulation of the retina. Orientation and illumination of a simple light-dark stimulus were varied.
2. All neurons examined showed orientation selectivity.
3. Increases in stimulus intensity tended to increase firing rate.
4. Individual neurons varied considerably within these general trends. Moreover, for each of the neurons responses varied a great deal even to repeated presentations of a stimulus.
5. Interpolation of the results indicates that a given response of a neuron could result from several different stimuli.
6. A 'place' theory of pattern recognition does not adequately describe the behavior of these neurons.
7. It is suggested that the stimulus is uniquely identified by the relative activity across several neurons.

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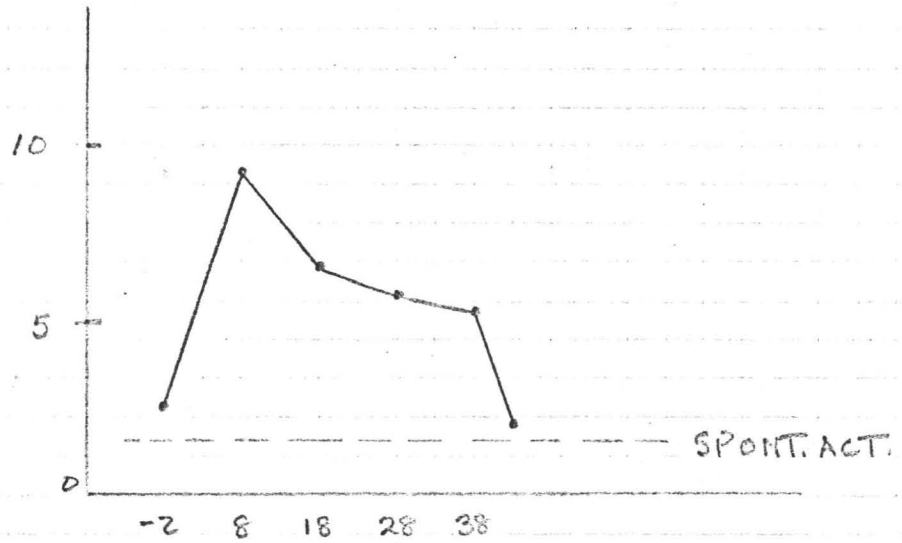
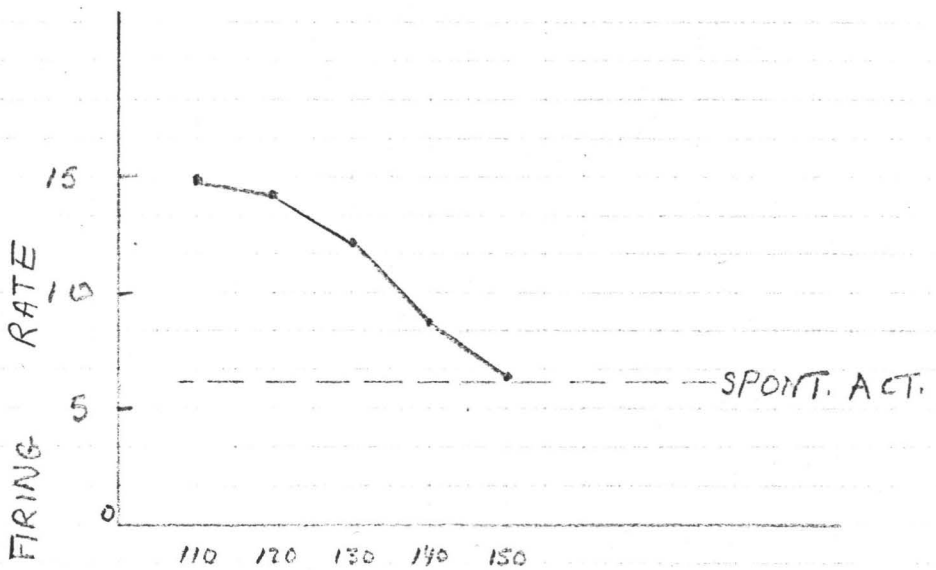
APPENDIX





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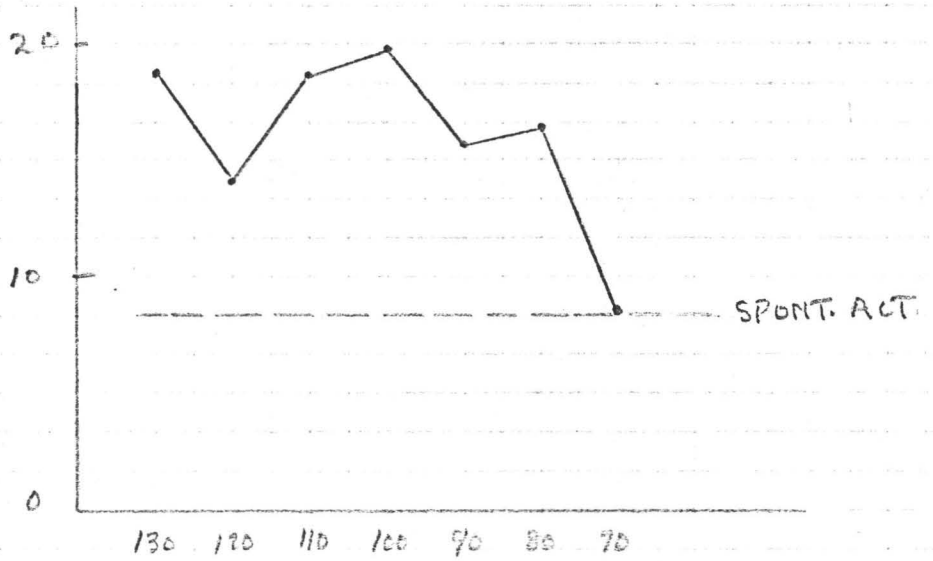

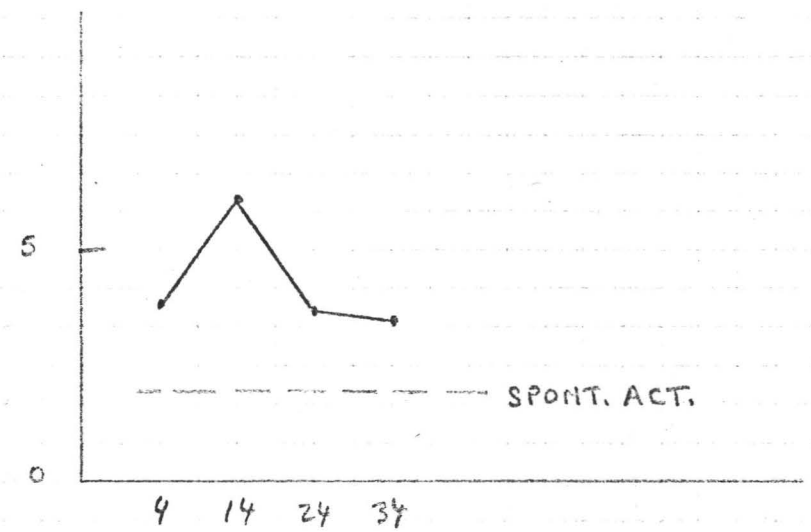

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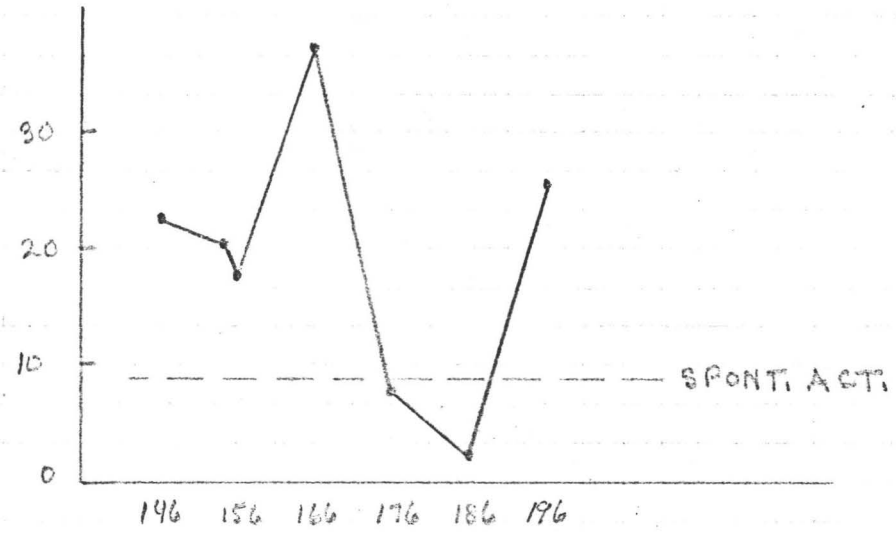

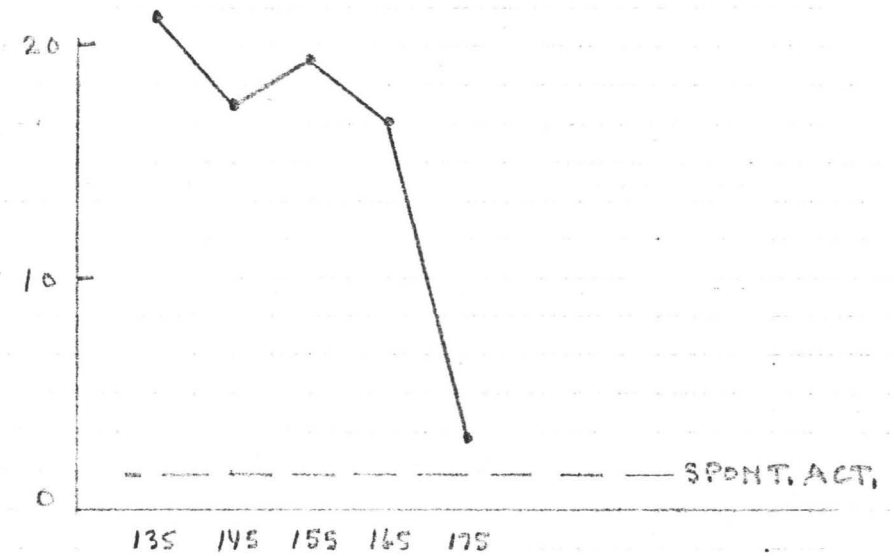

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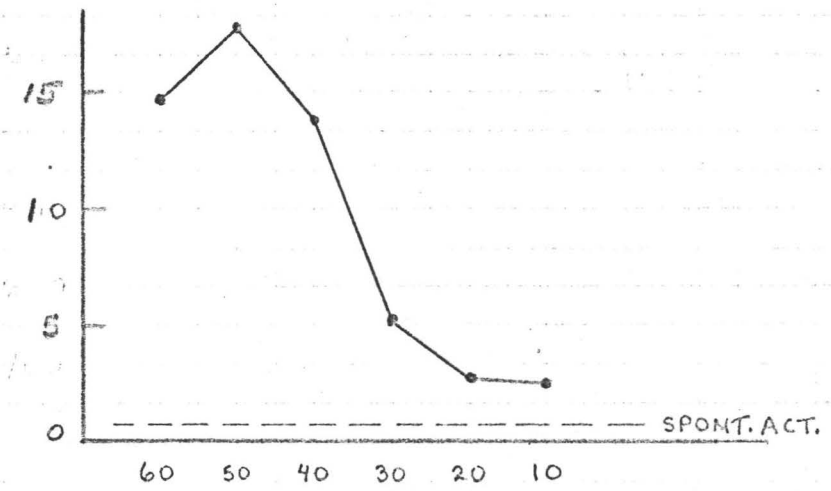

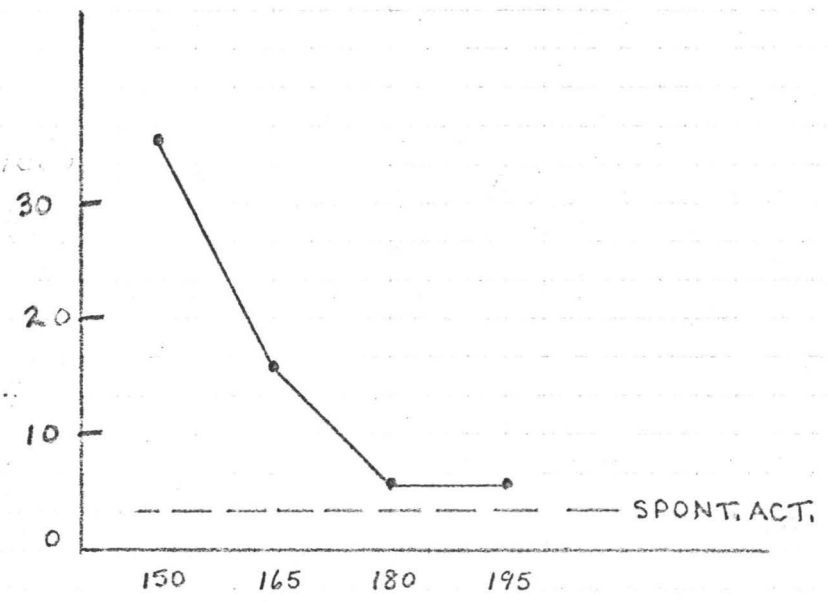

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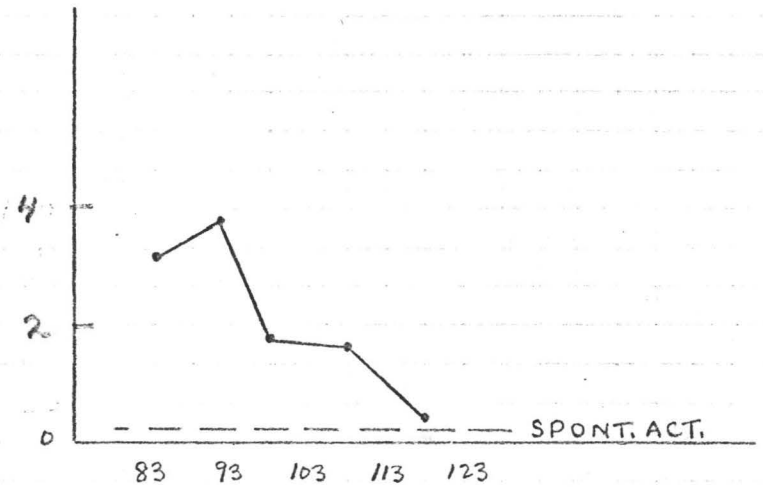

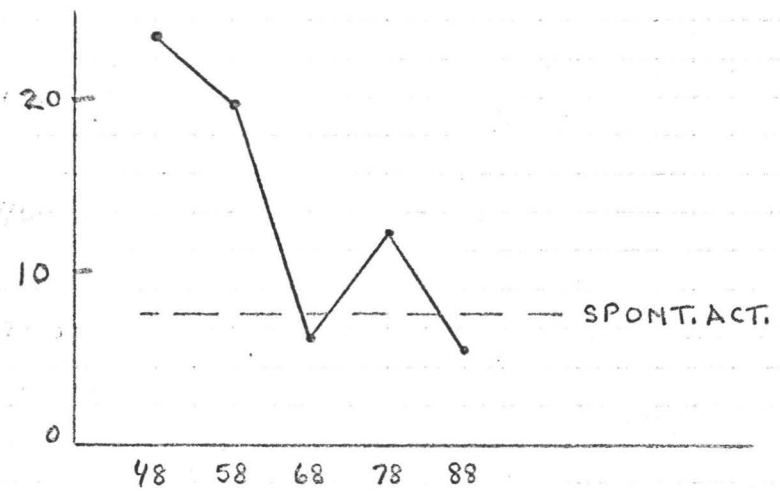

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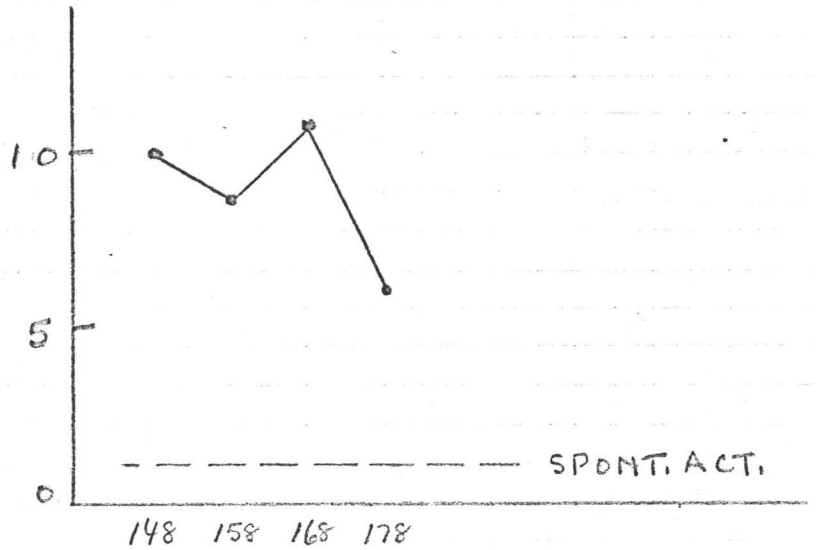

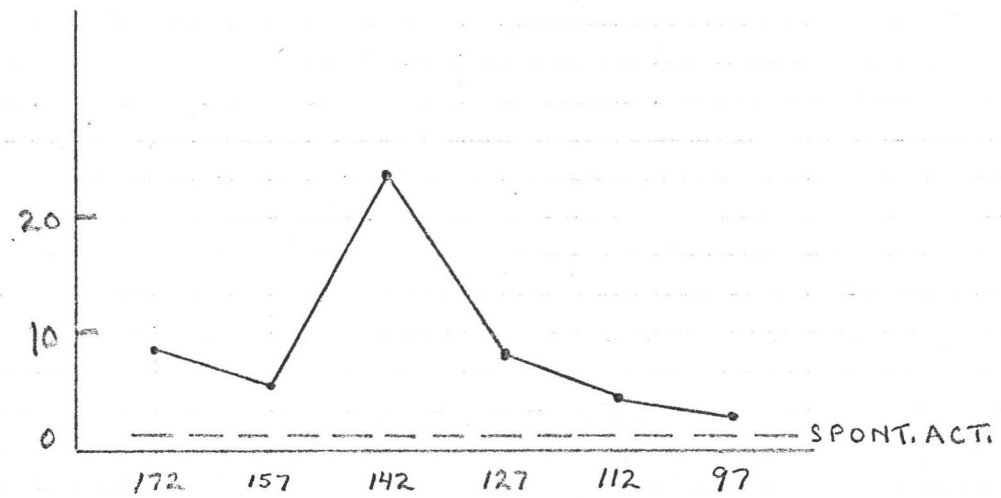

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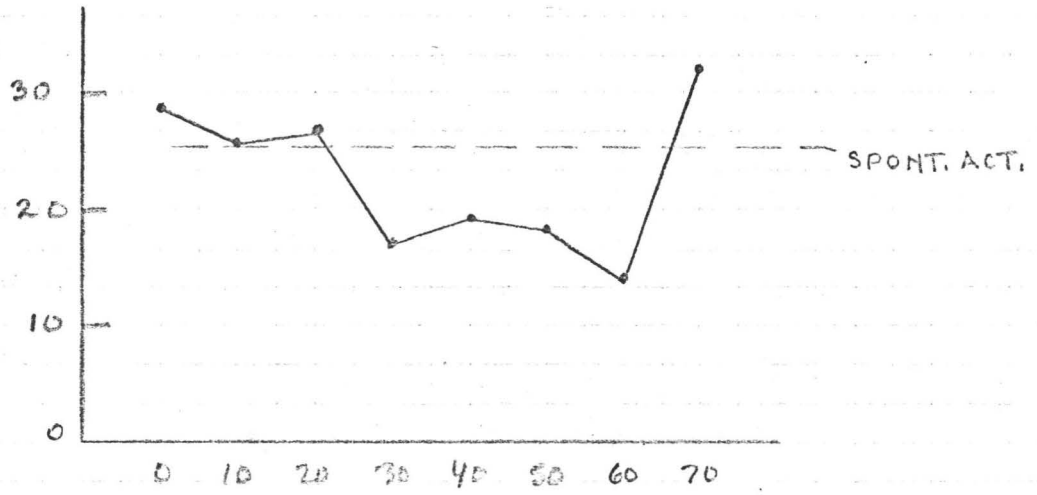

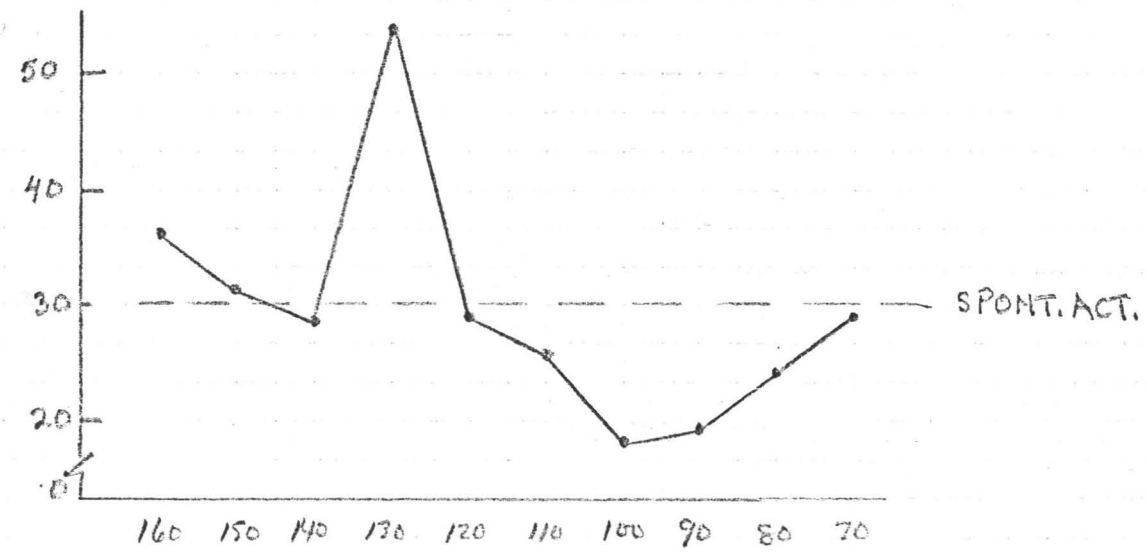

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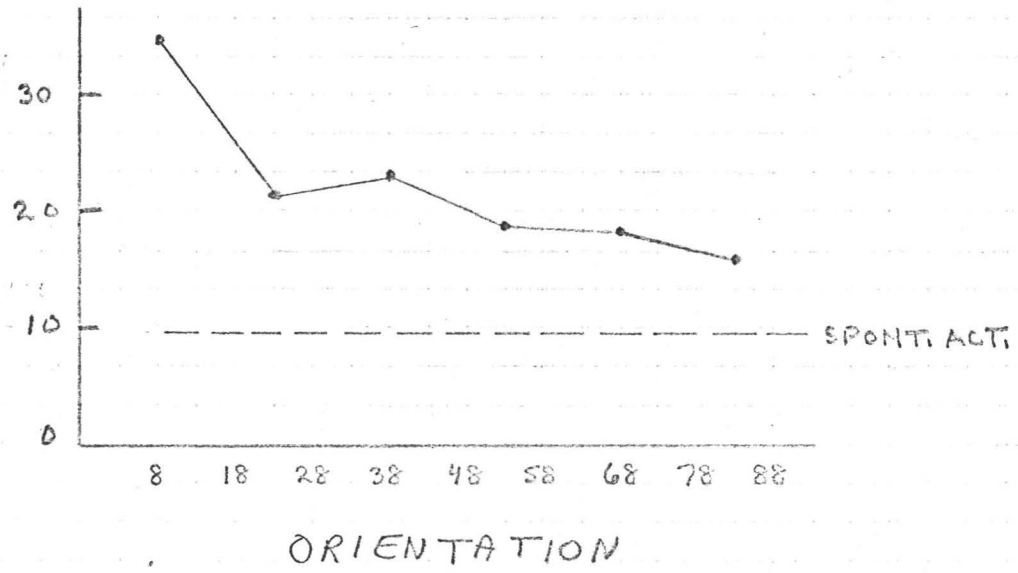
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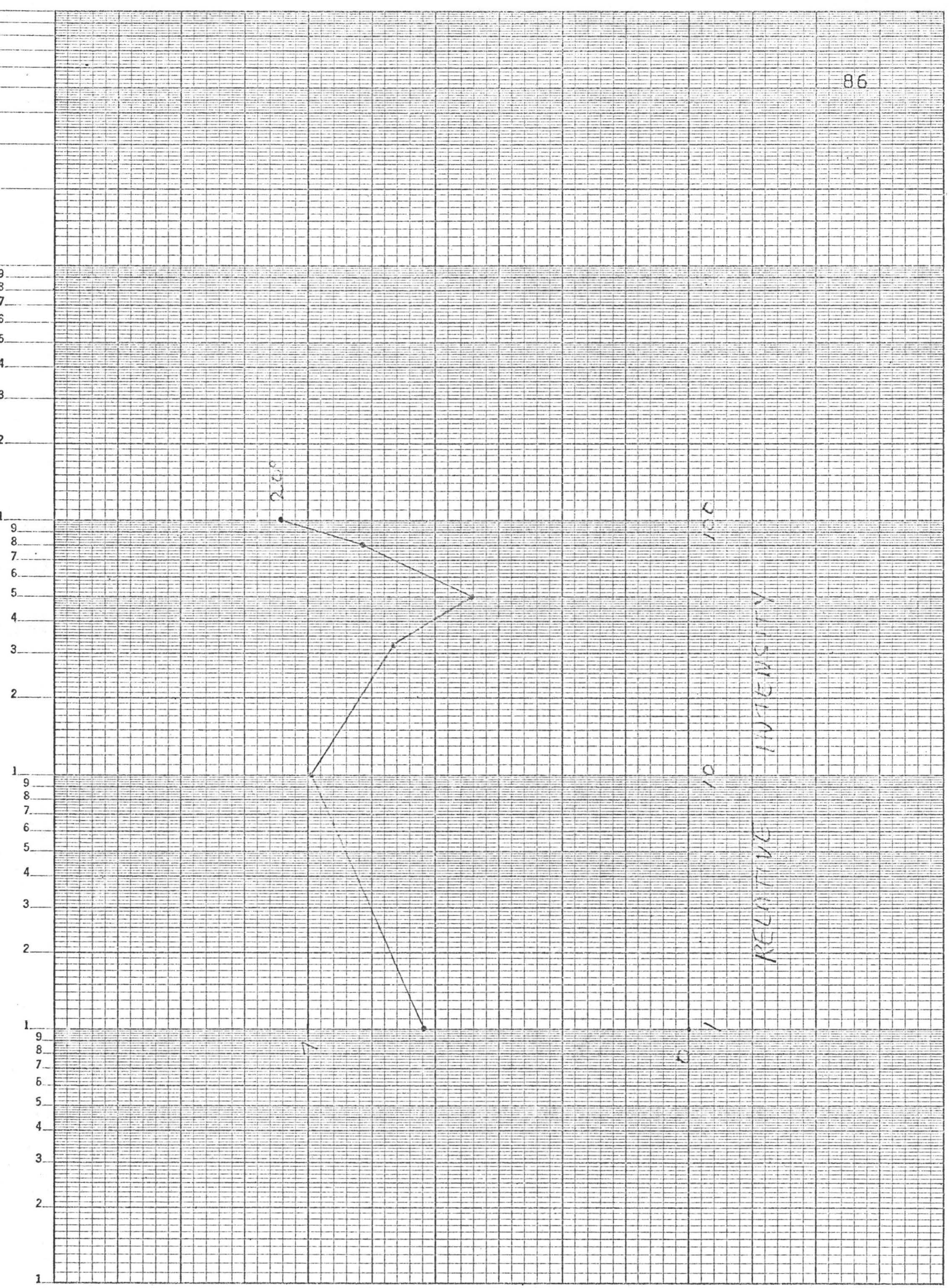

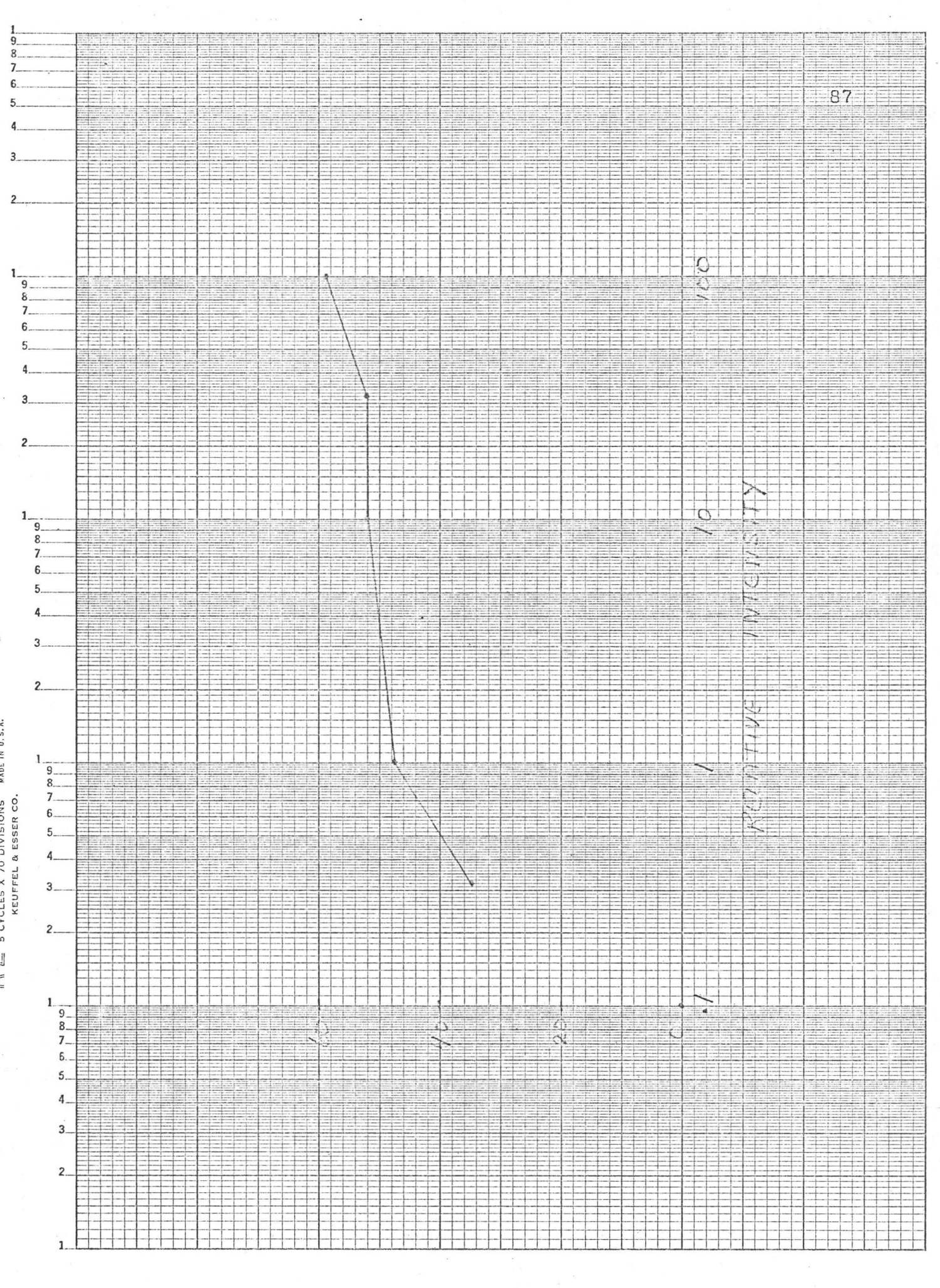

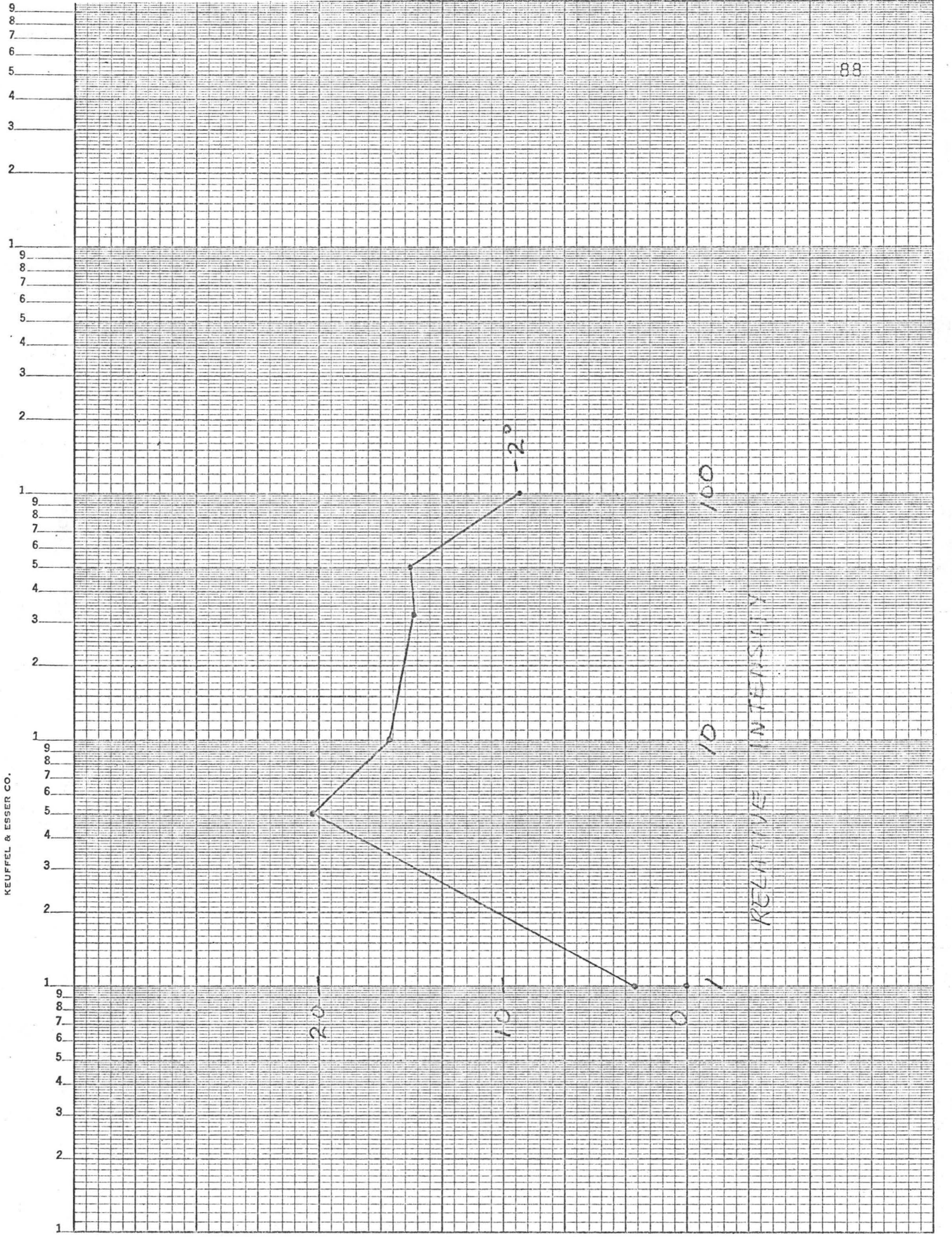

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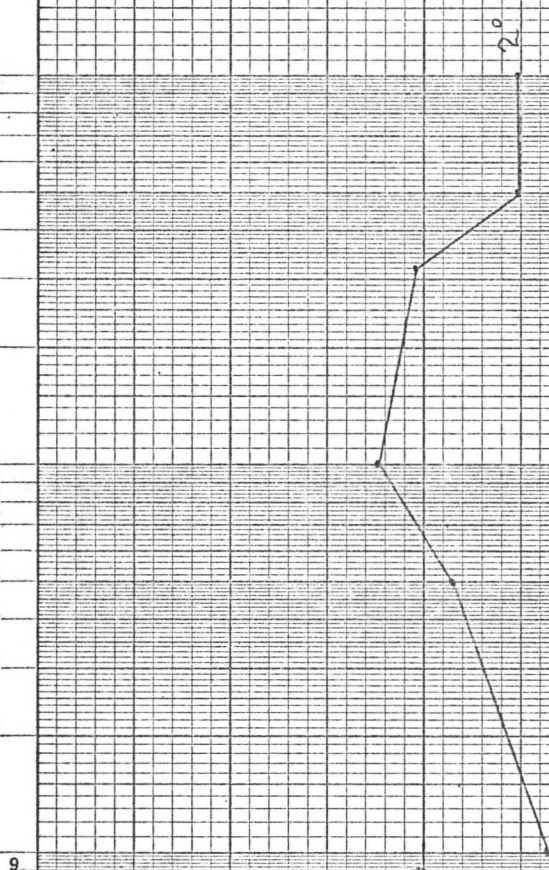

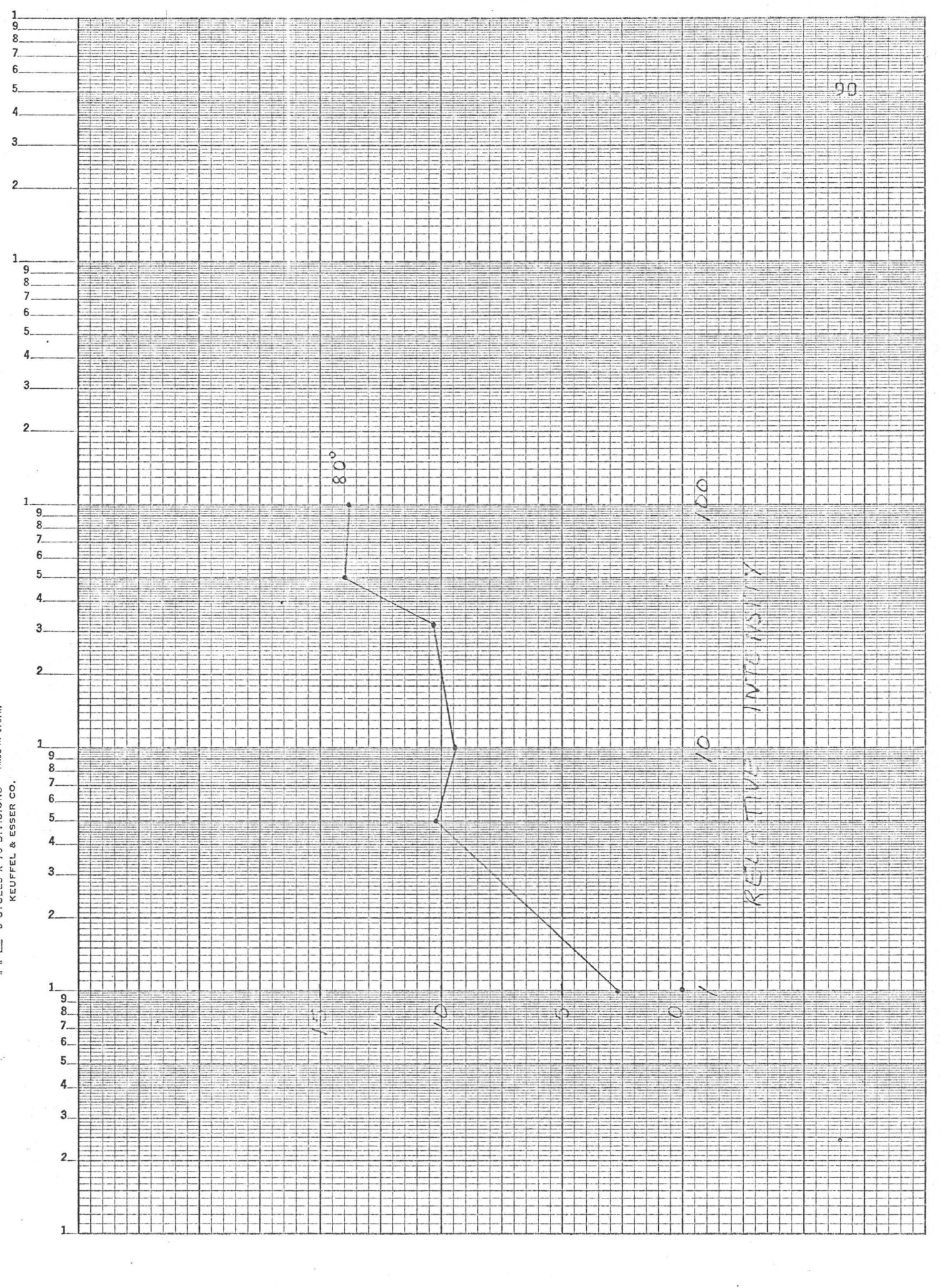
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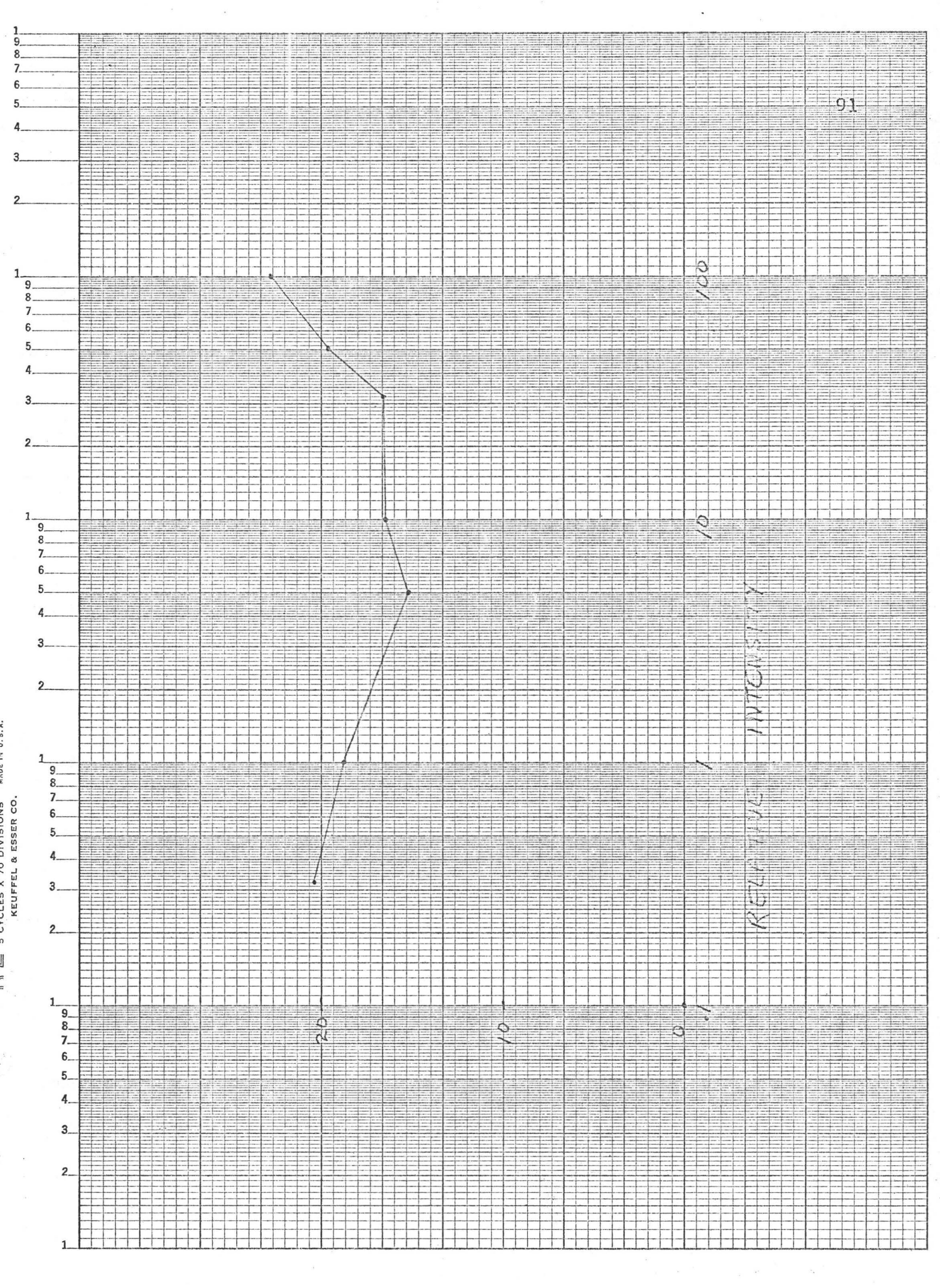
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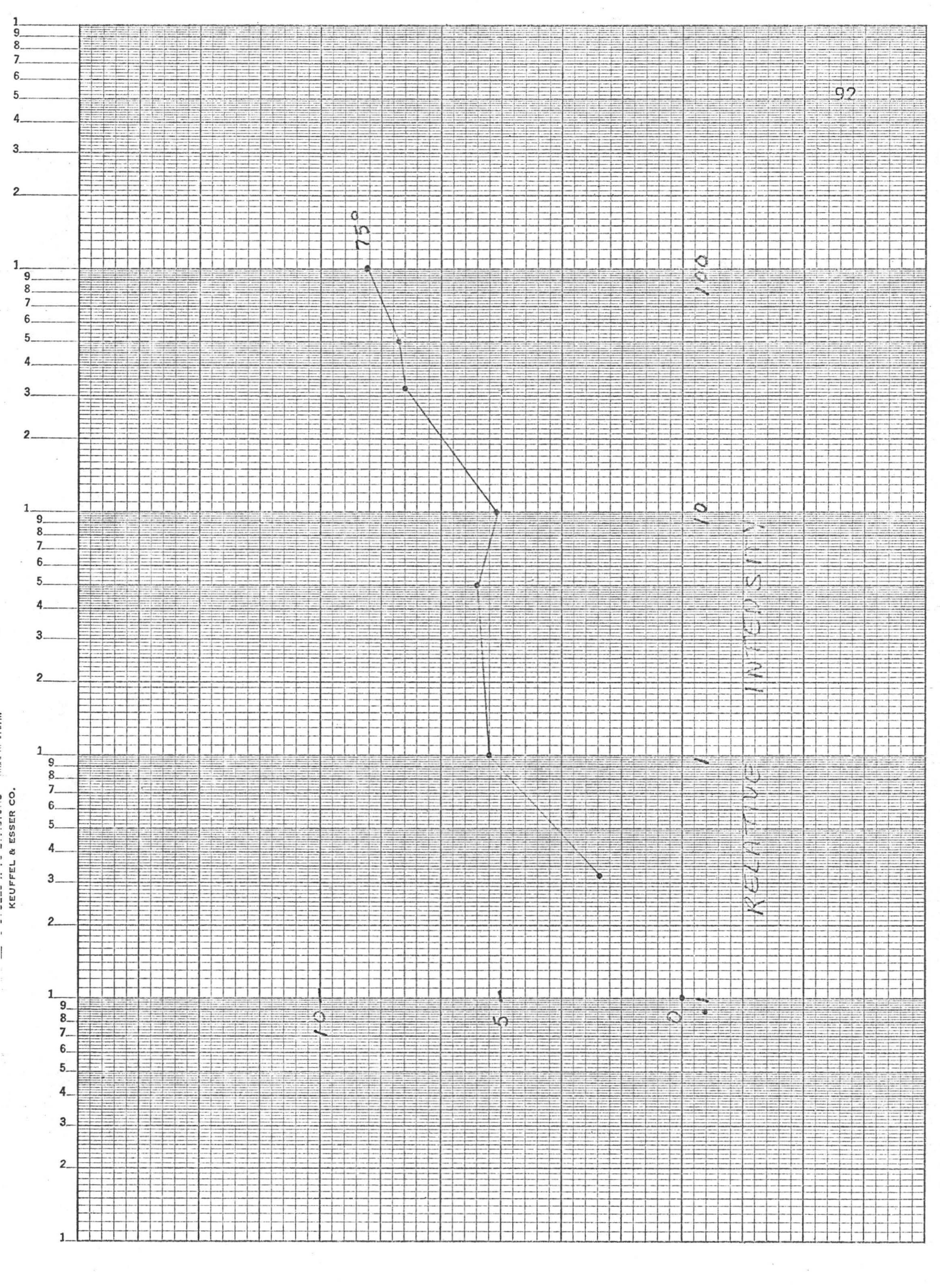

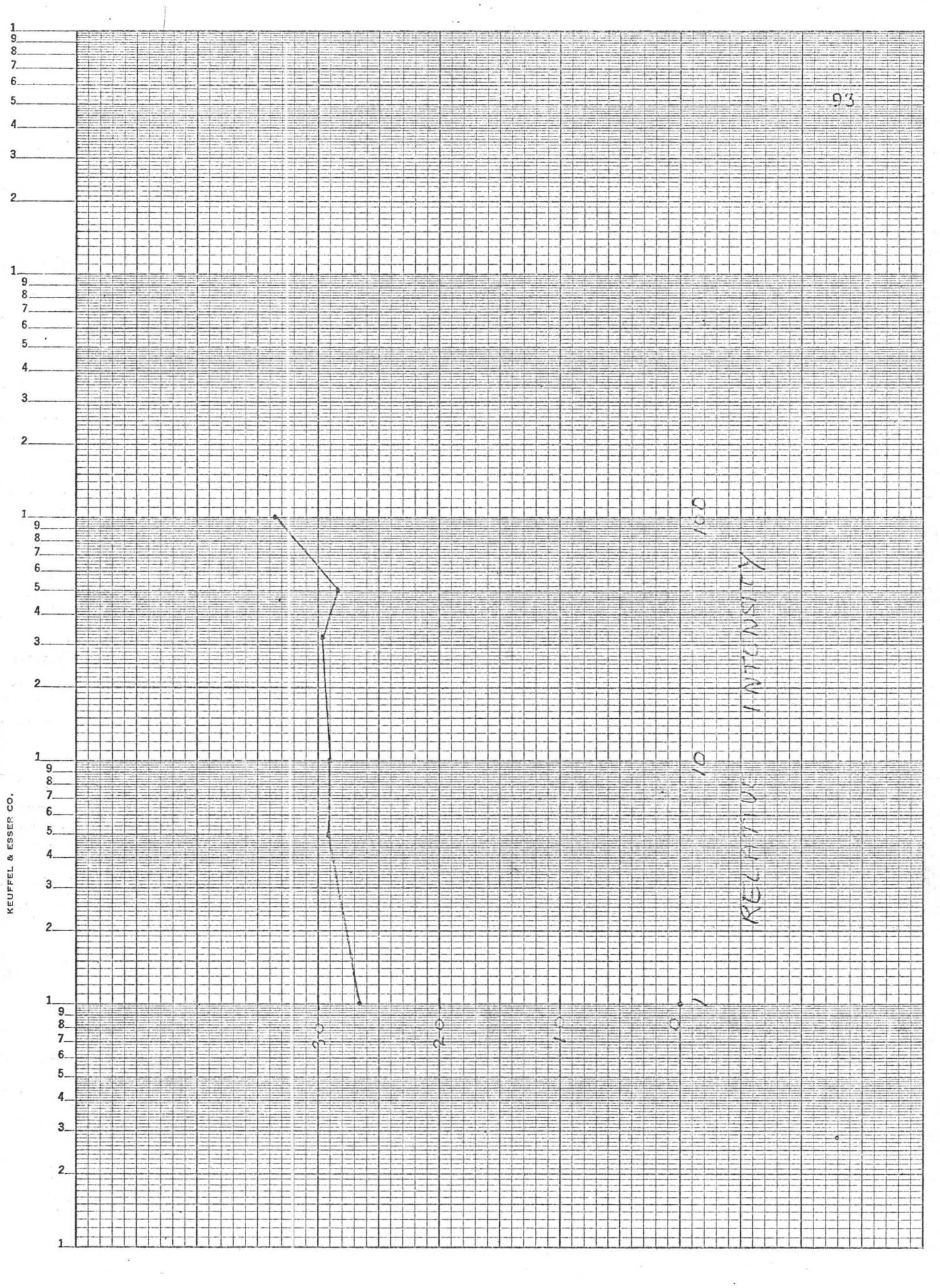

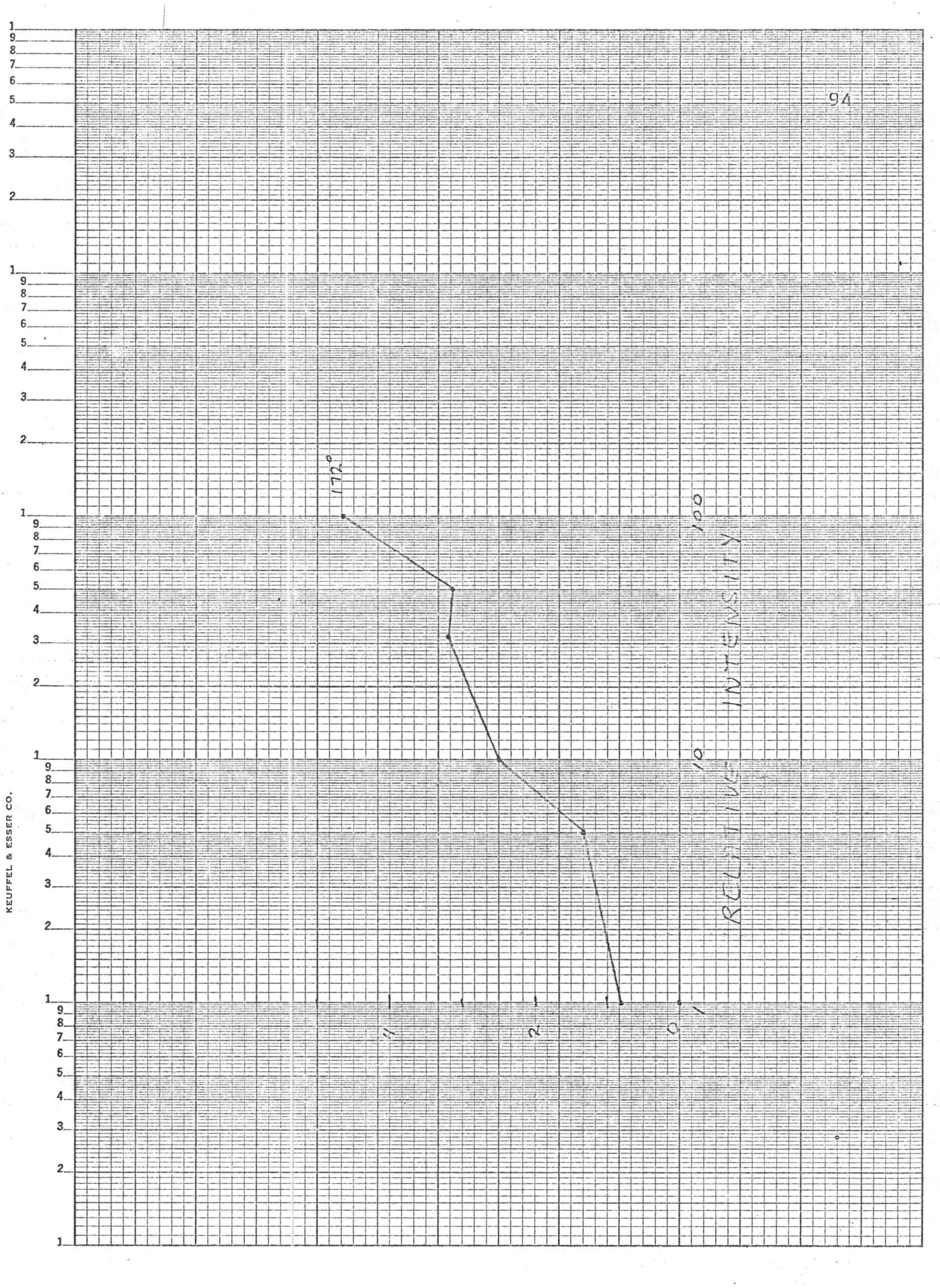
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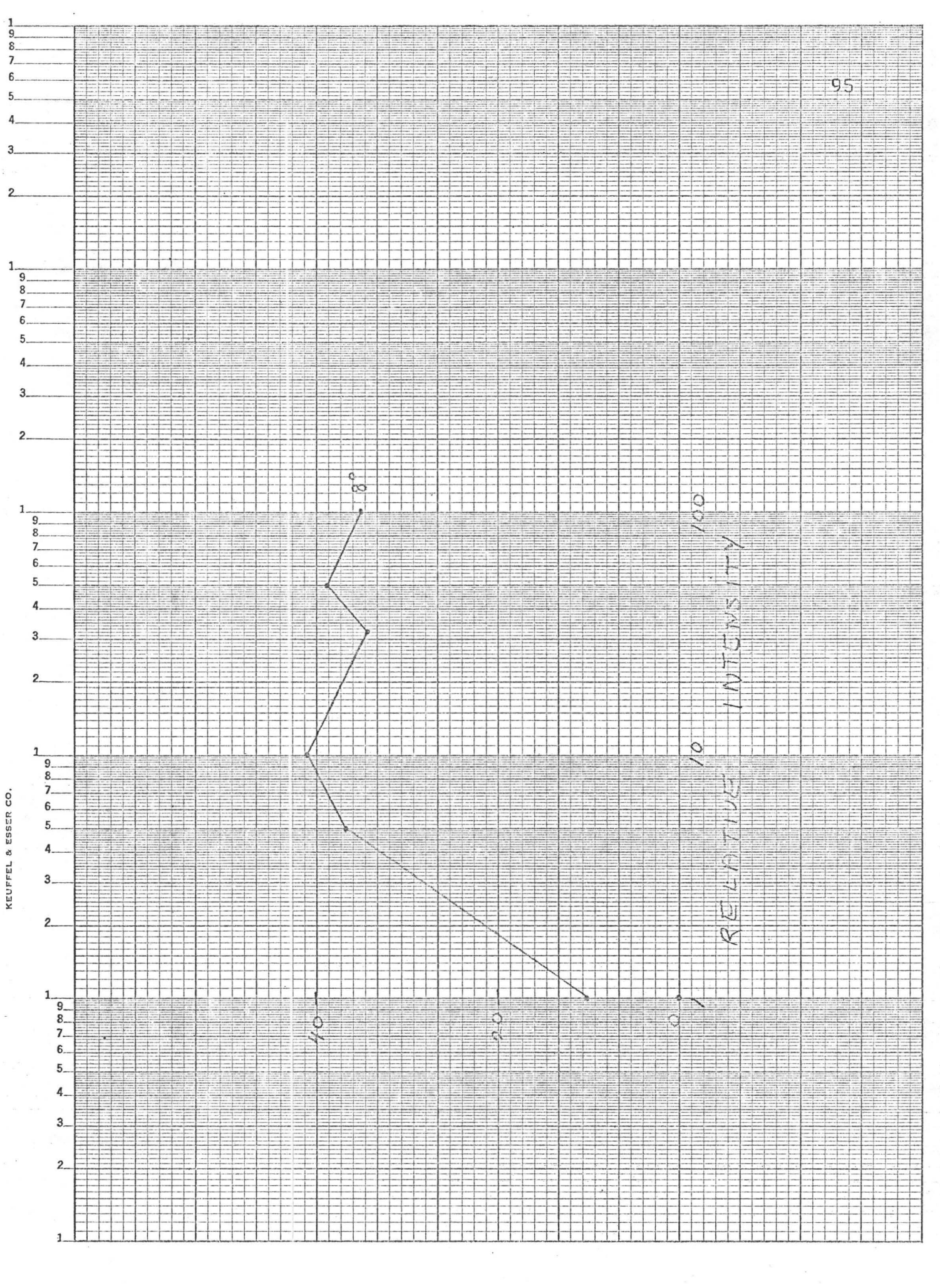

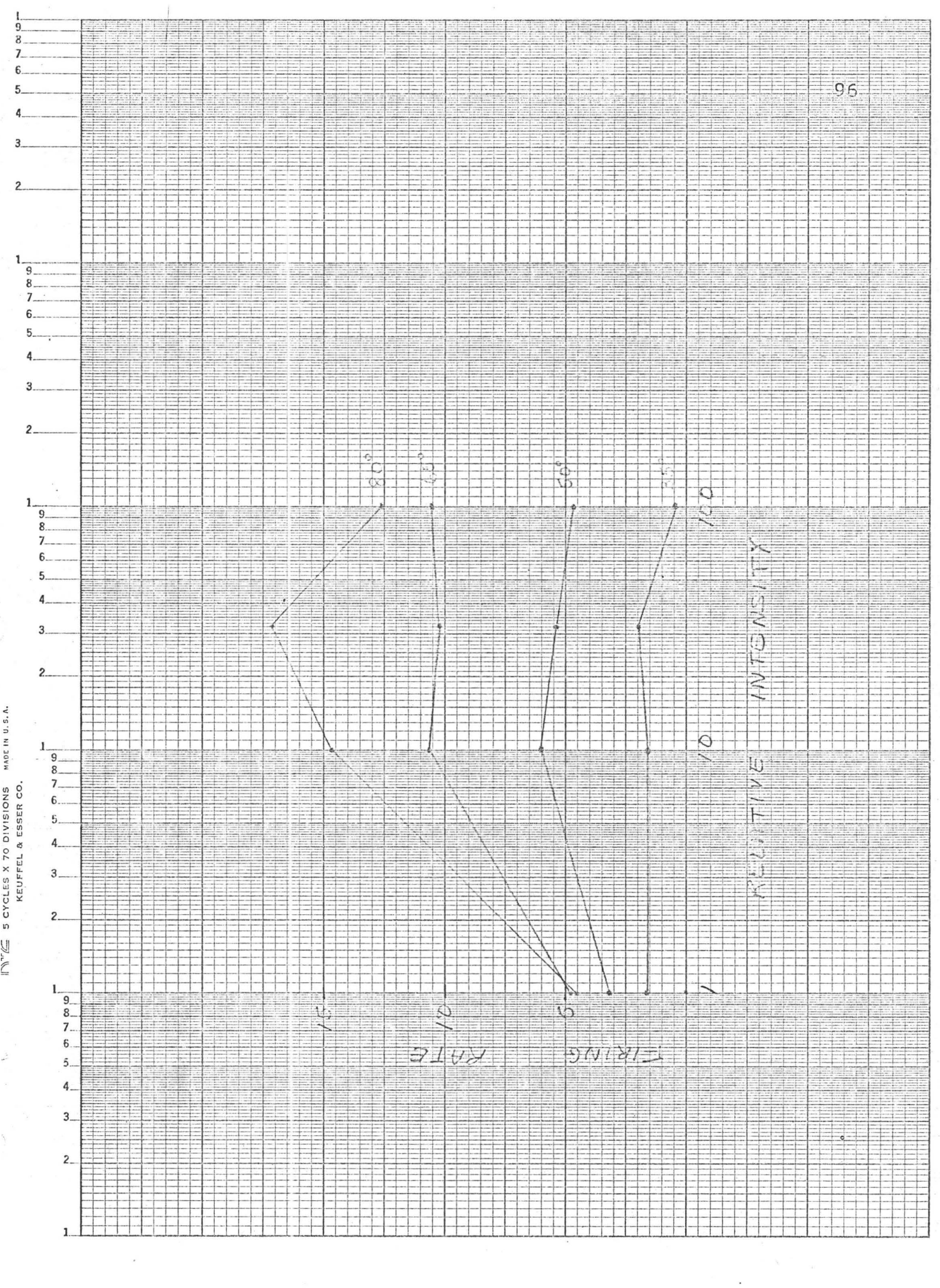

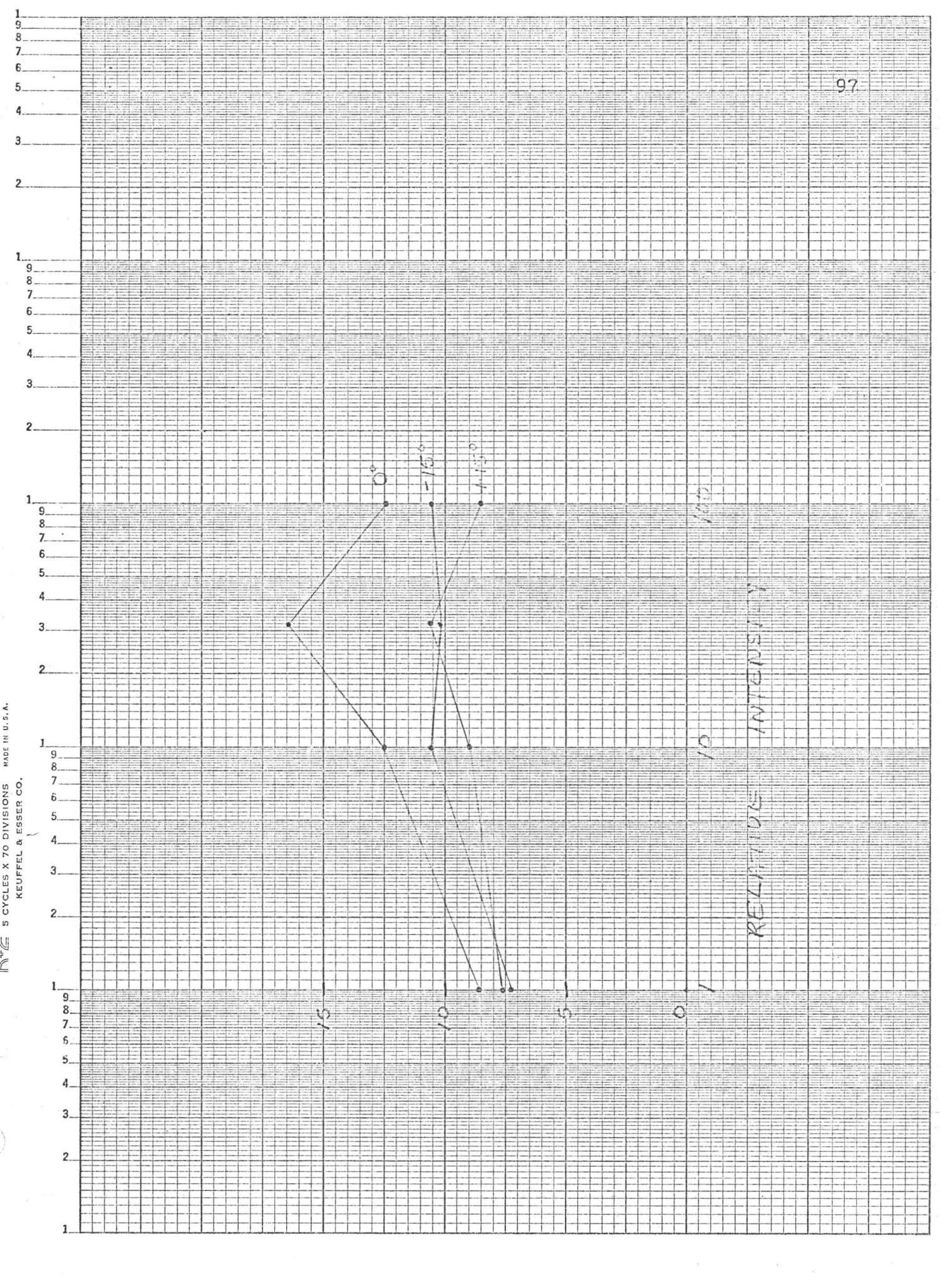

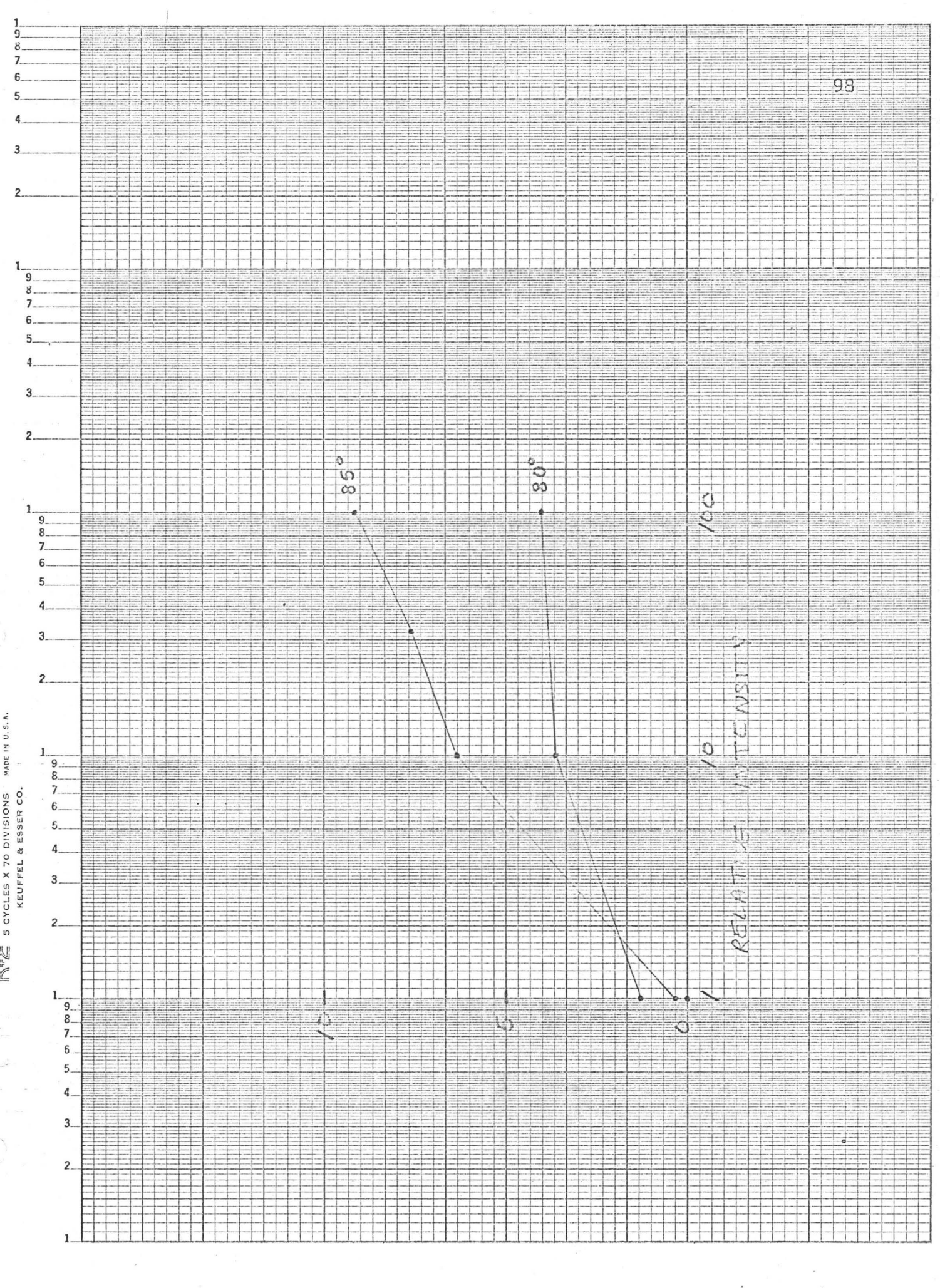

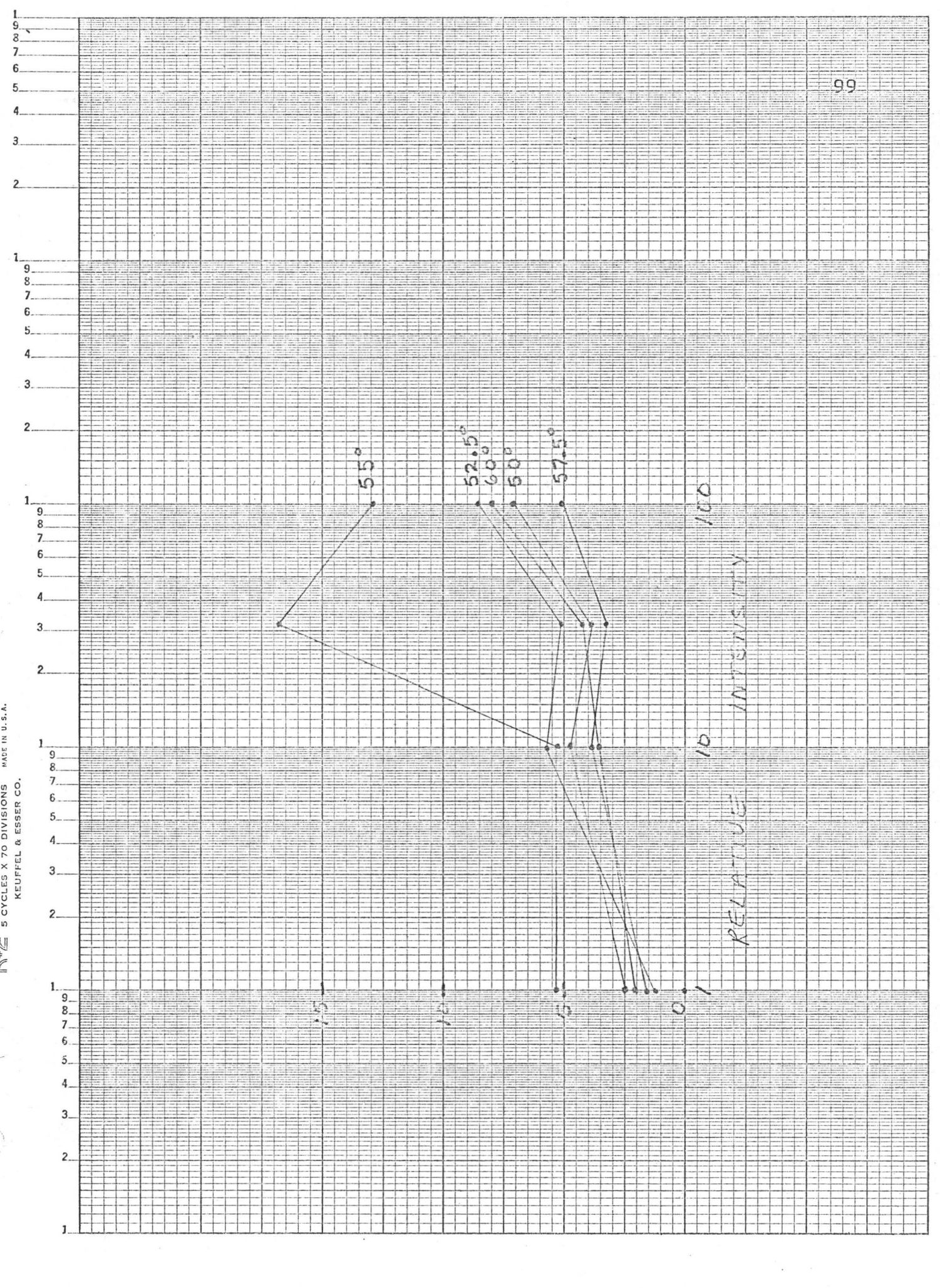

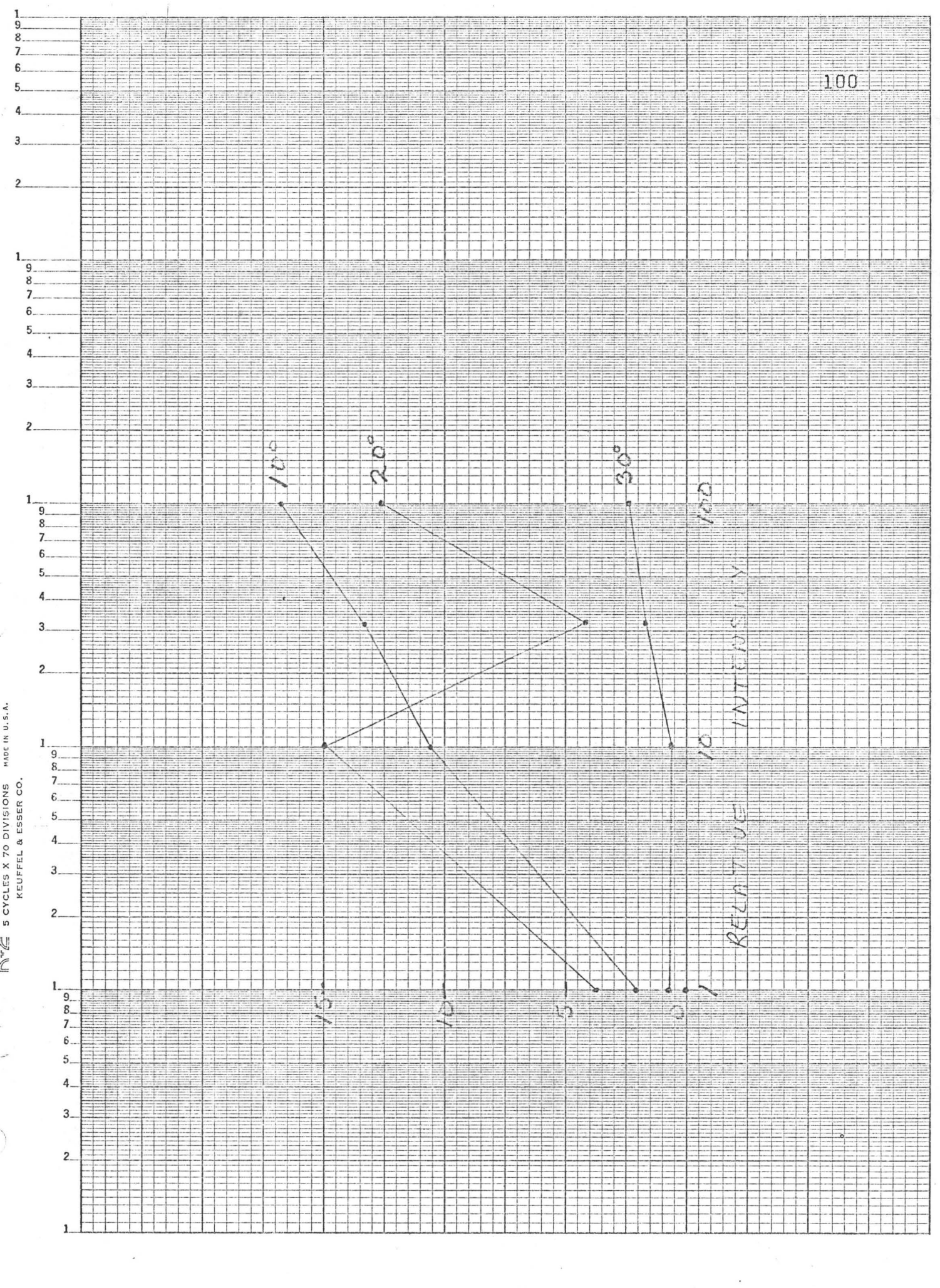

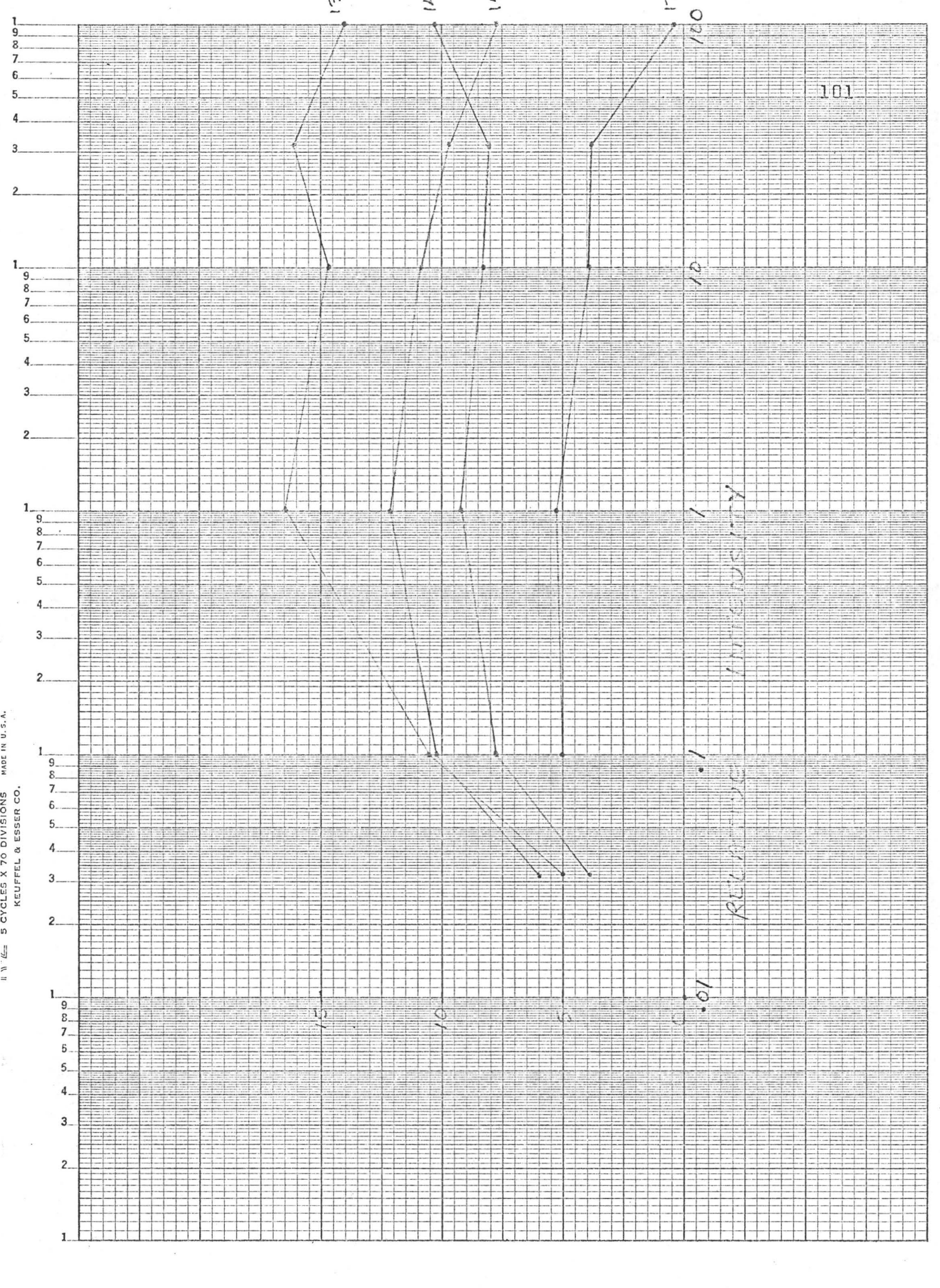

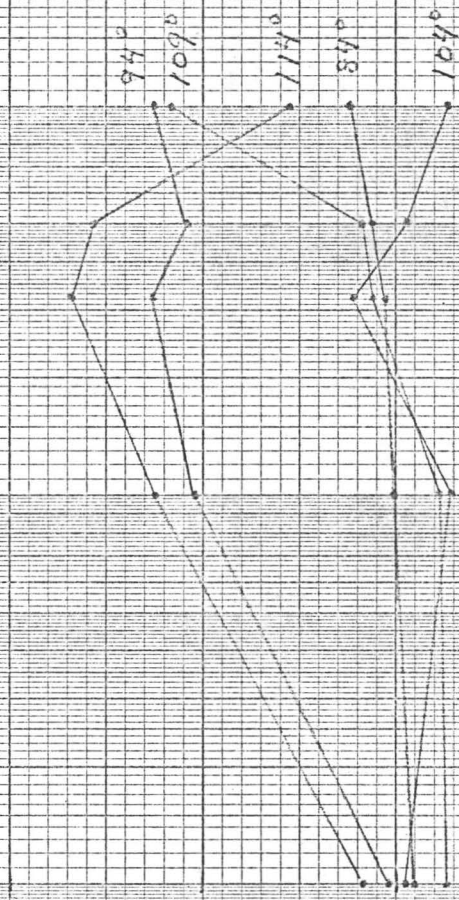

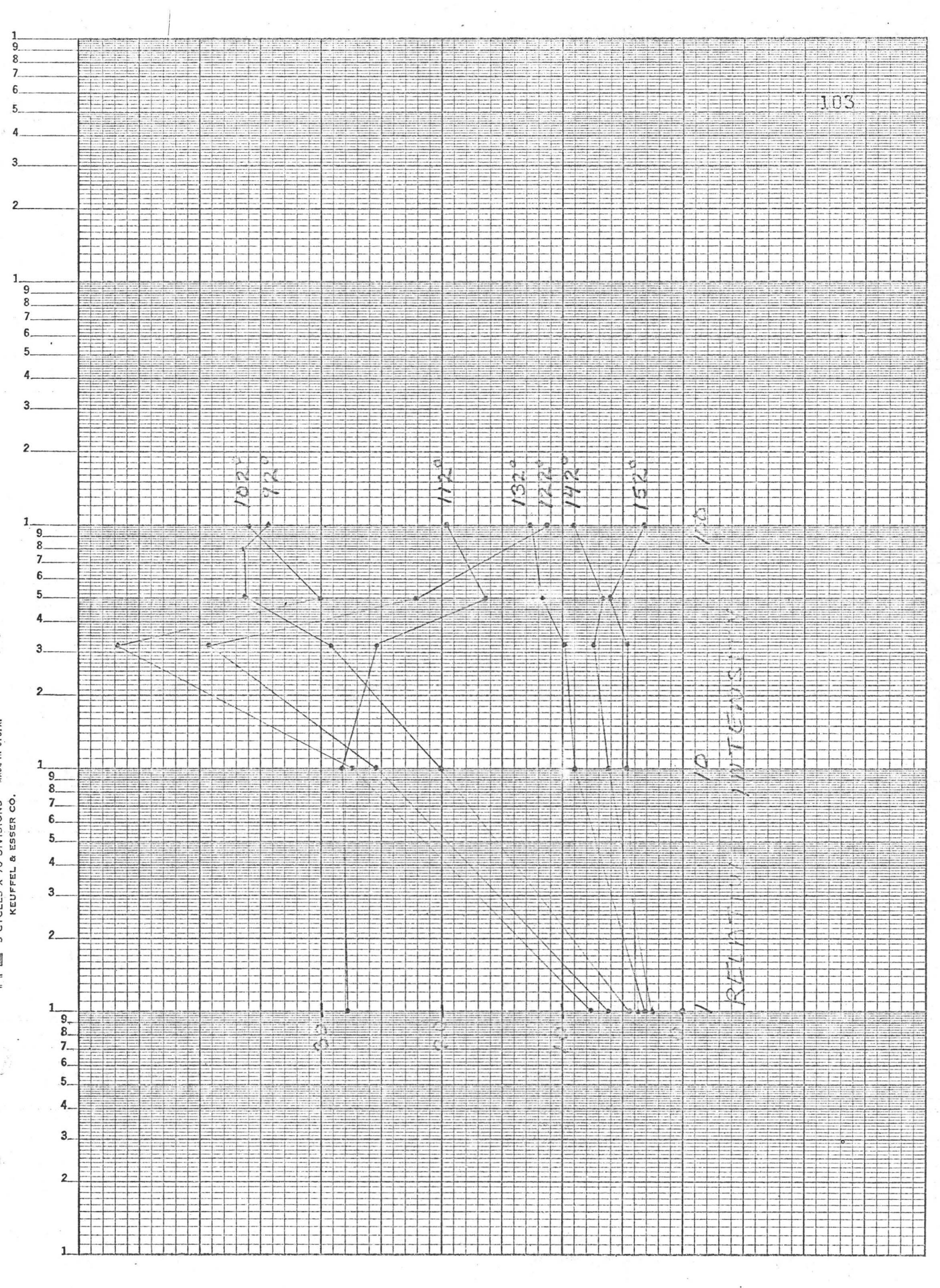

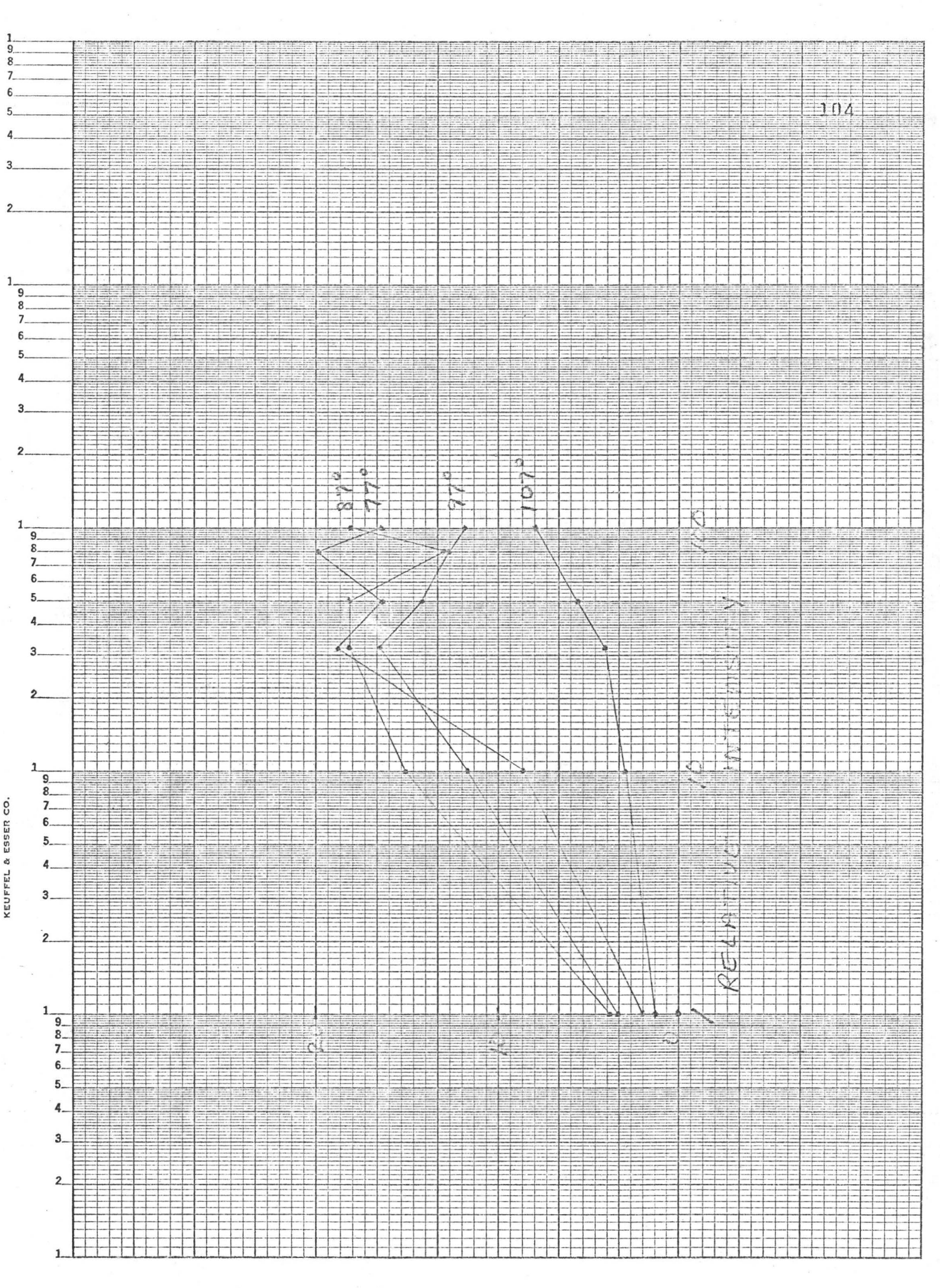

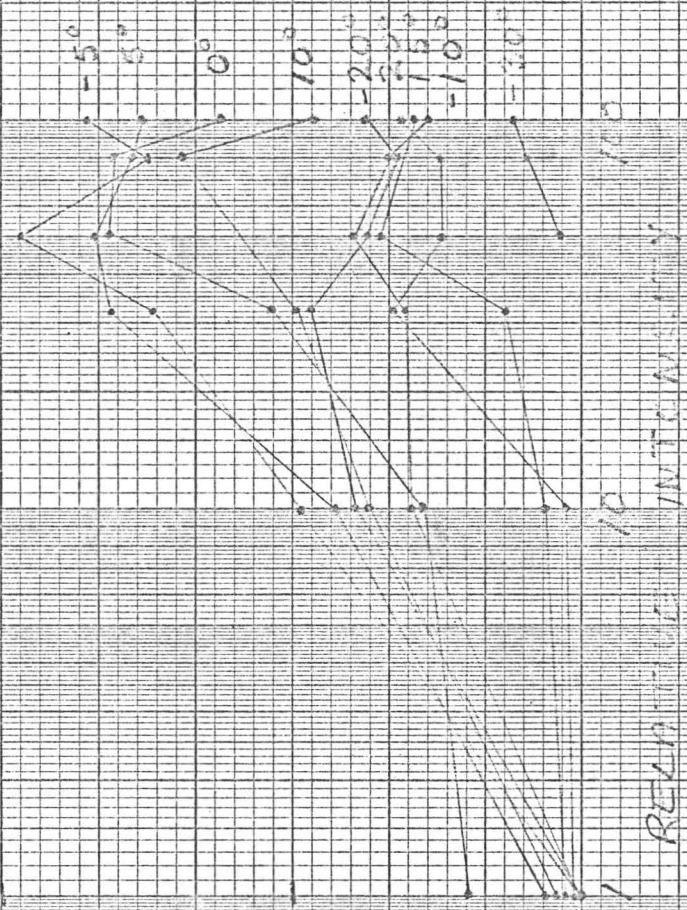

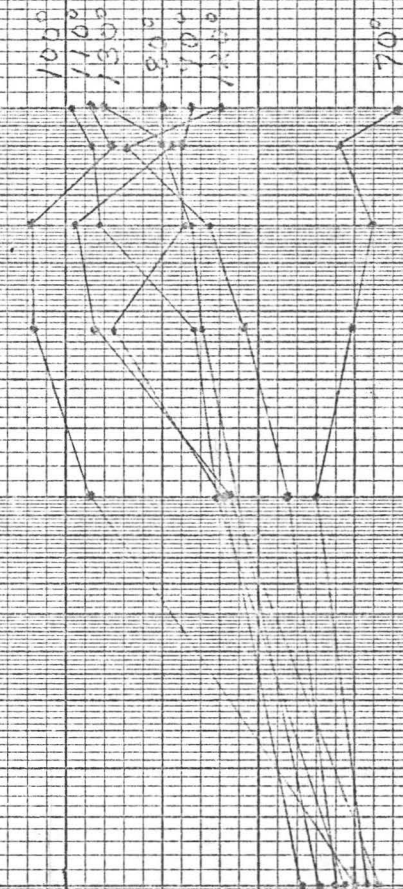

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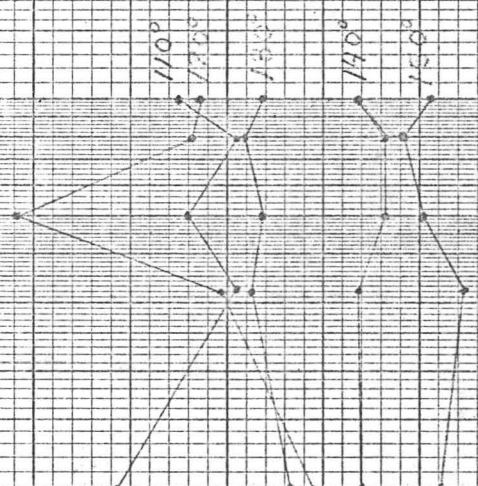

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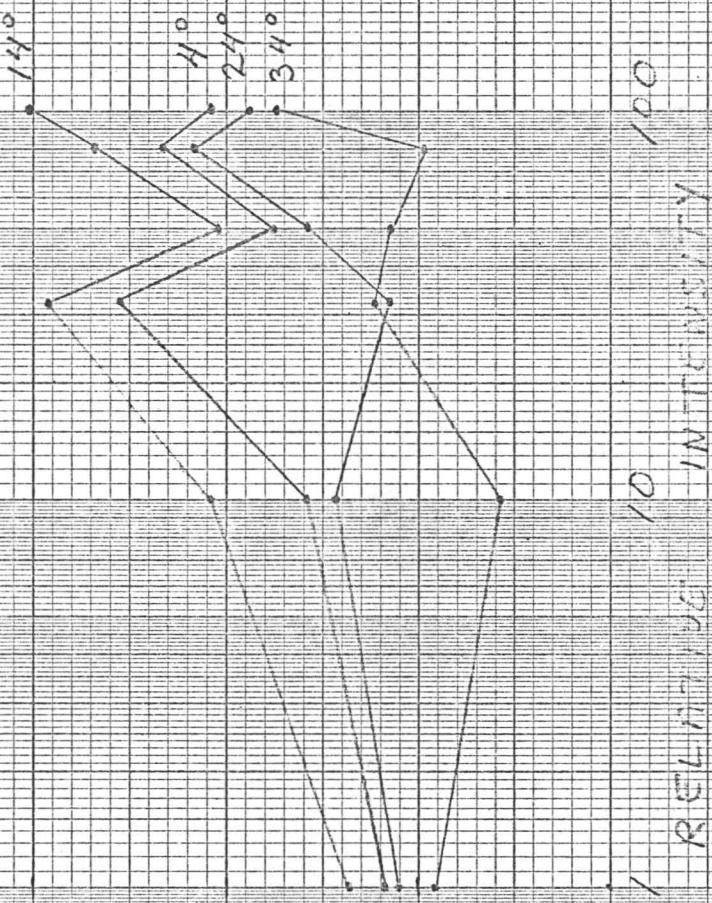
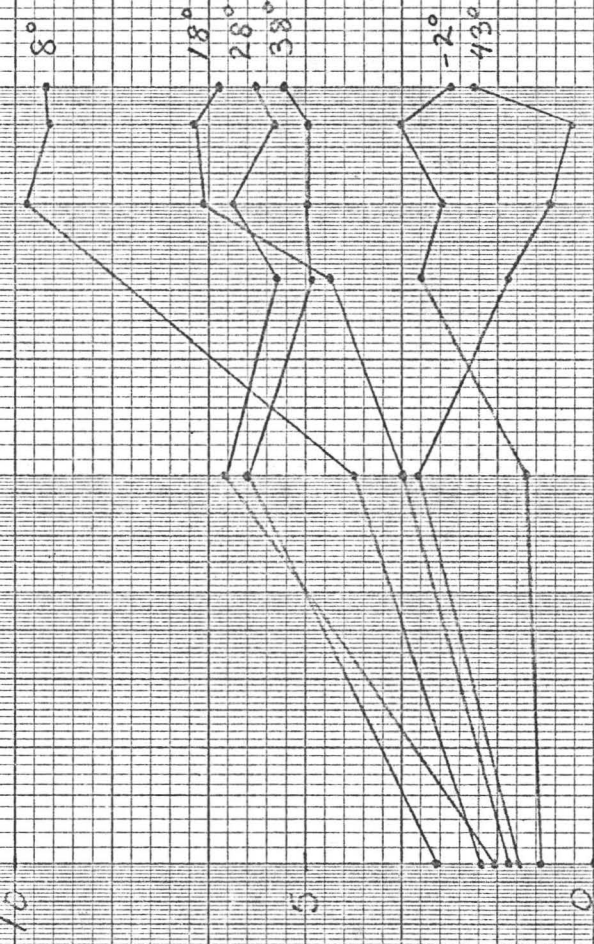
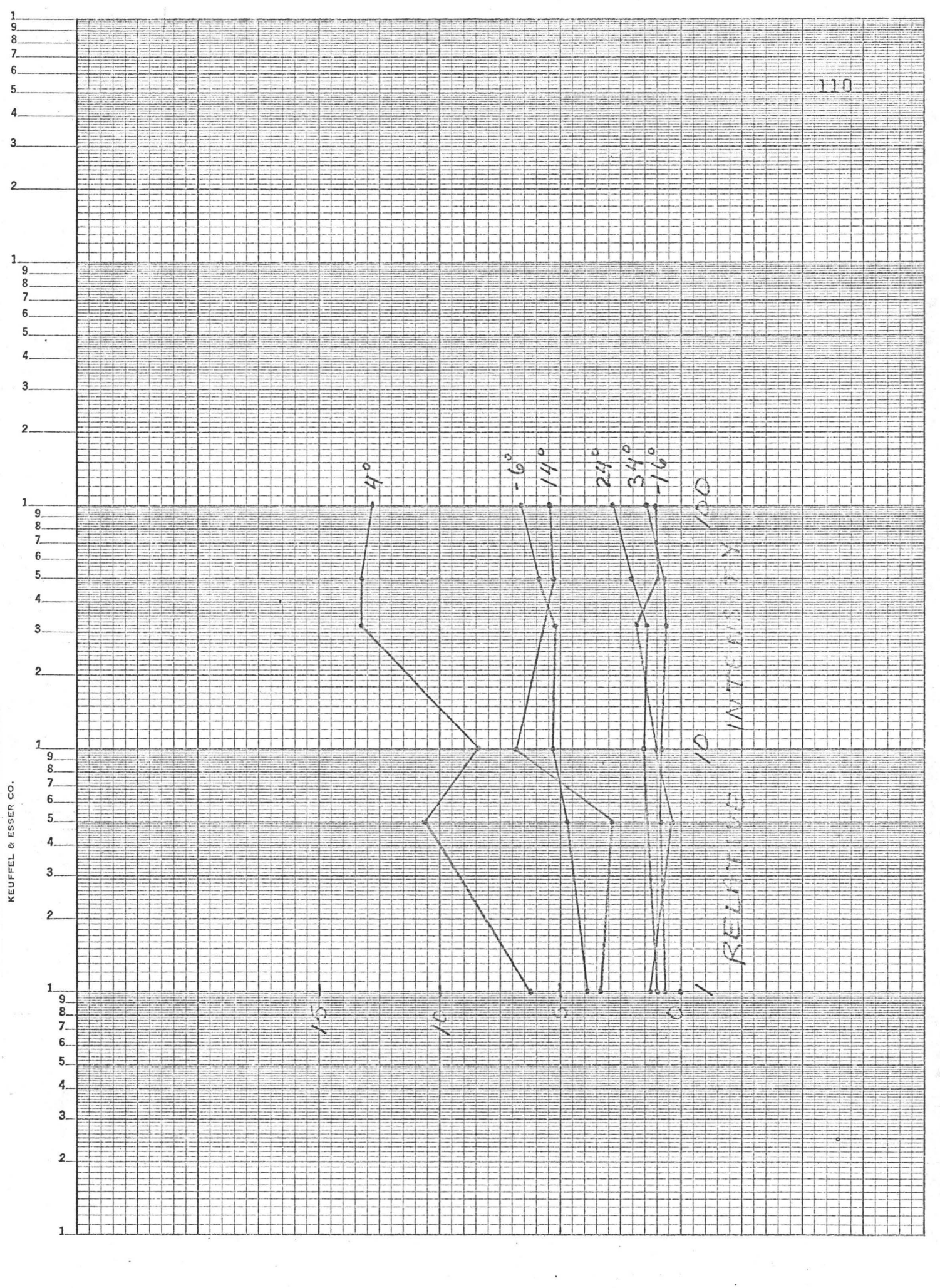
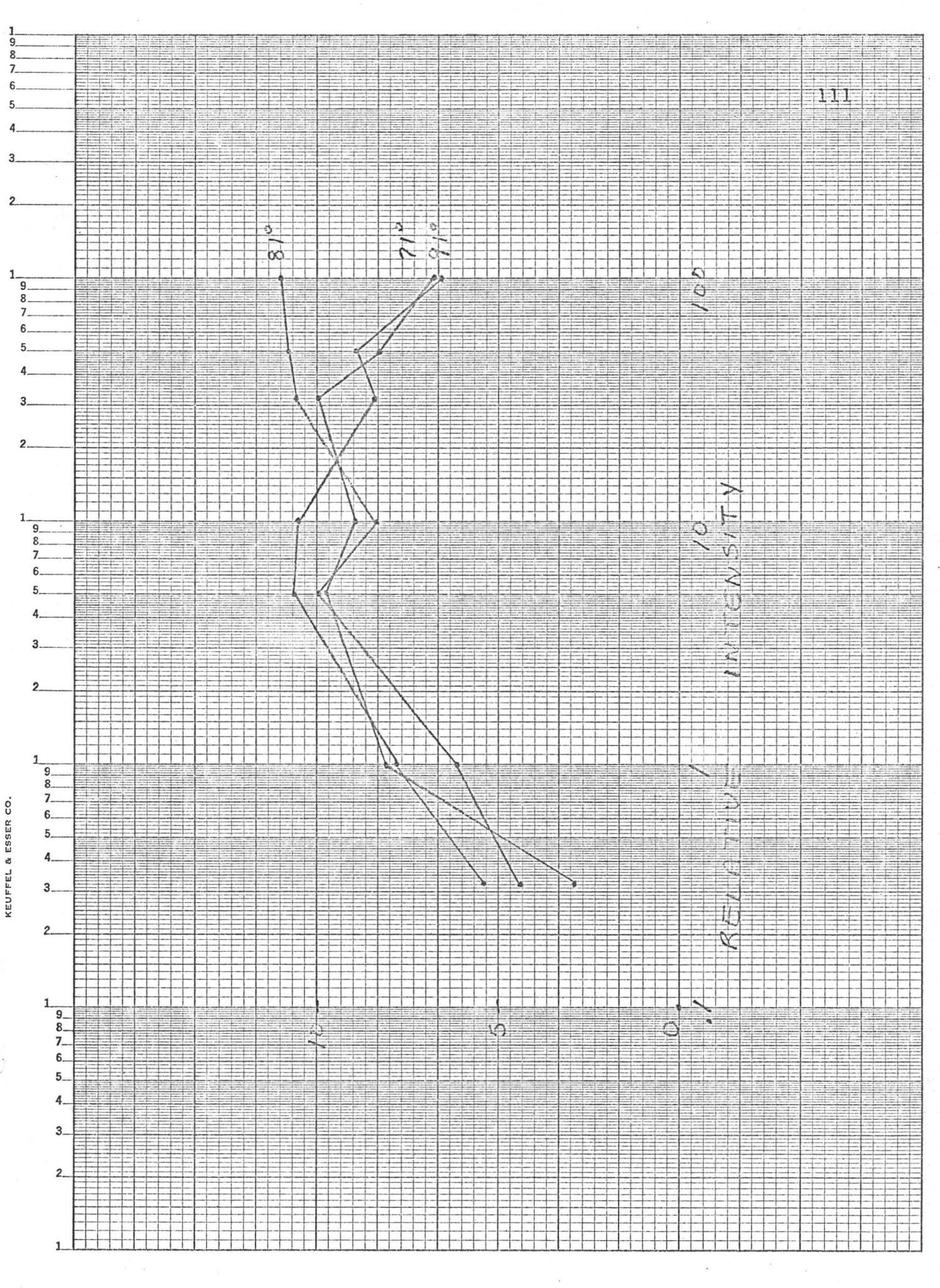
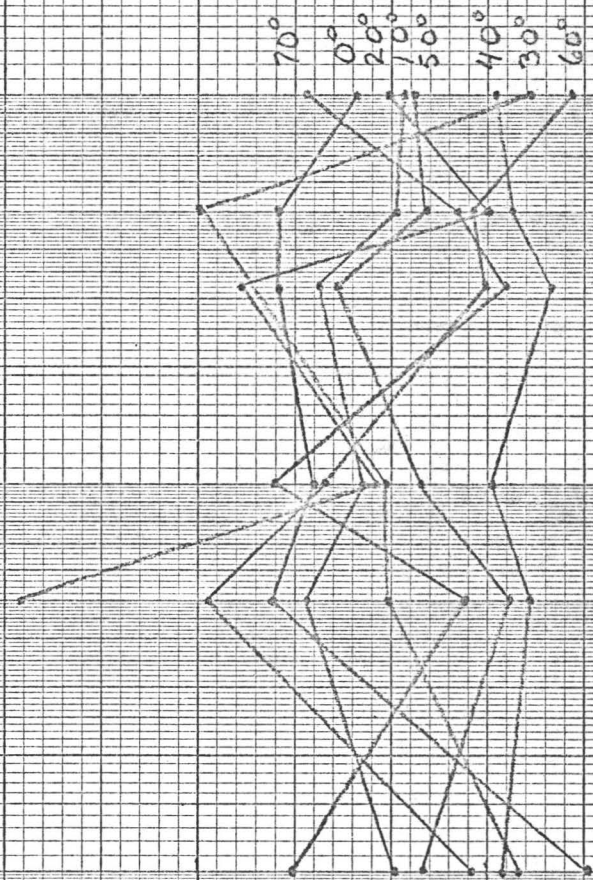




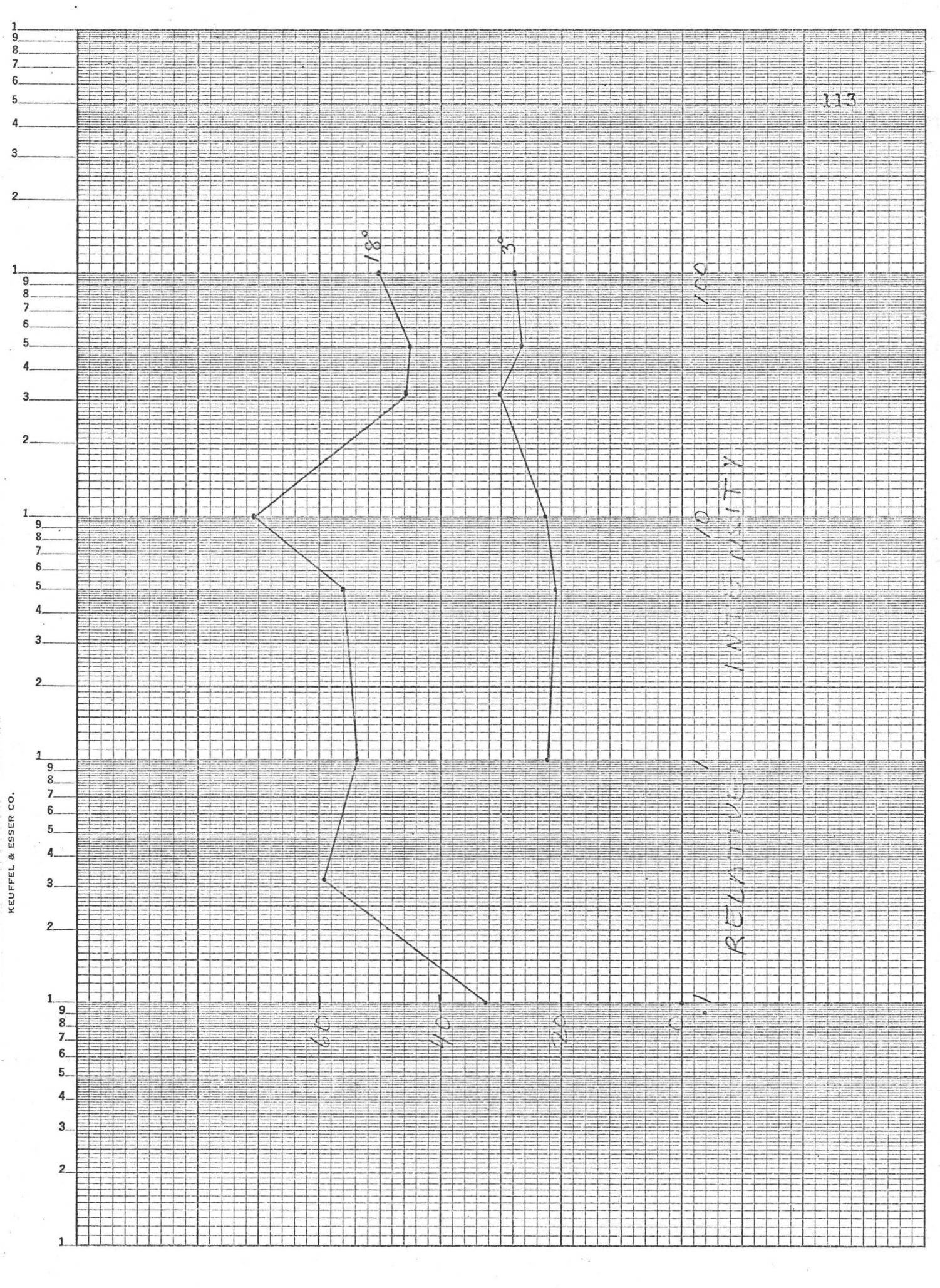


KEUFFEL & ESSER CO.

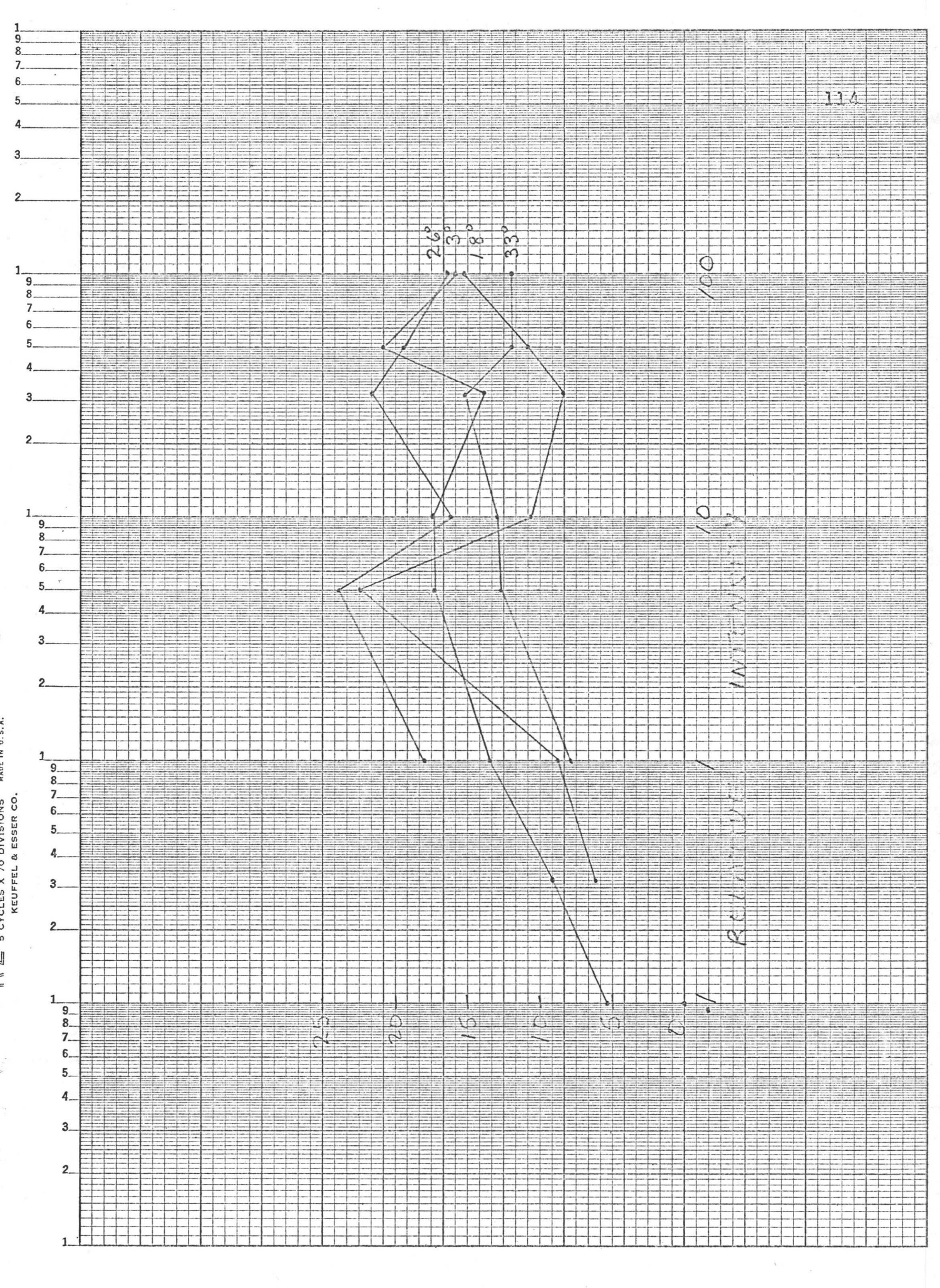

81°
71°
91°
10°
10
RELATIVE INTENSITY
0.1
5
KEUFFEL & ESSER CO.

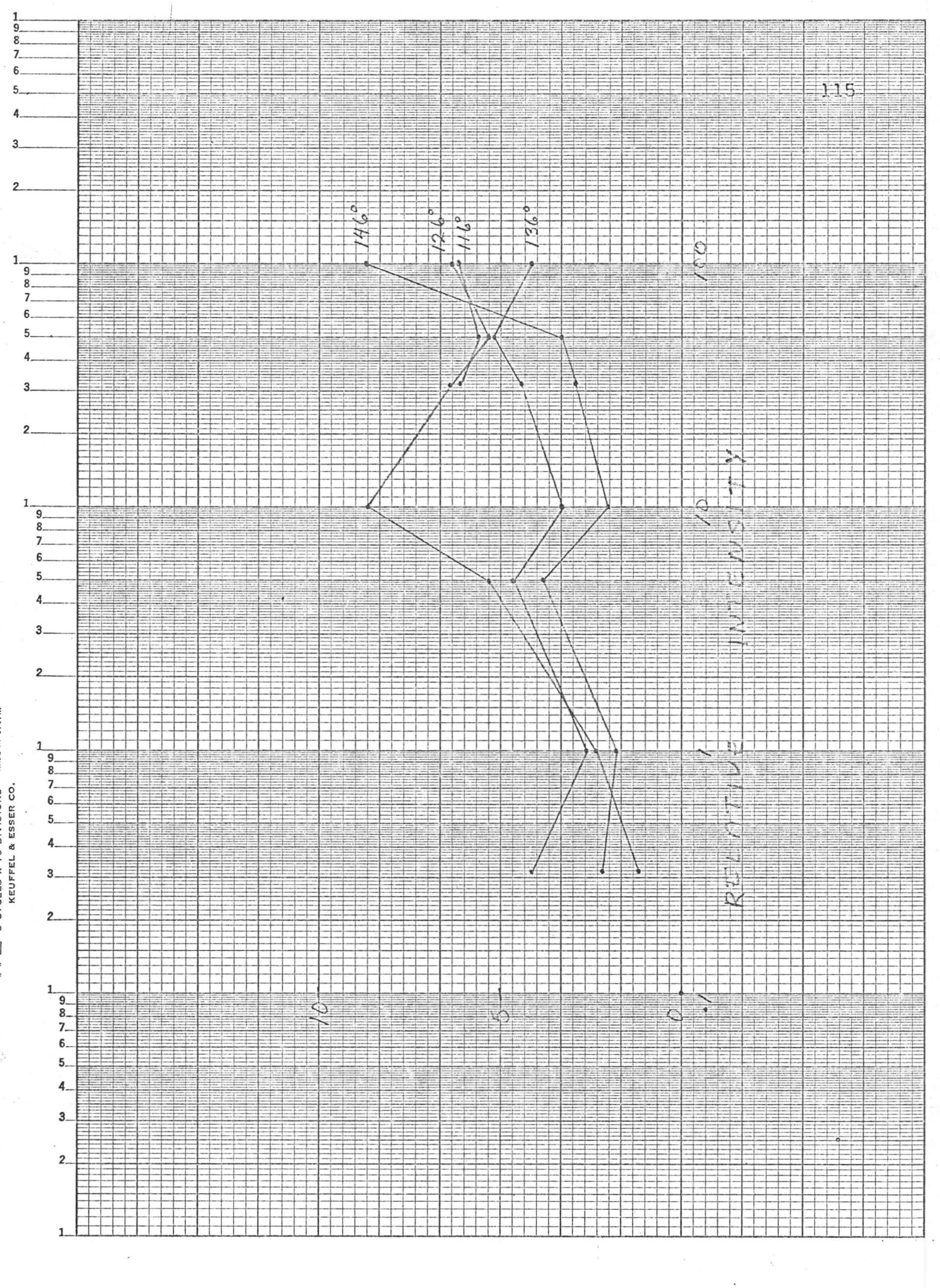


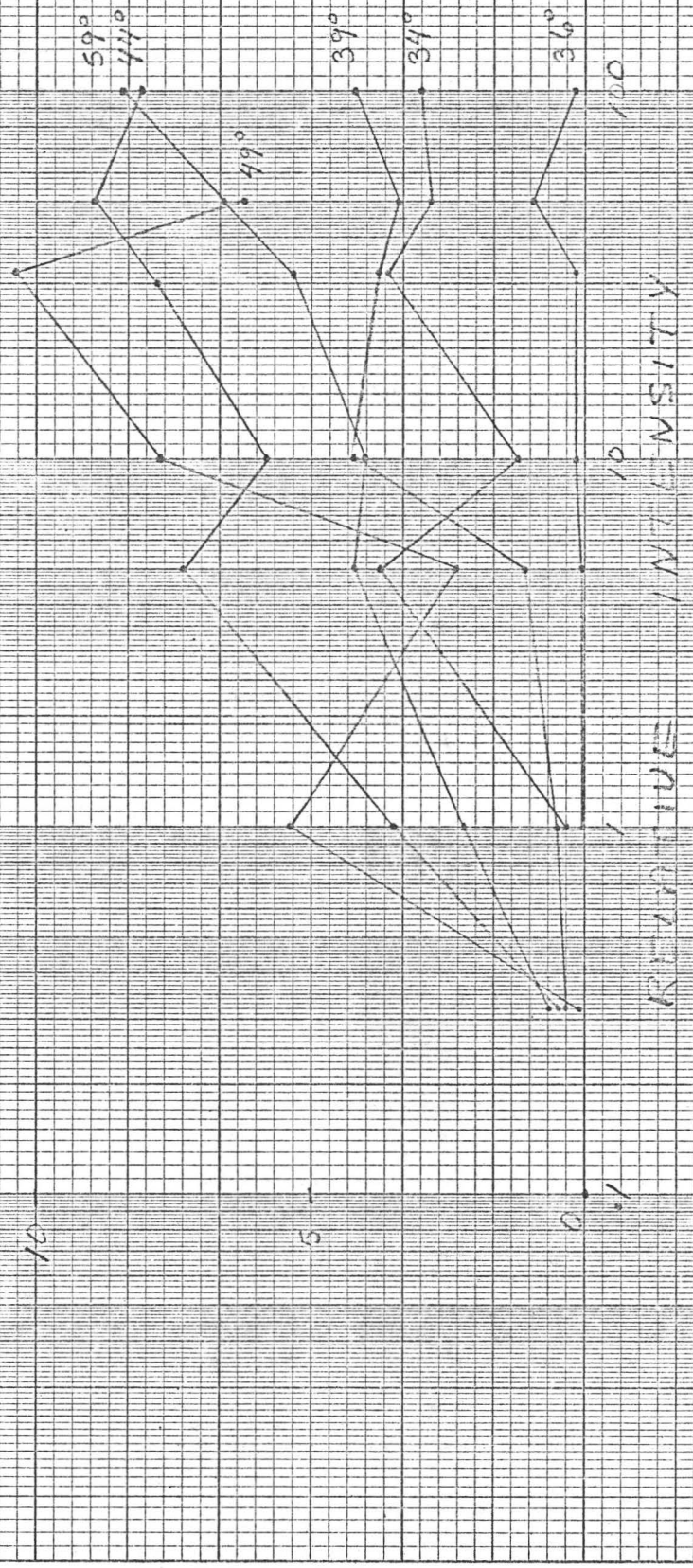
KEUFFEL & ESSER CO.



KEUFFEL & ESSER CO.







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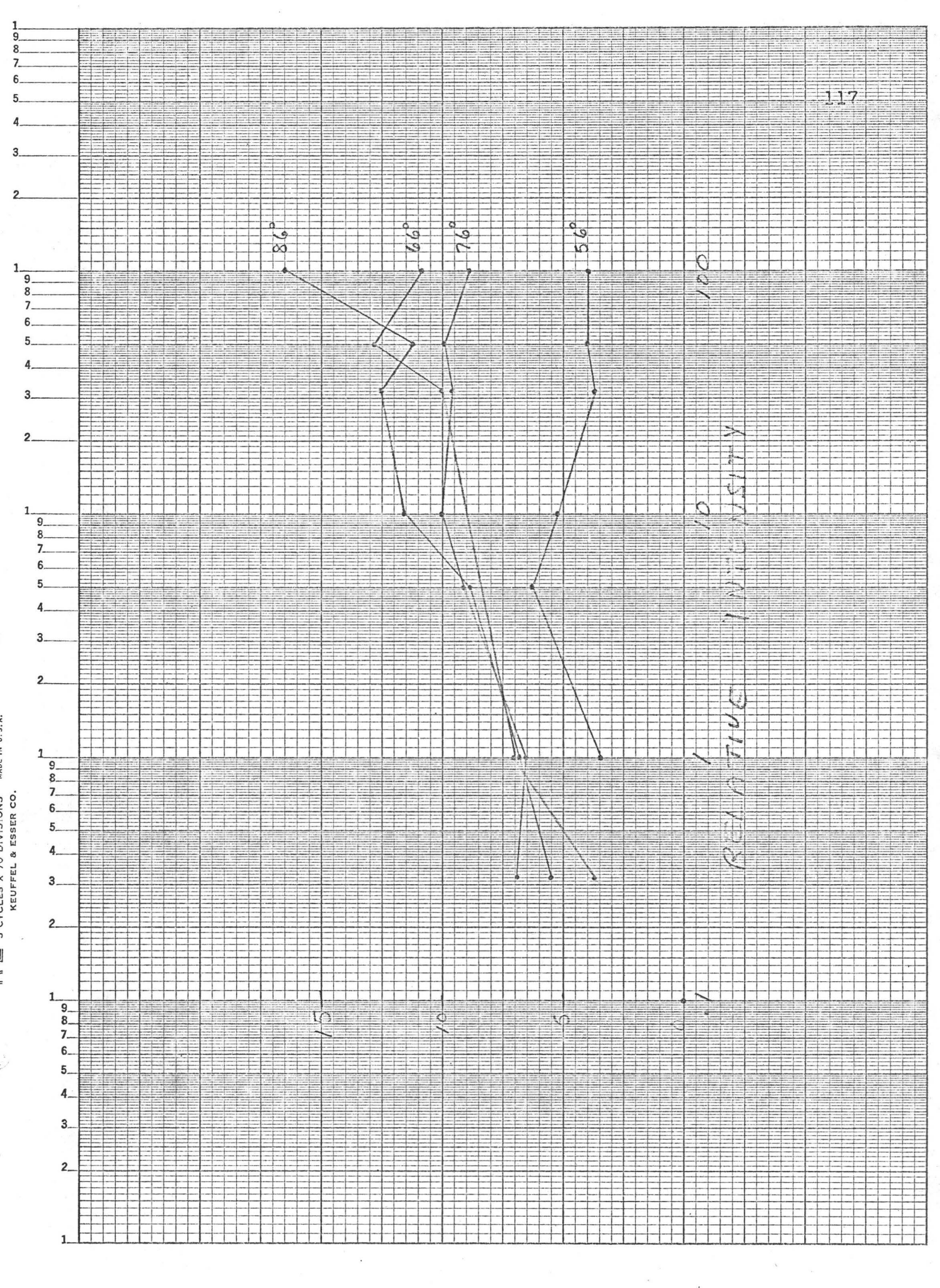
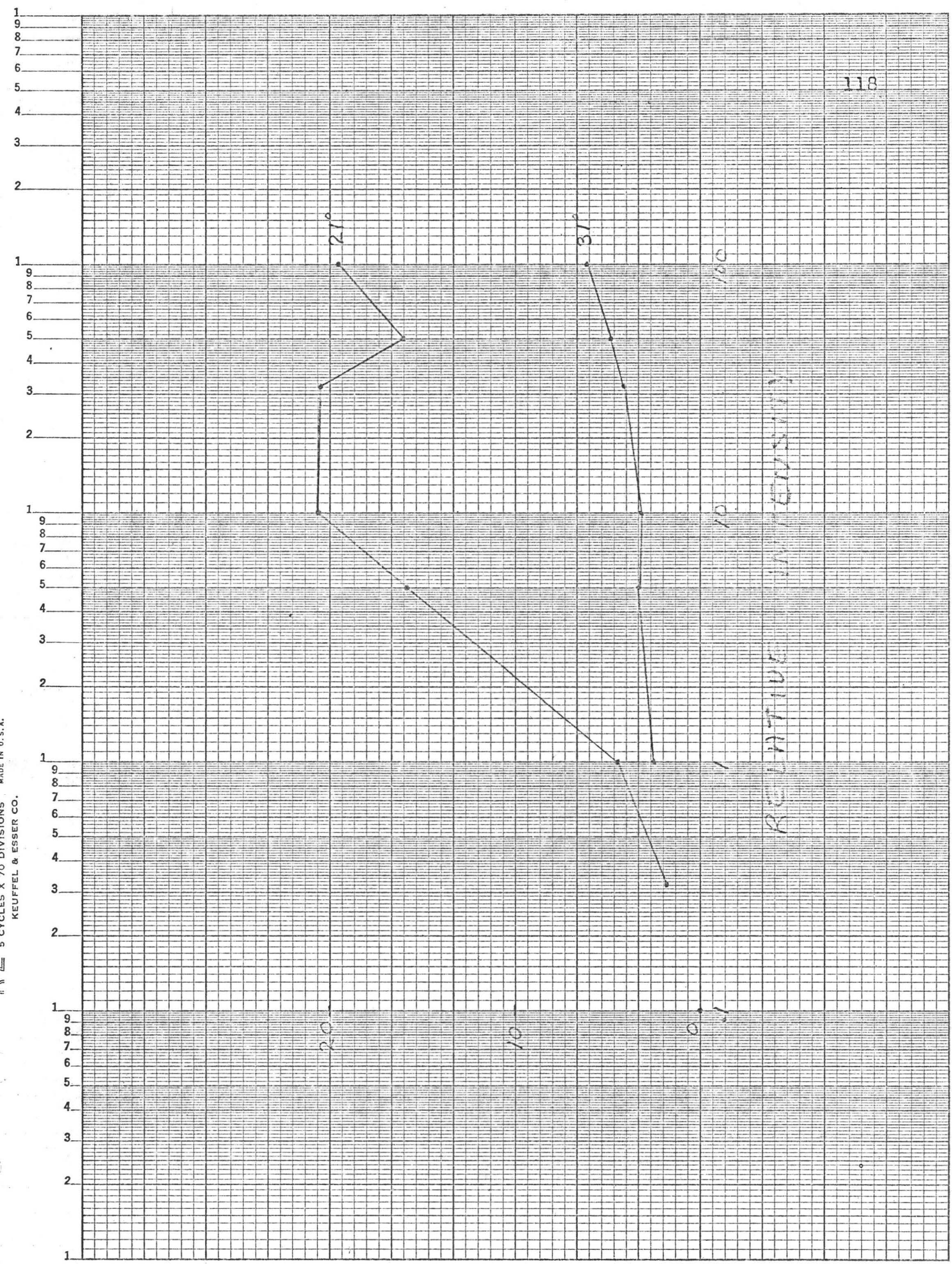
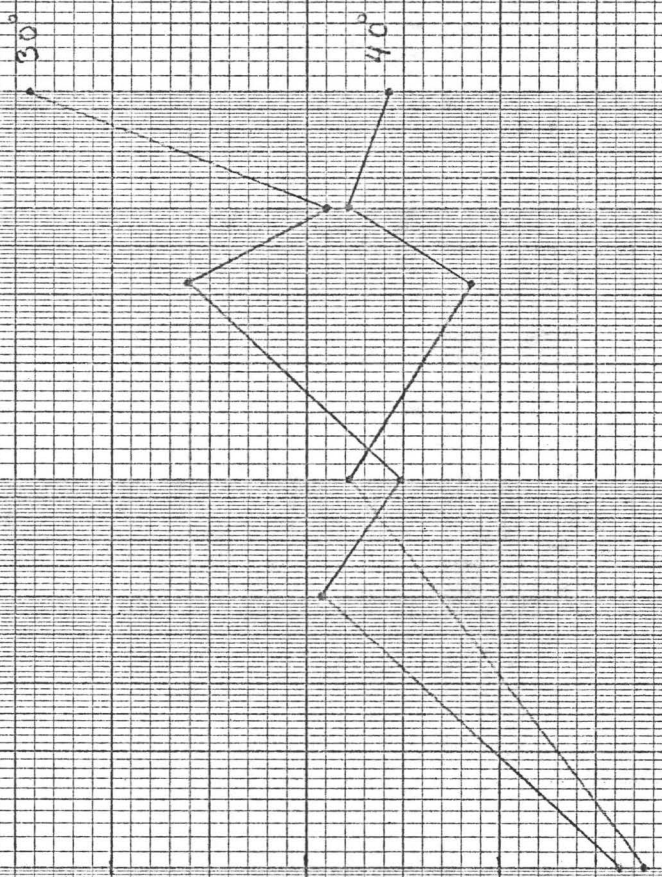
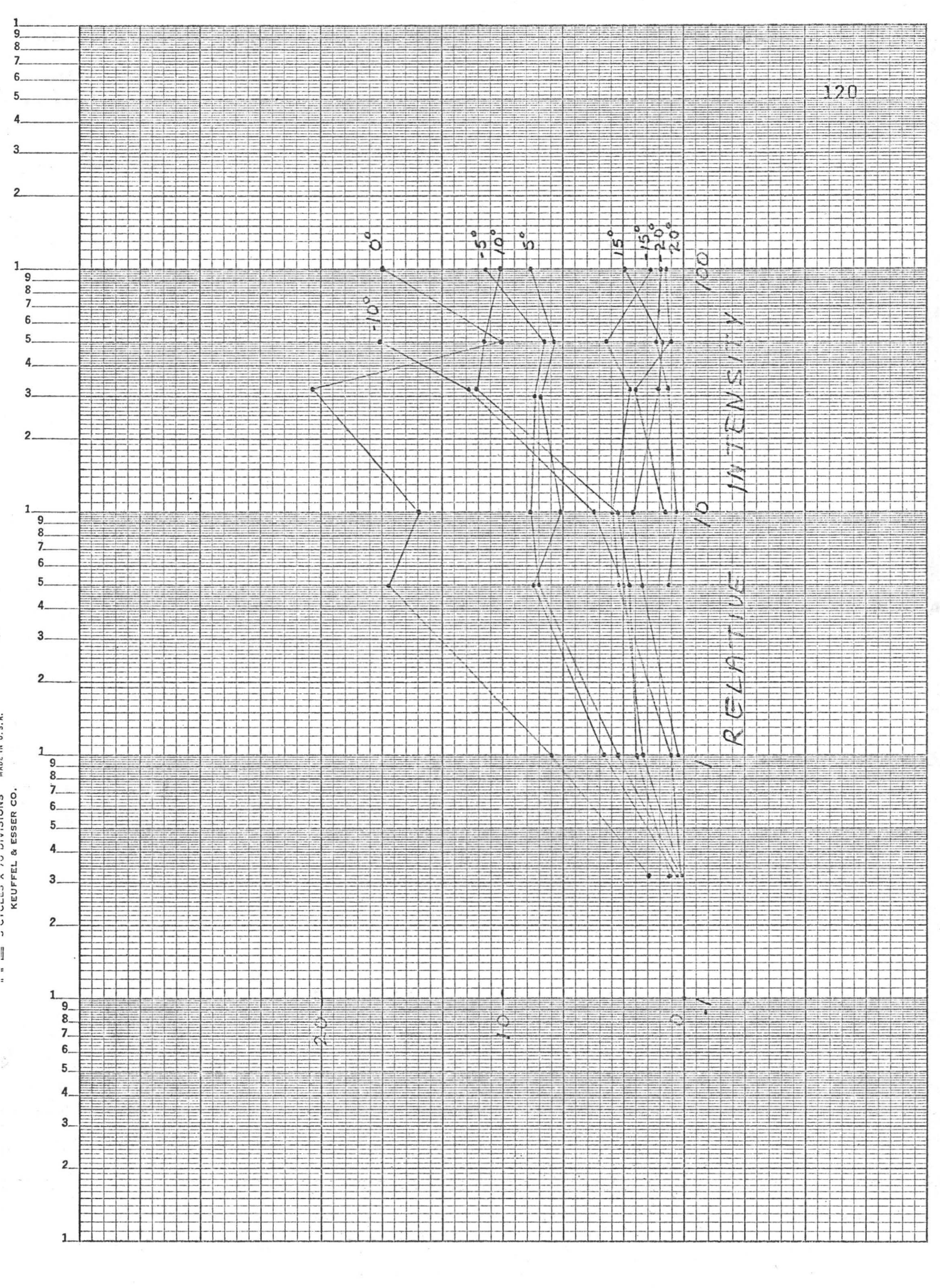
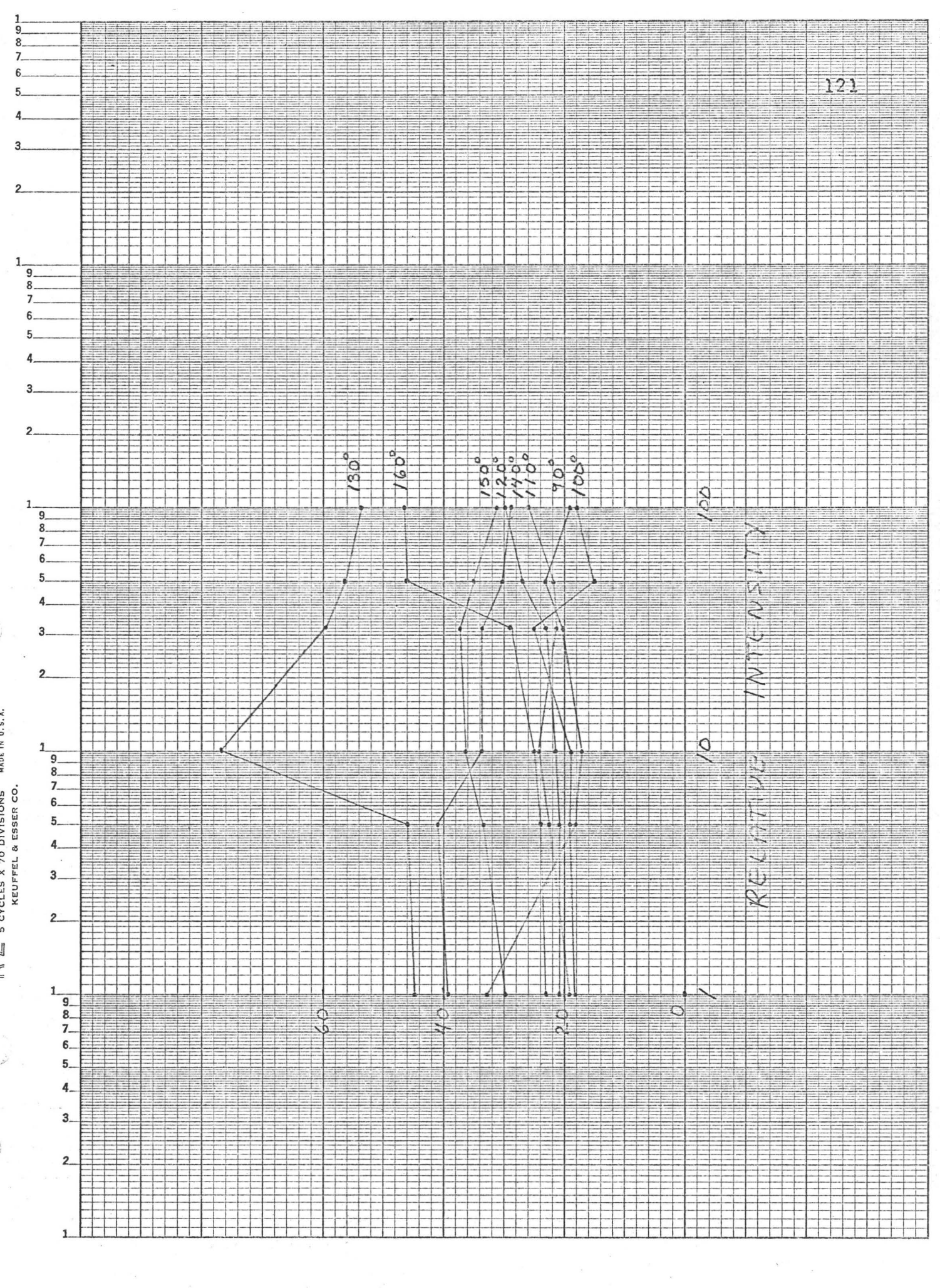
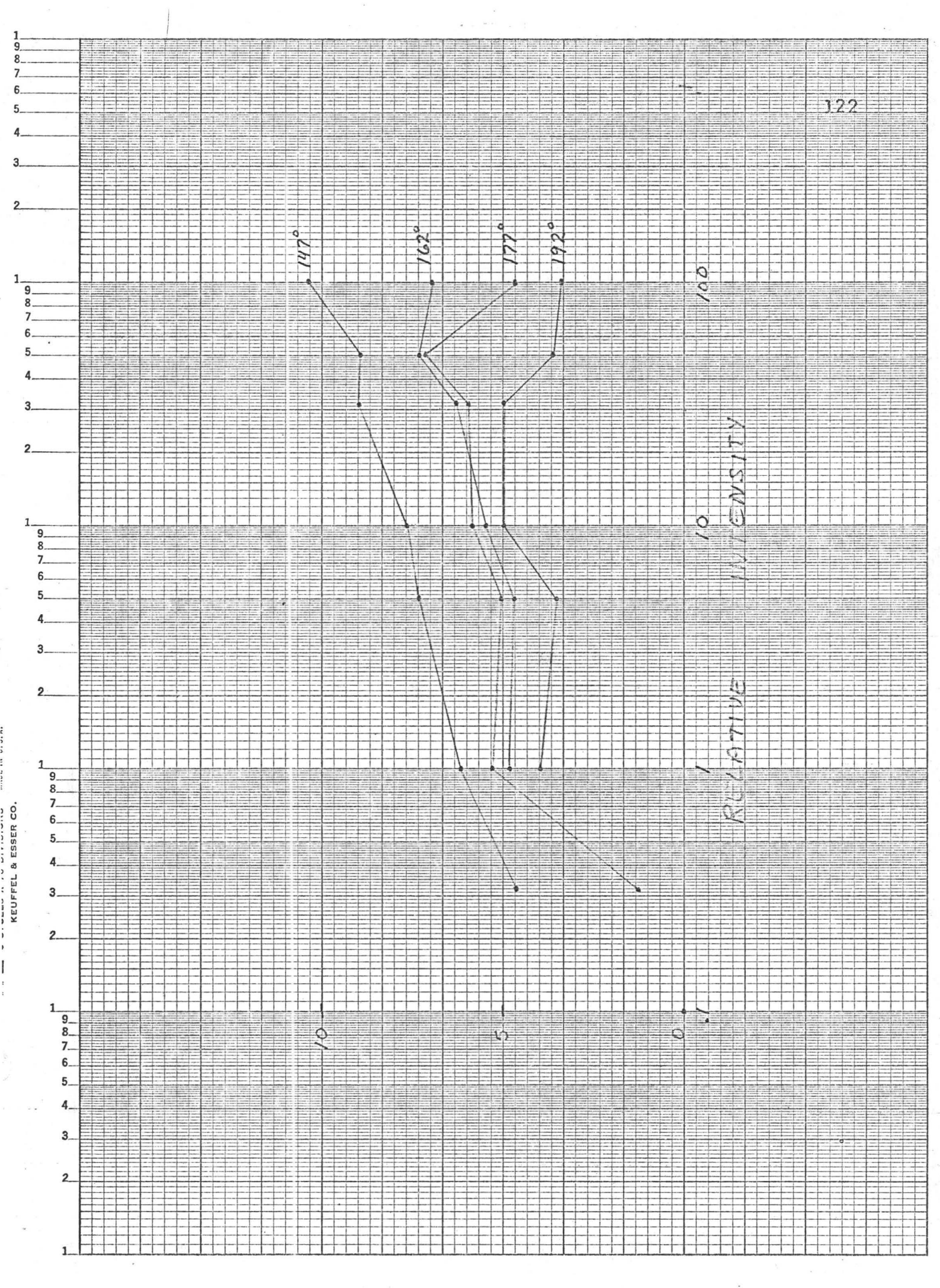


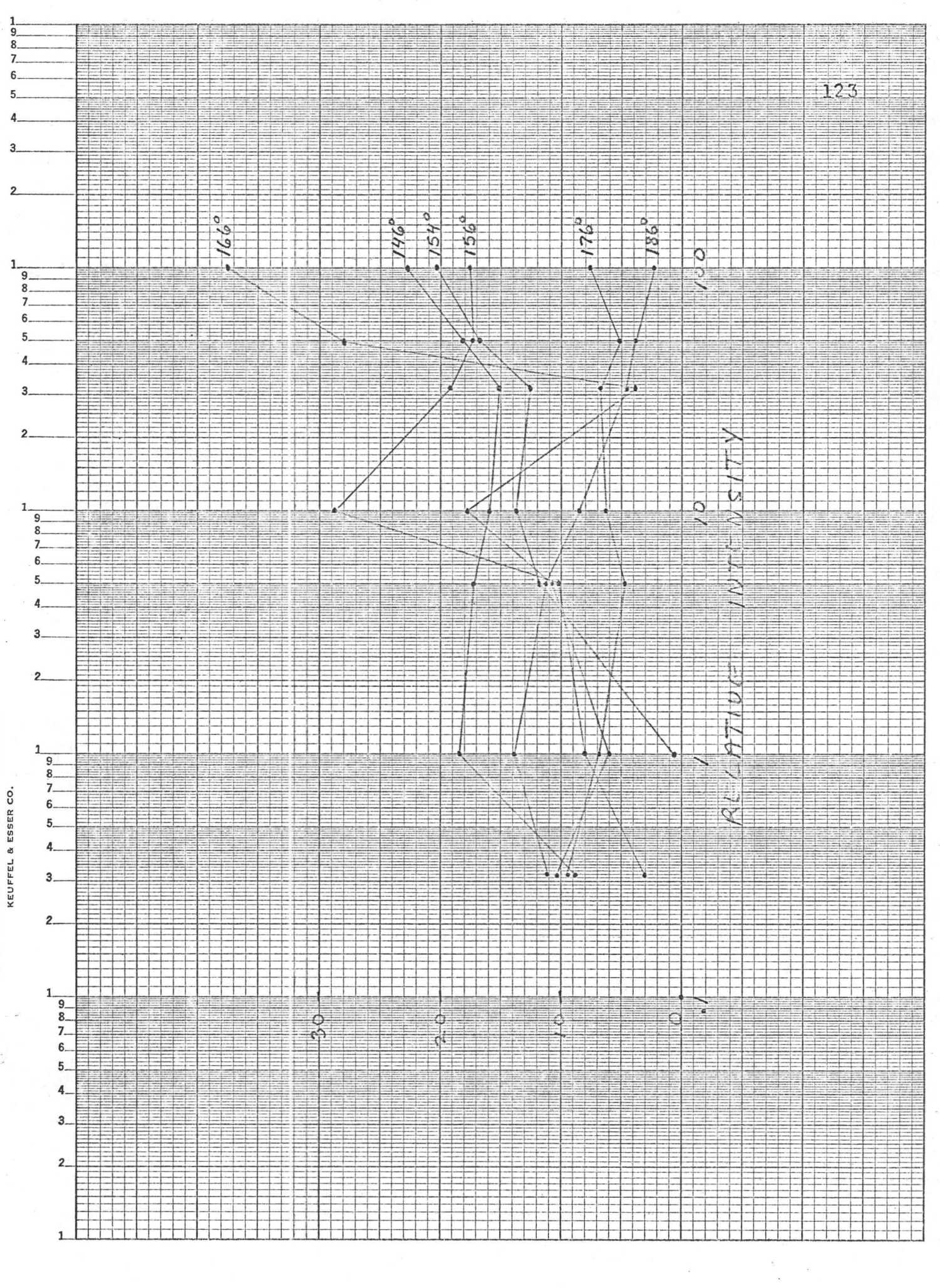


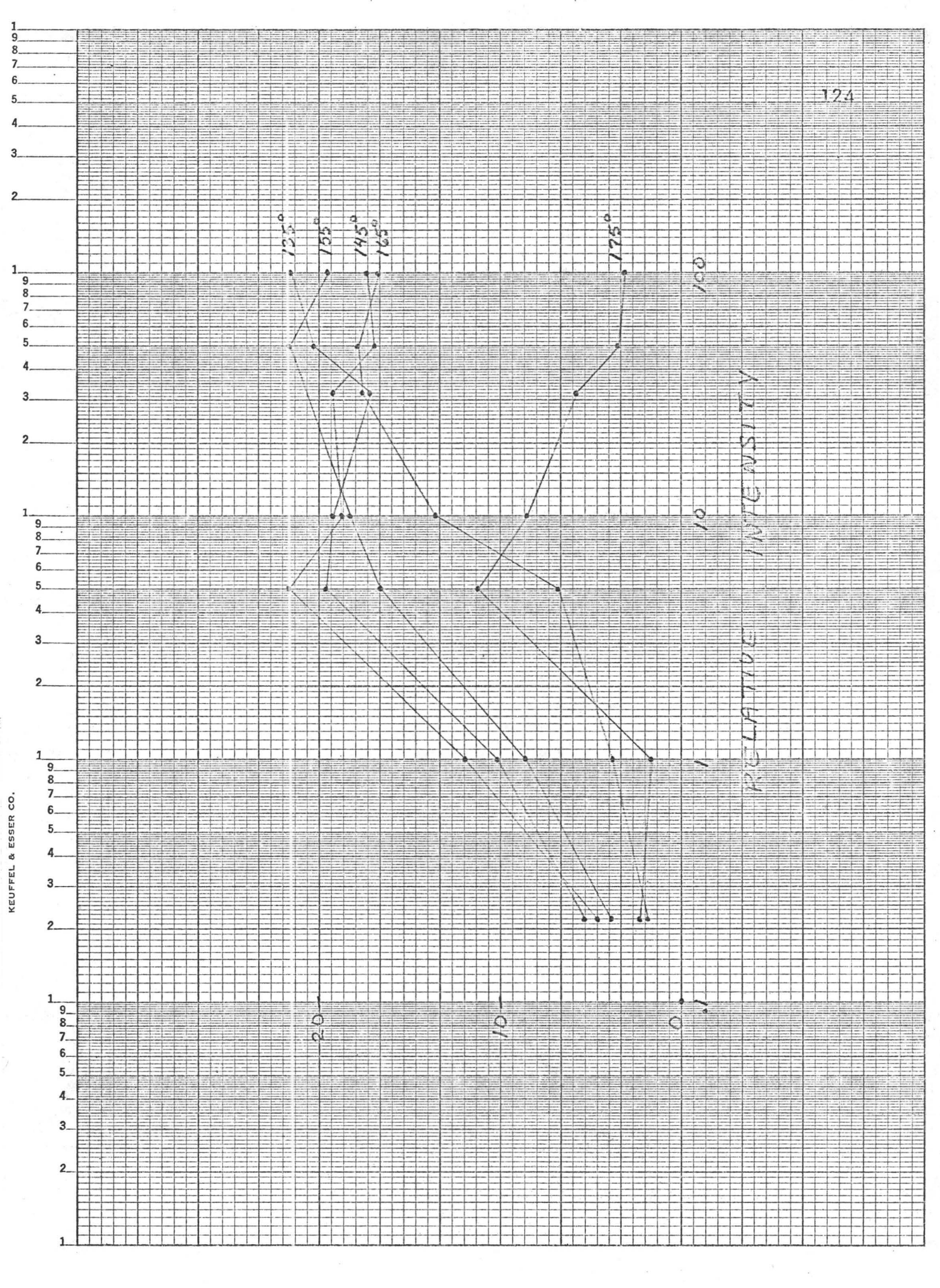



120
0°
-5°
10°
5°
15°
-15°
-20°
20°
-10°
120
10
1
RELATIVE INTENSITY
KEUFFEL & ESSER CO.

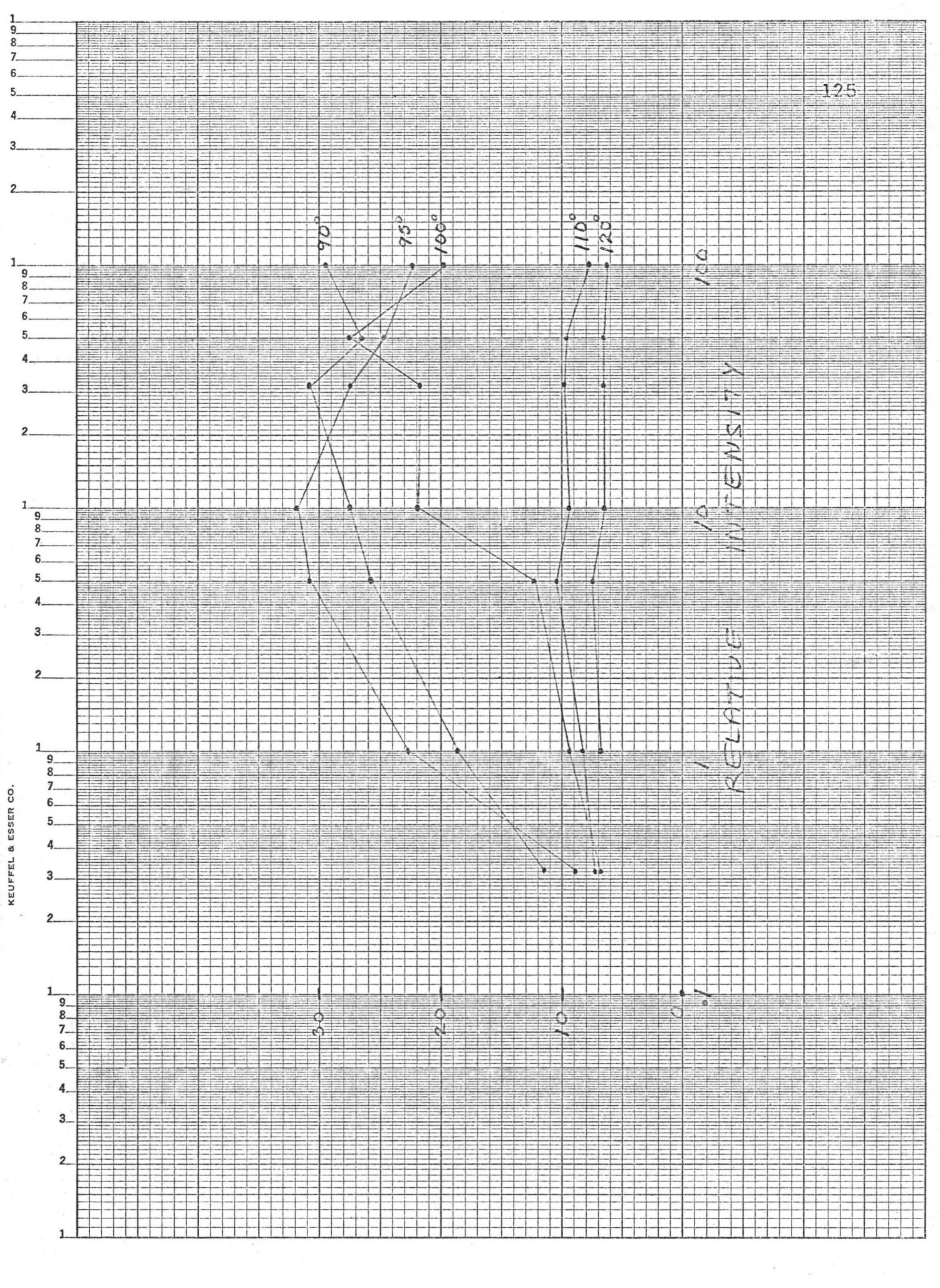


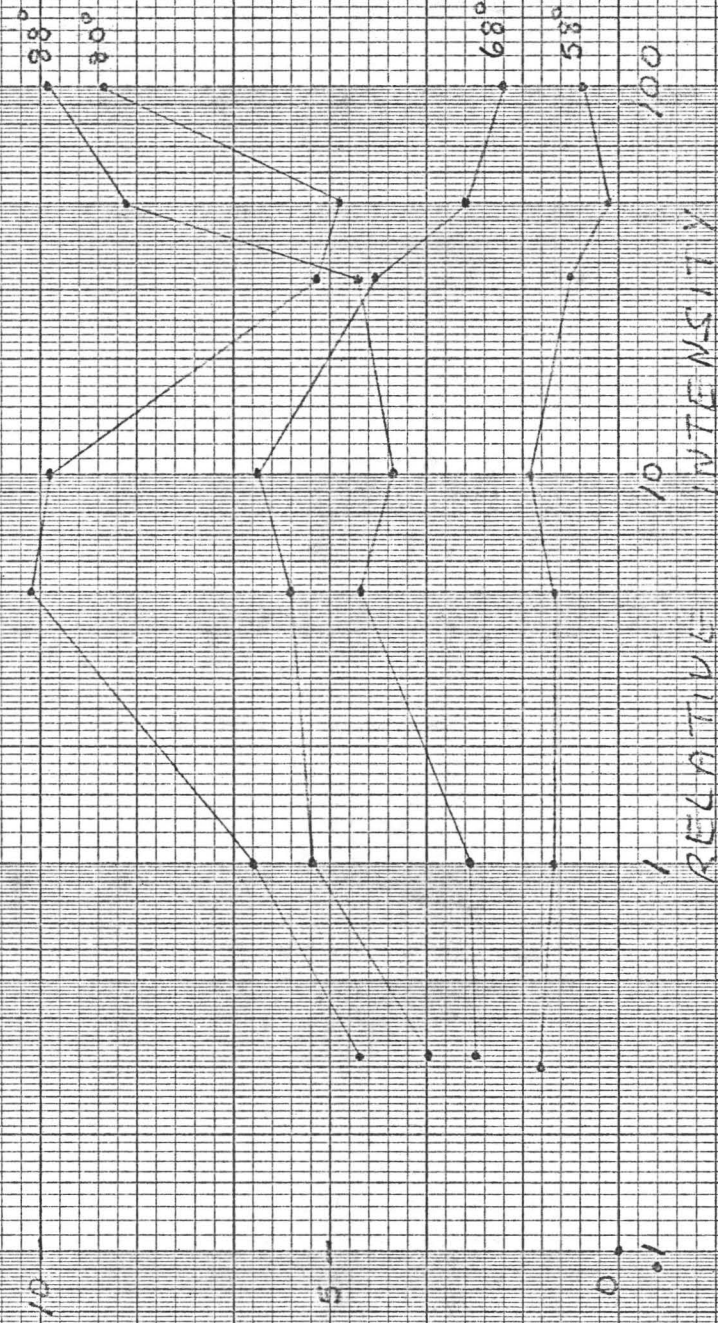


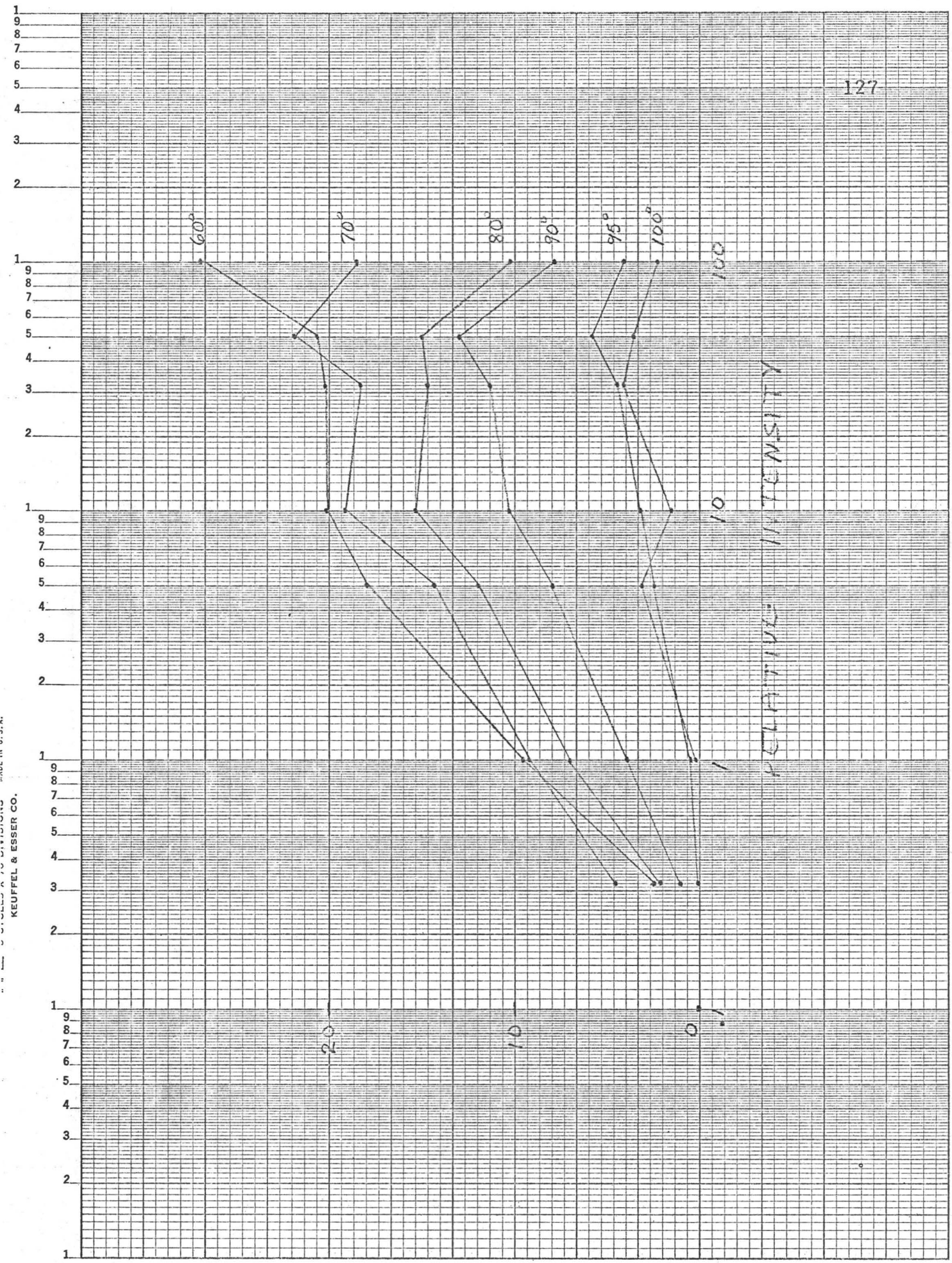


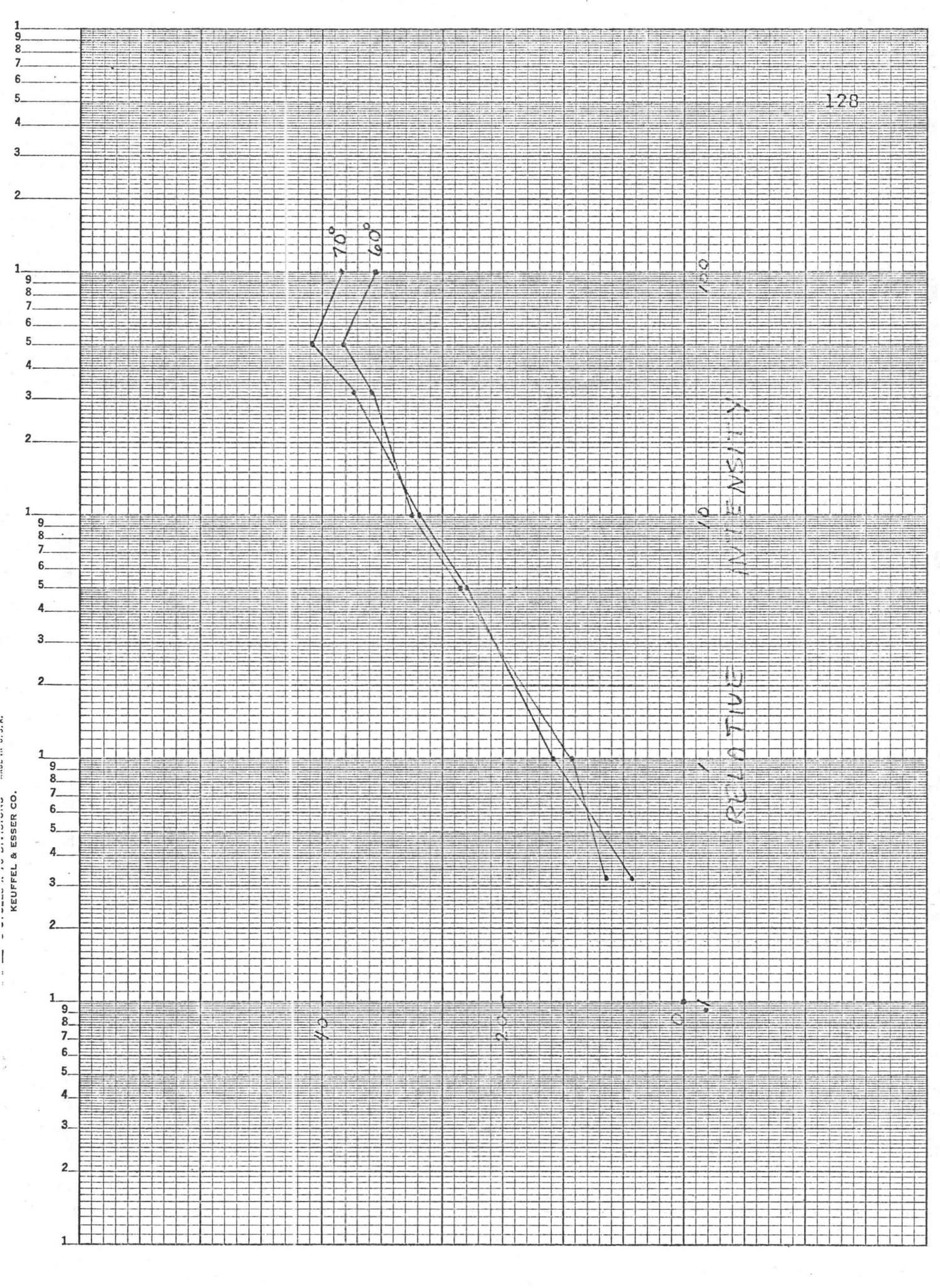


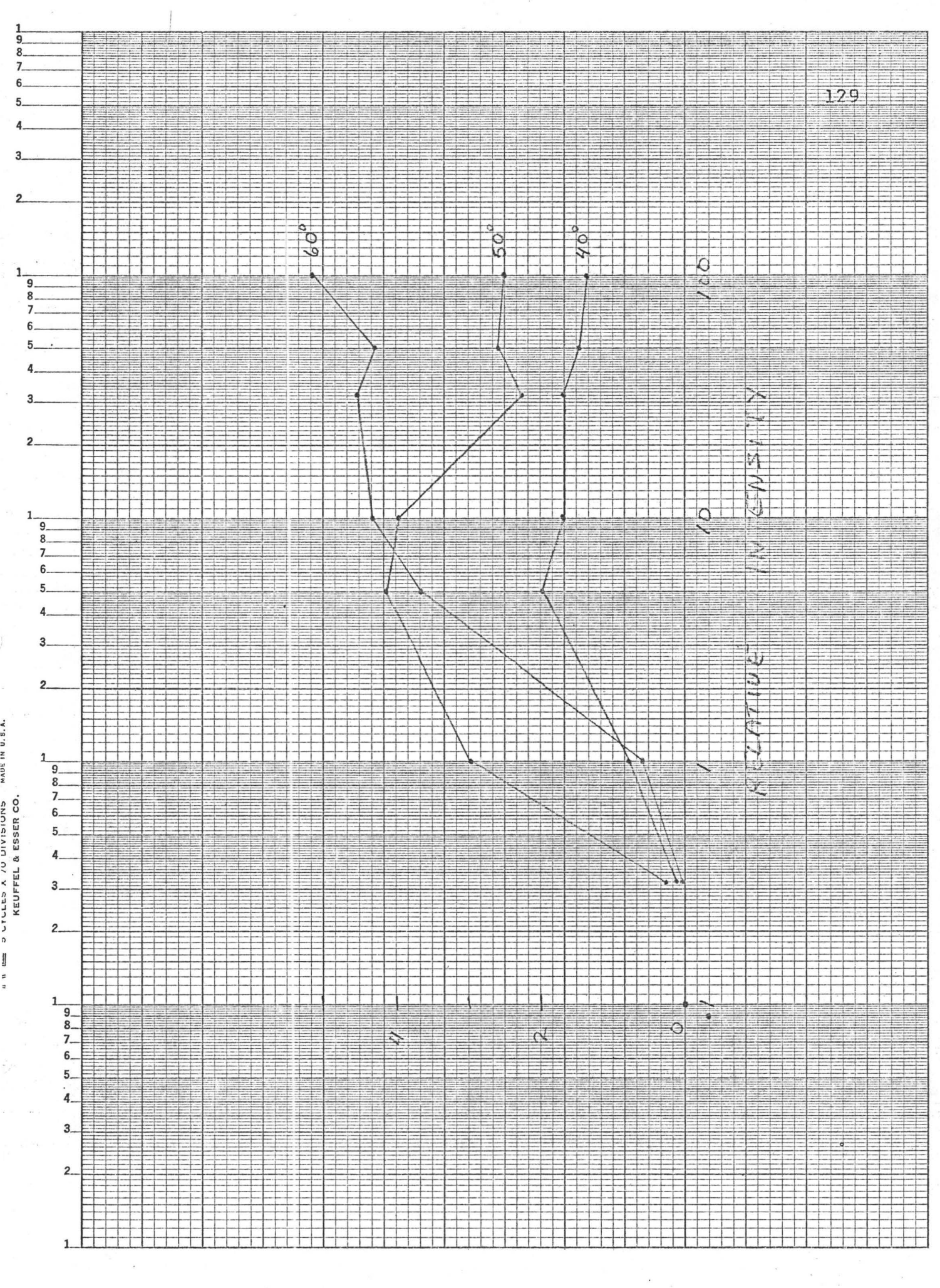
KEUFFEL & ESSER CO.

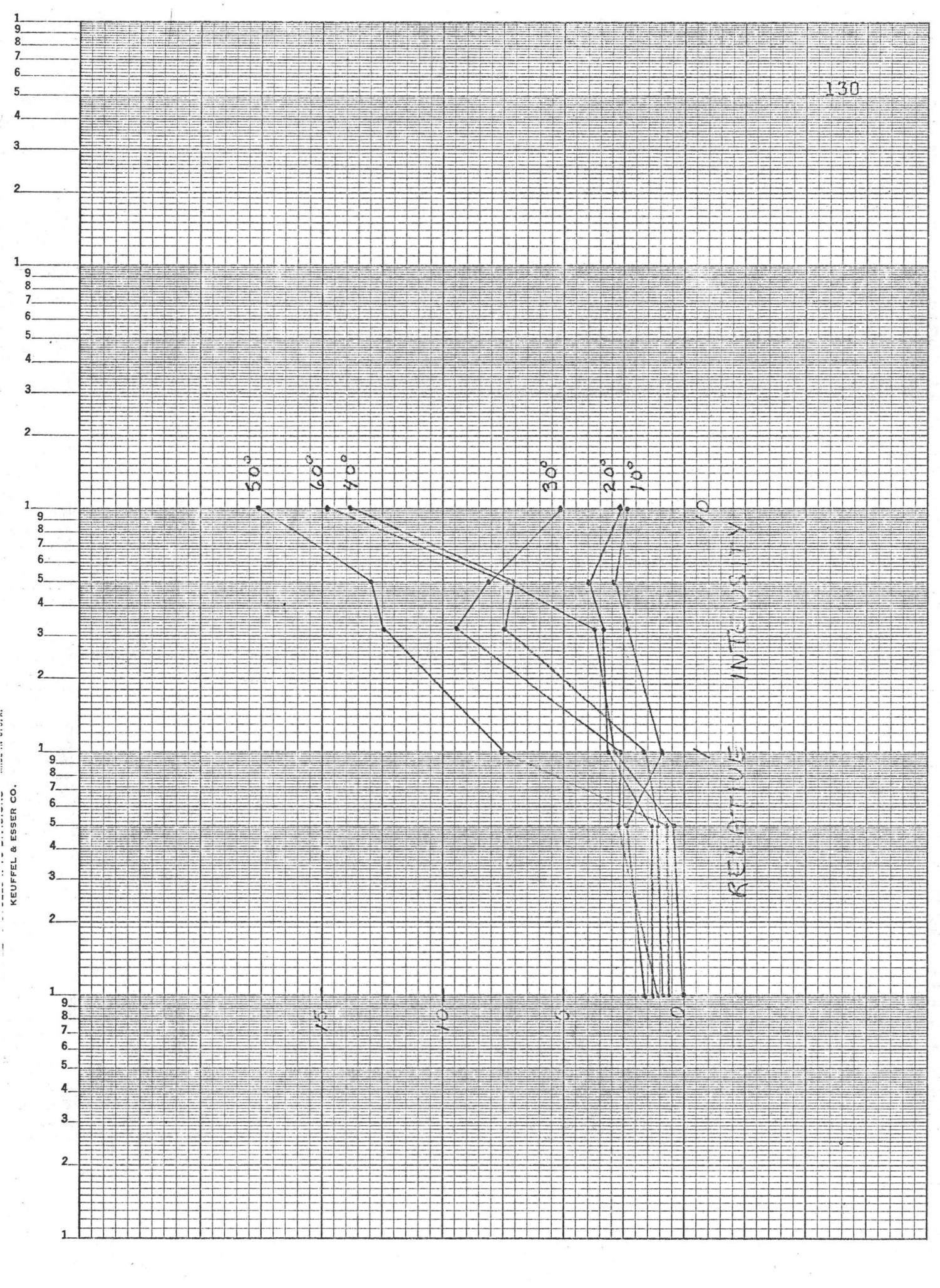


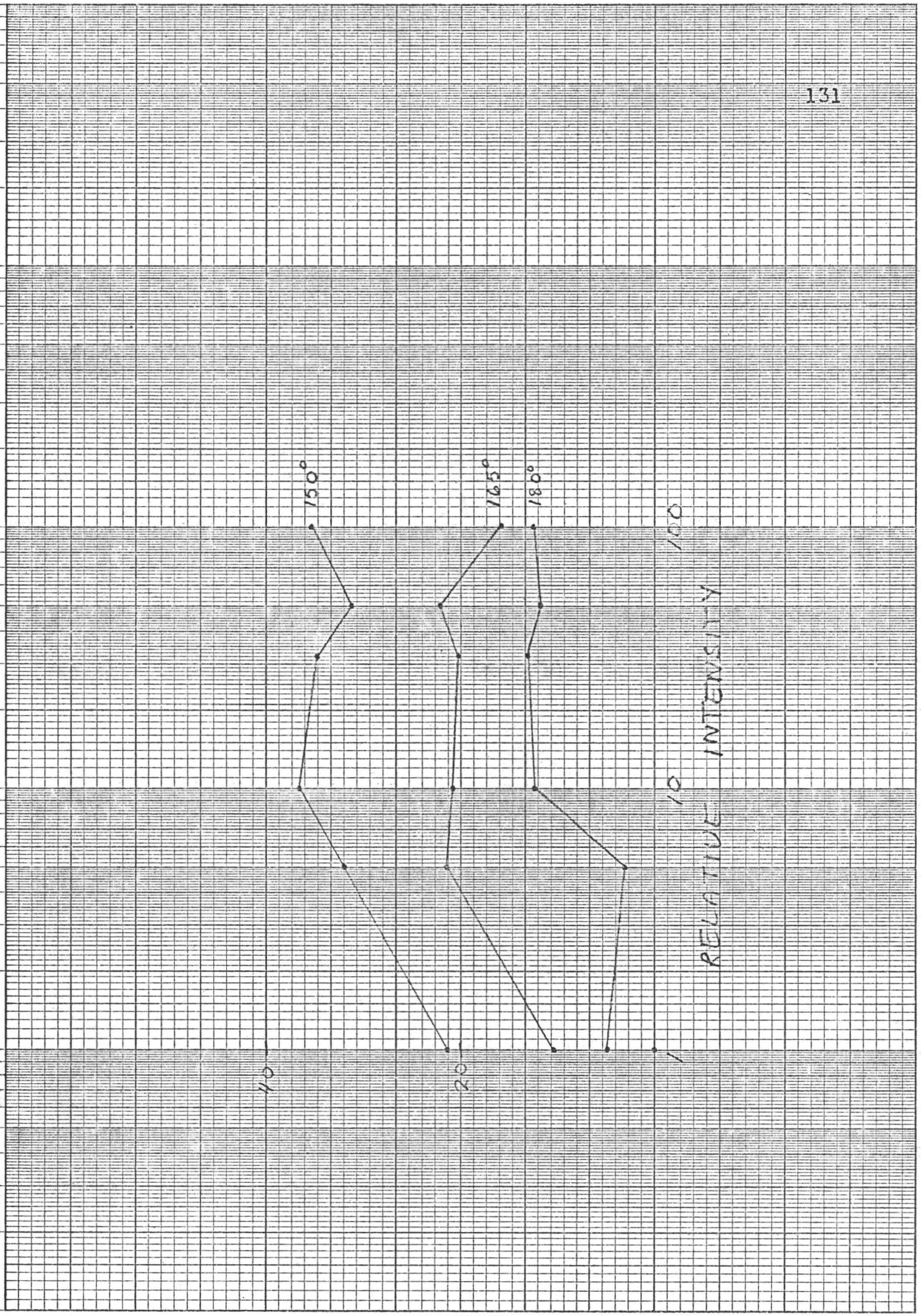


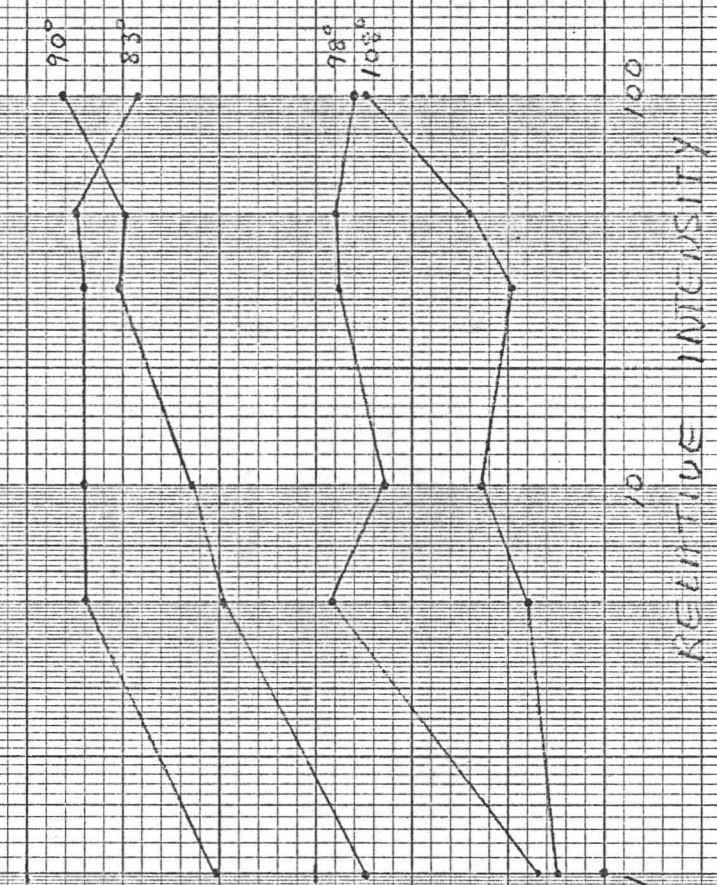

60°
70°
80°
90°
95°
100°
RELATIVE INTENSITY
20
10
0.1
KEUFFEL & ESSER CO.

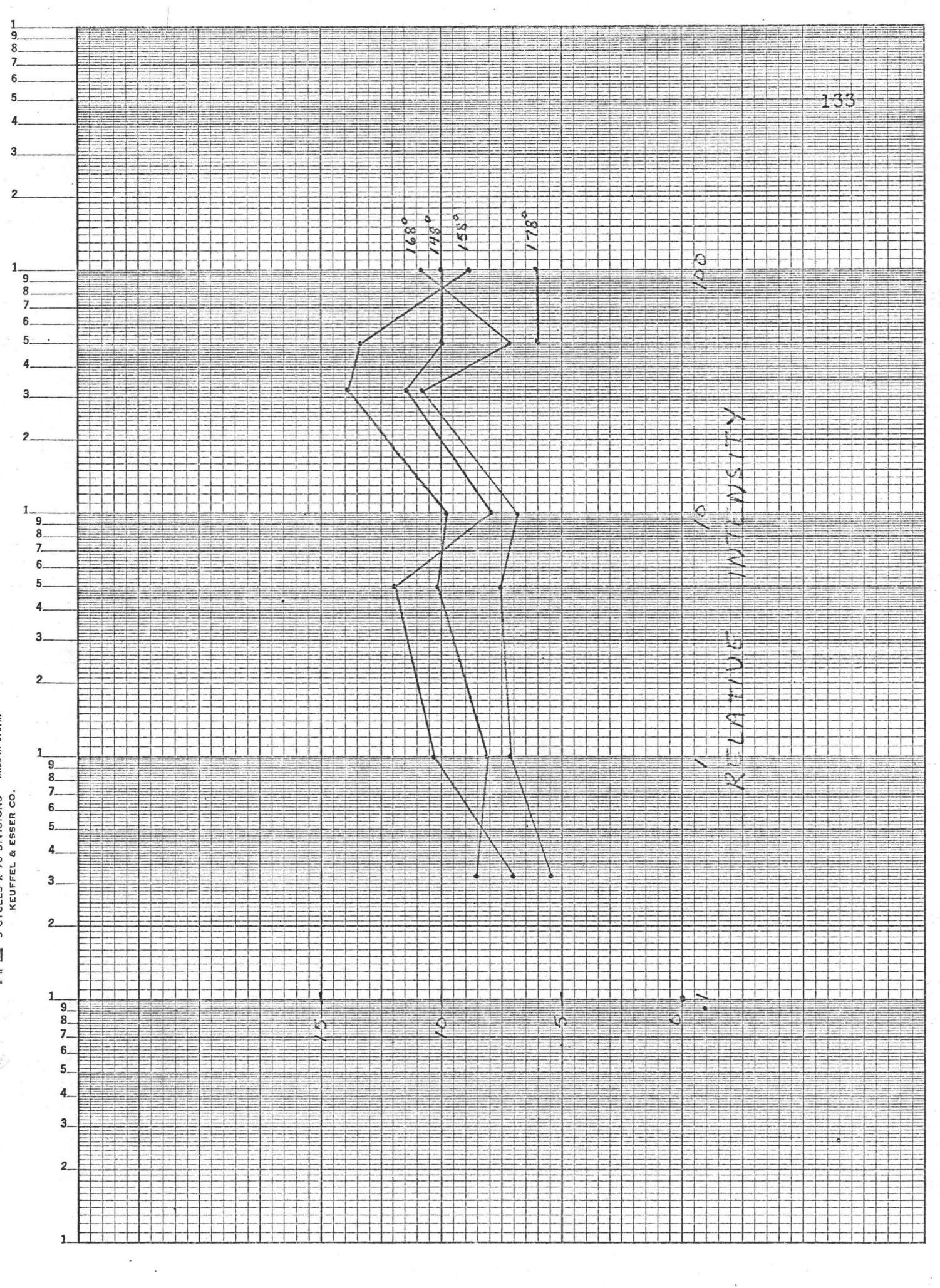


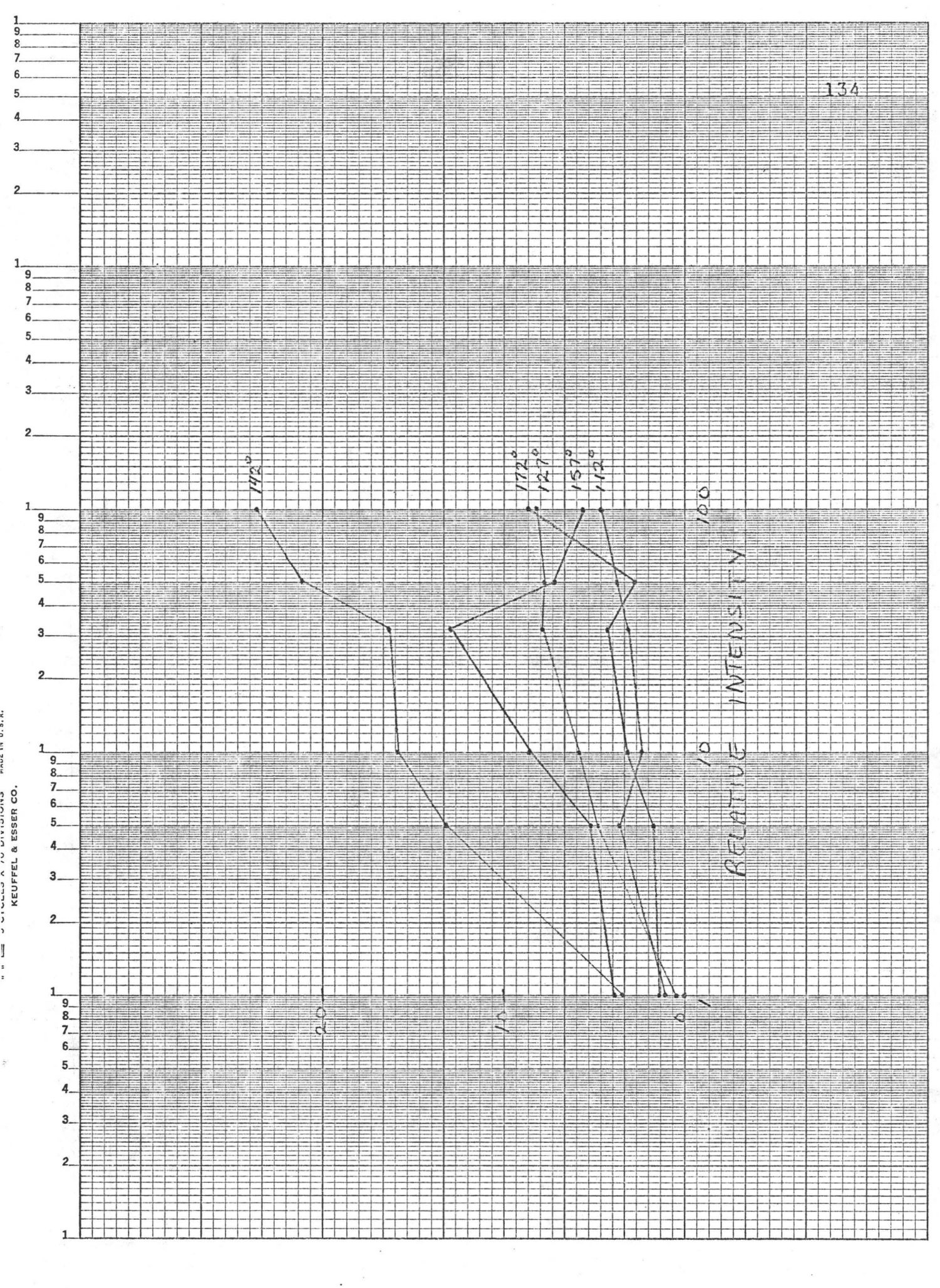


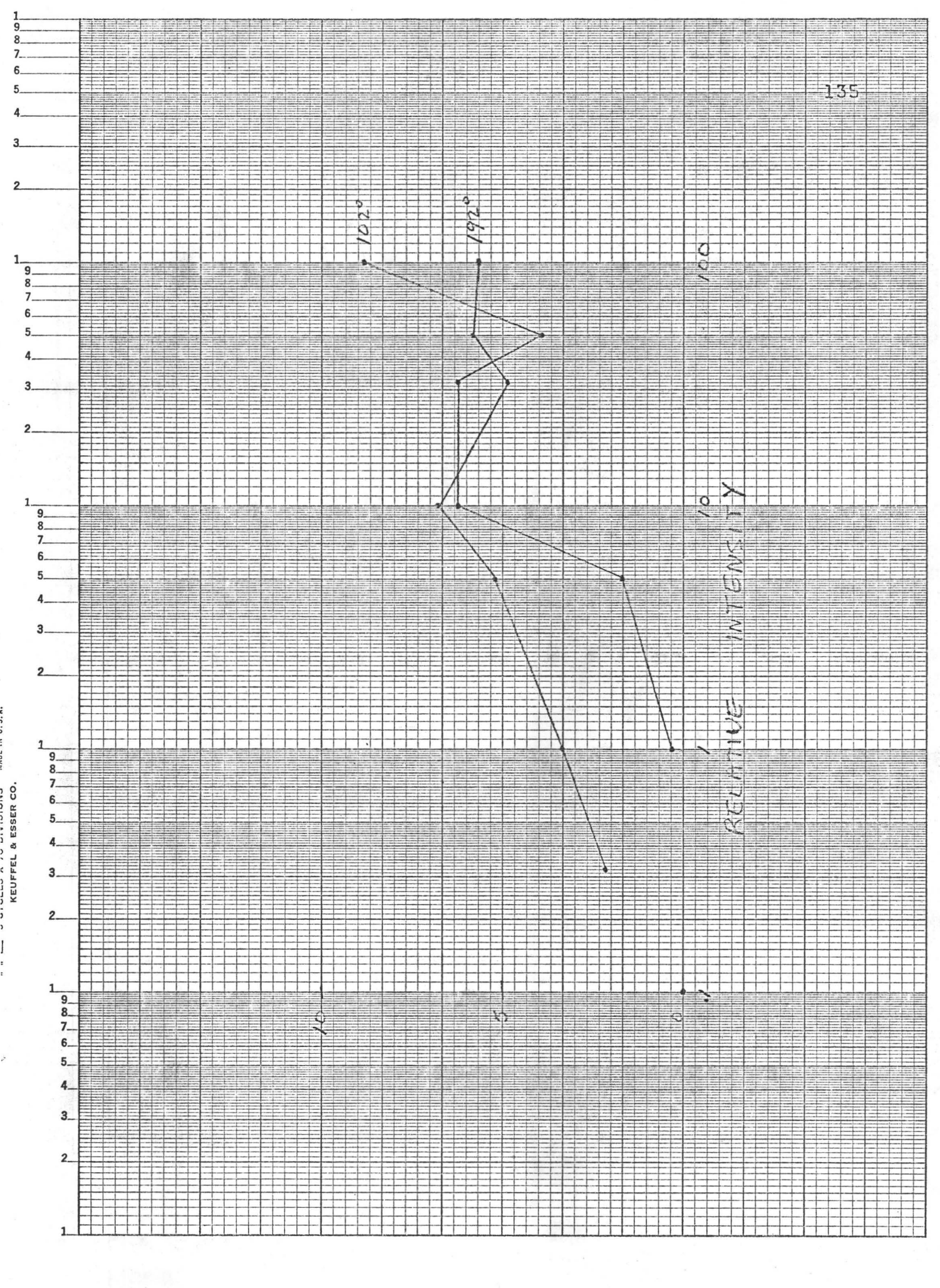


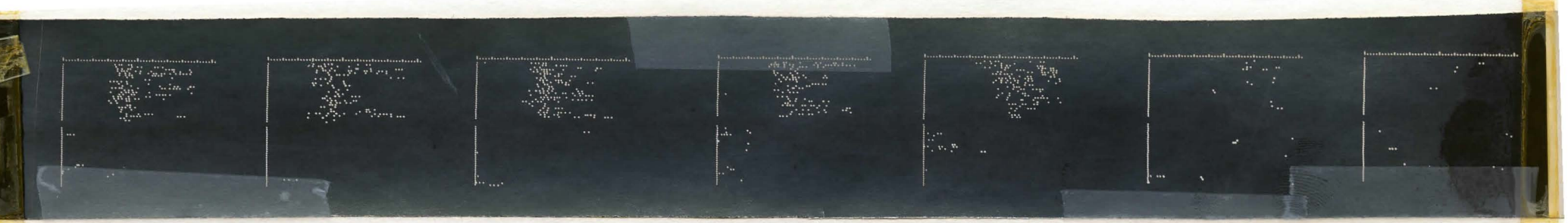








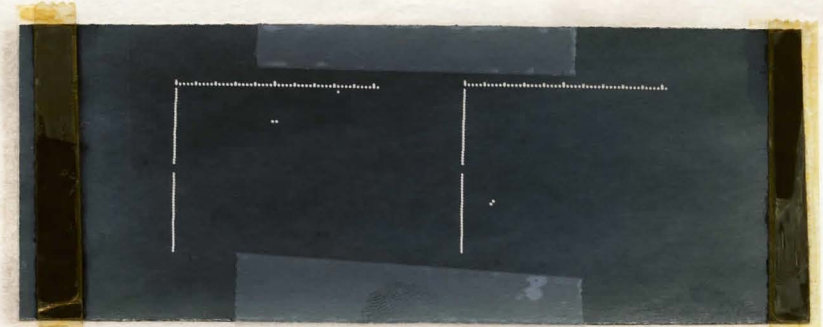




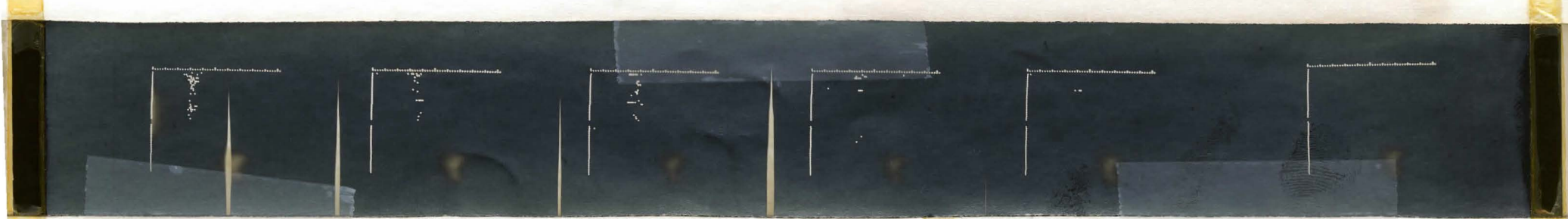
100 50 32 10 5 1 .3

INTENSITY (RELATIVE UNITS)

cell (i)



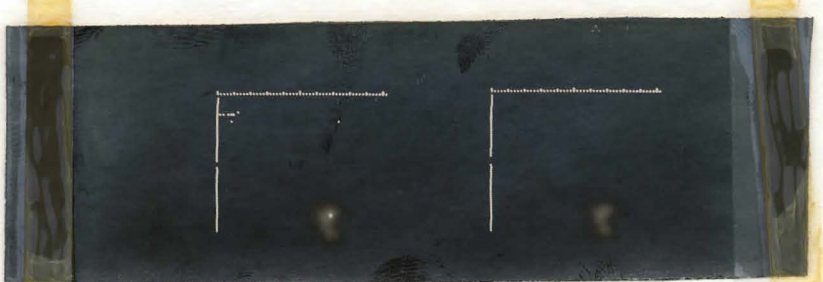
DARK LIGHT
SPONTANEOUS ACTIVITY



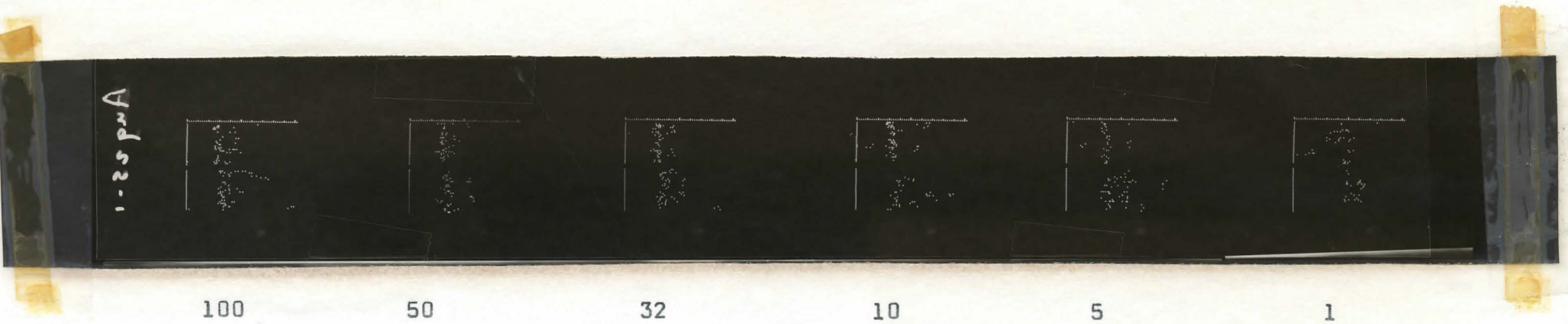
100 50 32 10 5 1

INTENSITY (RELATIVE UNITS)

cell (ii)



DARK LIGHT
SPONTANEOUS ACTIVITY

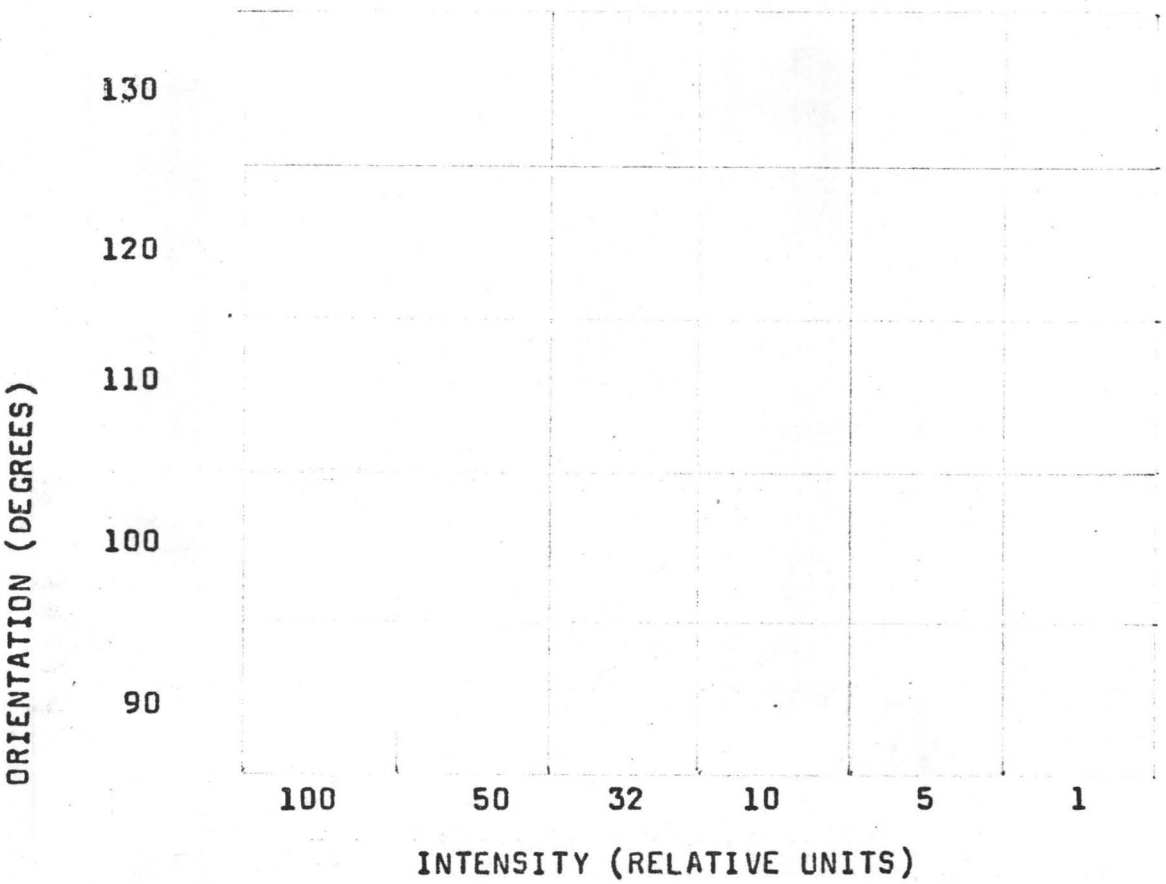


100 50 32 10 5 1

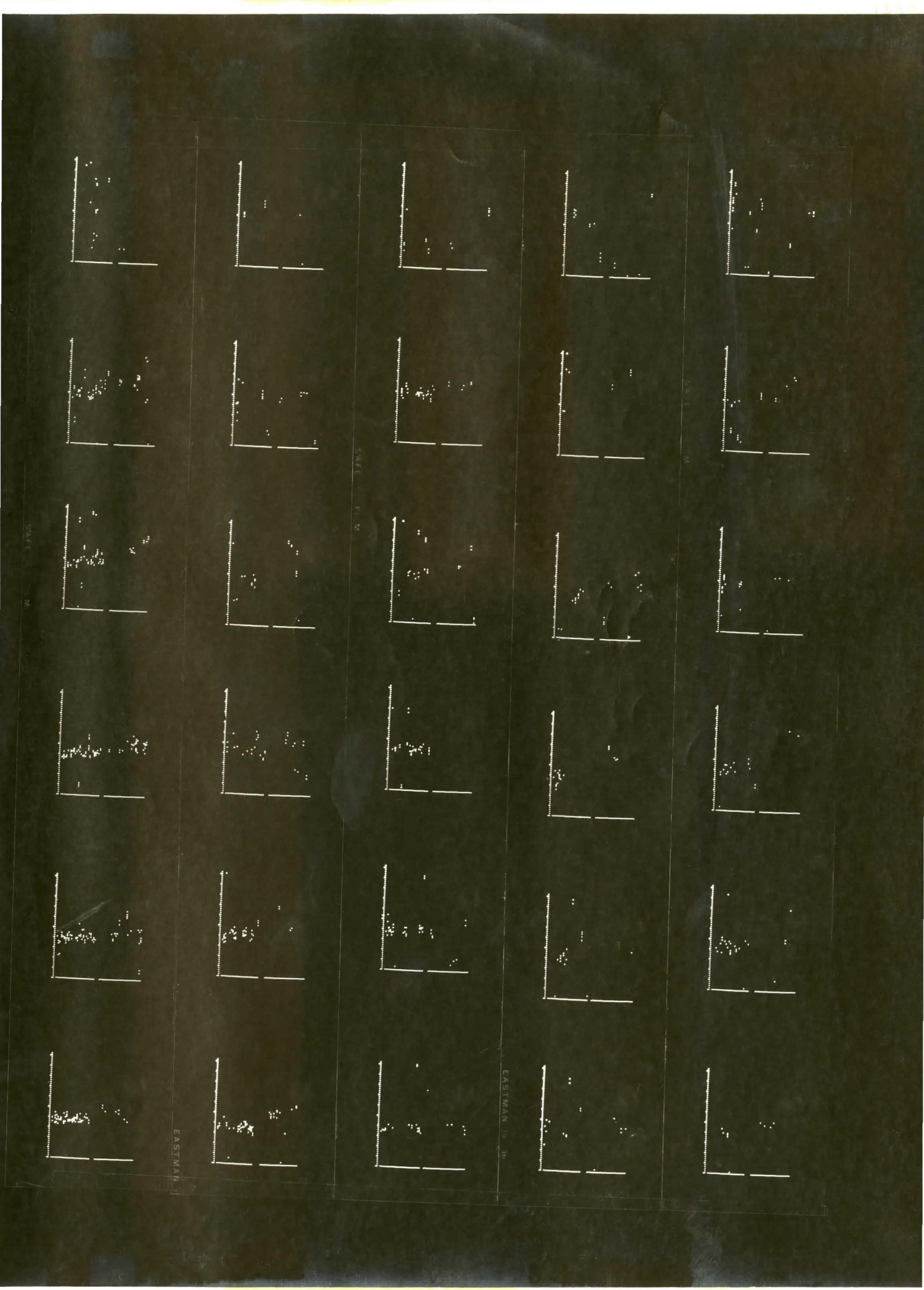
INTENSITY (RELATIVE UNITS)

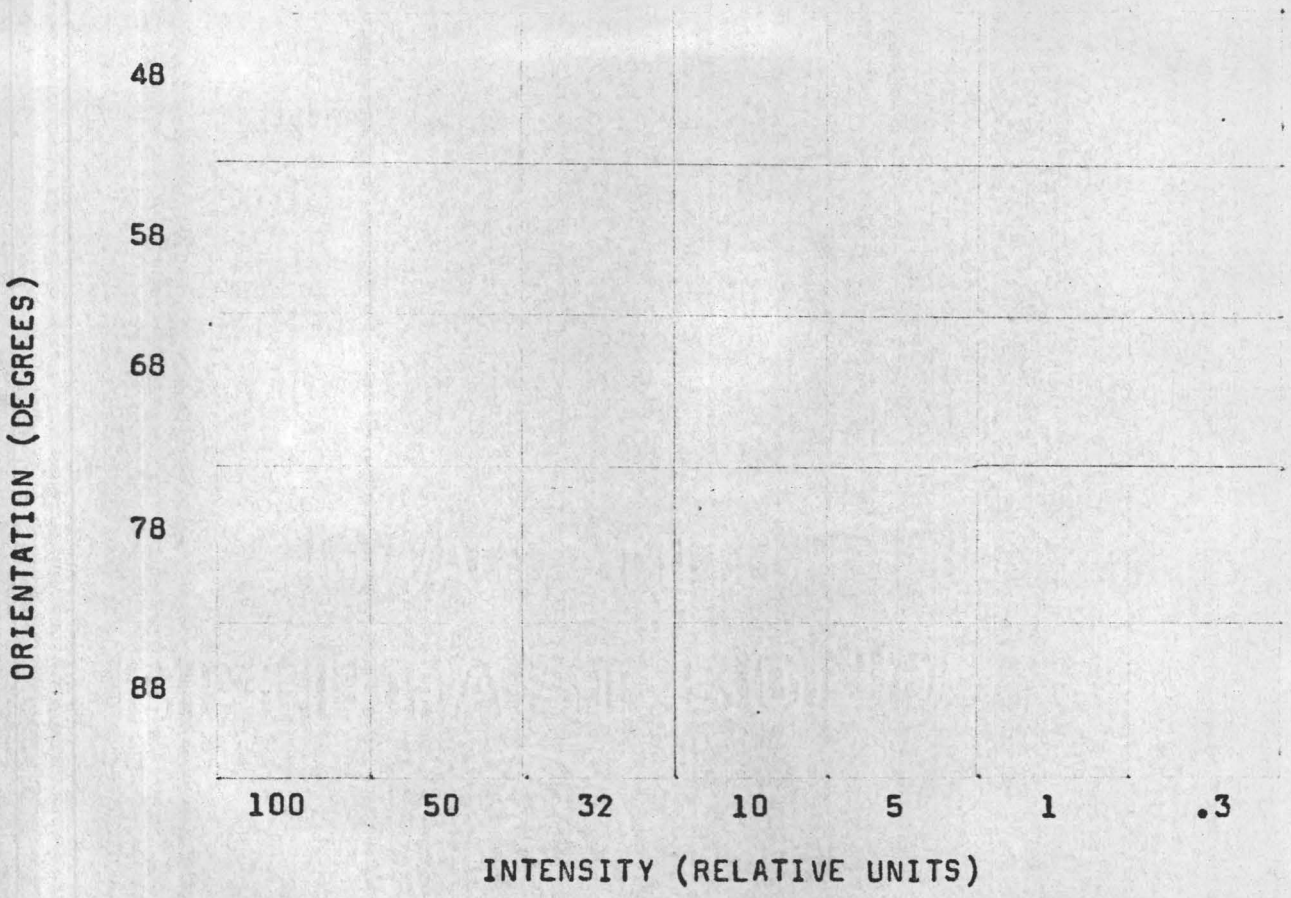
cell (iii)

The firing rate of this cell was relatively unaffected by intensity changes. Note the high spontaneous rate and the effect of stimulation on the pattern of response.

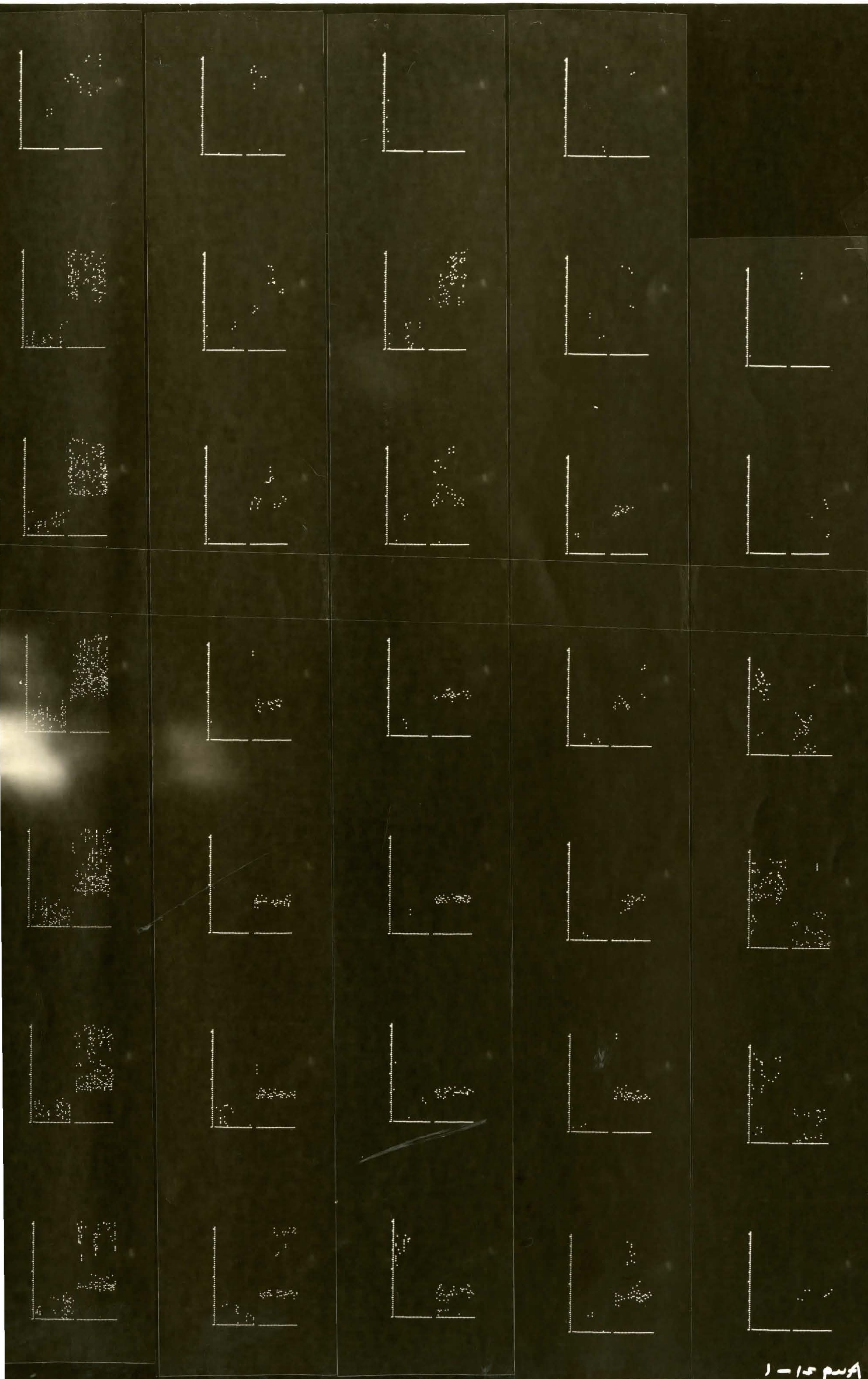


Pattern of response to an oscillating light-dark border at various orientations and intensities. A single unit.

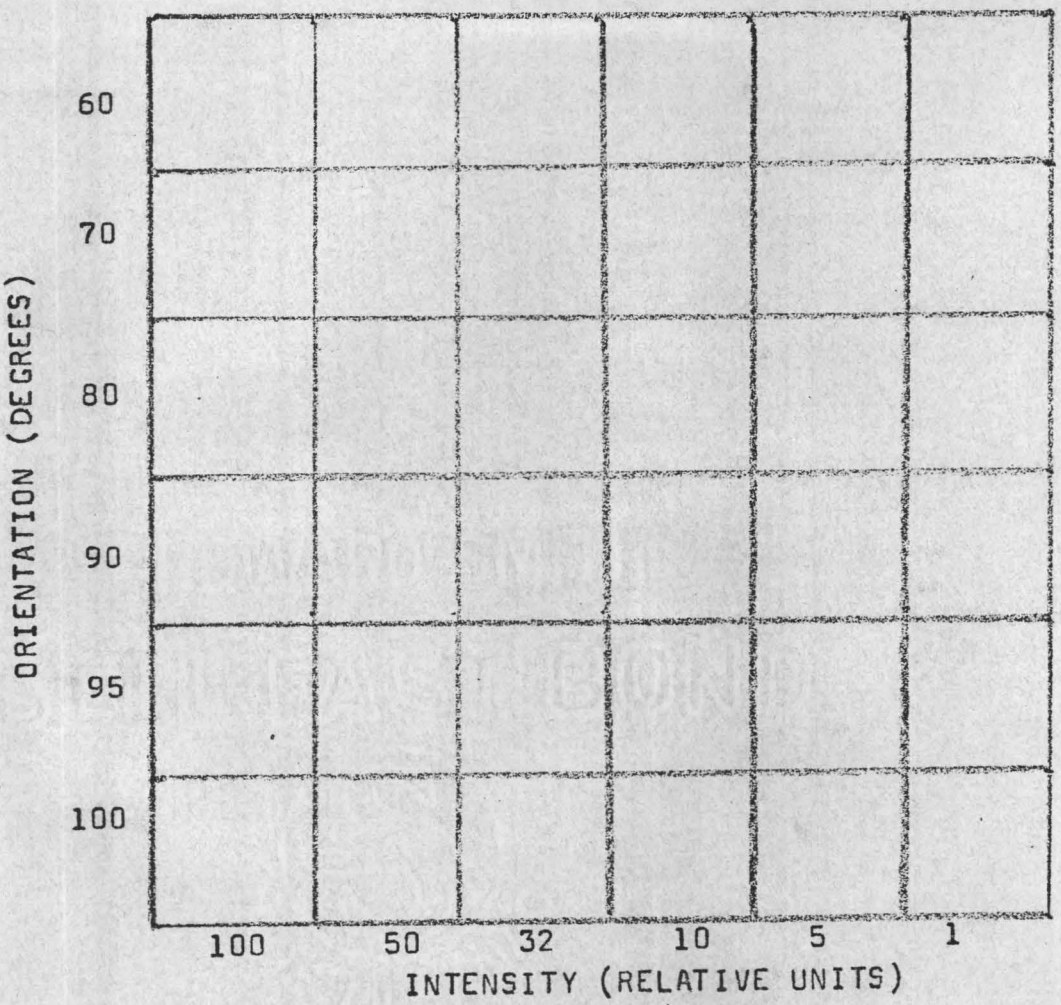




Pattern of response to an oscillating light-dark border at various orientations and intensities. A single unit showing radical changes in firing pattern i.e. from 48° to 58°, from 78° to 88°, along the intensity dimension at 48°, 68° and 88°.



1 — 15 pwA



Pattern of response of a single cell to an oscillating light-dark border at various orientations and intensities.


SAFETY FILM
EASTMAN 19 TH
SAFETY FILM
SAFETY FILM