71-25,133

VERSTEEG, Arlen Dale, 1941-
THE EFFECT OF STIMULUS AREA ON THE REACTION TIME TO THE ONSET AND CESSATION OF VISUAL STIMULATION IN THE PERIPHERY.

The University of Arizona, Ph.D., 1971
Psychology, experimental

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THE EFFECT OF STIMULUS AREA ON THE REACTION TIME TO THE ONSET AND CESSATION OF VISUAL STIMULATION IN THE PERIPHERY

by

Arlen Dale Versteeg

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF PSYCHOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Arlen Dale Versteeg

entitled THE EFFECT OF STIMULUS AREA ON THE REACTION TIME TO THE ONSET AND CESSATION OF VISUAL STIMULATION IN THE PERIPHERY

be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

Dissertation Director — Date: 13 May 1971

After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

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*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.

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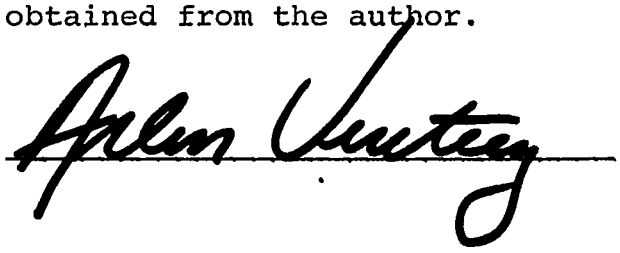
SIGNED: 

PREFACE

In our Perceptual and Human Resources Laboratory in the Department of Psychology, at The University of Arizona, we have been studying the nature of the "on-off" response in the human visual system. There have been numerous electrophysiological investigations which have shown that various retinal and higher order neurons in many species respond differentially to the onset and cessation of visual stimulation.

In our laboratory we have studied these on-off effects in the human visual system employing reaction time (RT) as the response measure. These psychophysical investigations have provided certain generalizations. (1) In the peripheral system, there are consistent differences, apparently dependent upon luminance, between onset and offset RTs. The onset of stimulation elicits faster RTs than the cessation of stimulation (V. P. Pease and T. G. Sticht, Reaction time as a function of onset and offset stimulation of the fovea and periphery, 1965; N. R. Bartlett, T. S. Sticht and V. P. Pease, The effects of wavelength and retinal locus on the reaction time to onset and offset stimulation, 1968). (2) These onset-cessation RT differences appear to be independent of wavelength, but

are presumably related to the different functions of the foveal and peripheral systems (N. R. Bartlett, T. S. Sticht, and V. P. Pease, 1968). (3) Experiments using the fovea as the locus of stimulation have produced no clear evidence concerning any differences in onset-cessation effects (V. P. Pease, The effects of a surround upon onset and offset reaction times in the fovea, manuscript in preparation; A. Versteeg, The effect of a border on the reaction time to the onset and cessation of stimulation in the fovea, 1970). (4) RT, as a response measure for studying onset-cessation differences, is a sensitive psychophysical index of visual behavior under specified conditions (L. E. Hufford, Reaction time and the retinal area--stimulus intensity relationship, 1964; V. P. Pease and T. G. Sticht, 1965; N. R. Bartlett, T. S. Sticht and V. P. Pease, 1968; A. Versteeg, 1970).

The origin of these on-off retinal responses is typically attributed to the effects of excitatory and inhibitory influence, exerted over retinal structure, interposed between the ganglion cells and the photoreceptors. The experiments were initiated to determine the effects in the periphery. If stimulus area is significantly reduced (i.e., area 1 min) the interaction effects within the receptive field may be attenuated and thus, the on-off RT effects would dissipate.

This was not the case. Onset-cessation RT differences occurred throughout the range of stimulus areas tested, with the exceptions noted in the text.

I have had many mentors as a graduate student. Much of this completed work represents time spent under their tutelage. Whether in laboratory, union or classroom: wise and seasoned counselors they were.

It has been my good fortune to work under the leadership of Dr. Neil Bartlett. Without his forthright direction, my research would have floundered and probably never reached fruition. I wish to thank him for forgiving the overdue and oftforgotten deadlines; for the vitality and humor which abounded in our research meetings; for his insistence on clear reasoning and clear prose; and most significantly for the scholarliness and maturity from which I tried to borrow.

I am also most appreciative of the guidance provided by Dr. Lawrence Wheeler and Dr. Ronald Pool. Each has spent much of his energy and valuable time assisting me in the planning and progress of this dissertation.

Throughout my graduate program, Dr. Richard Coan and Dr. William Moore have granted me their consultations, cooperation, and enthusiasm for which I am grateful.

This research was conducted with the support of National Science Foundation Grant GB 3955 to The University of Arizona with Dr. Neil R. Bartlett serving as Project Director.

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ABSTRACT

Reaction times were taken to the onset and cessation of visual stimulation of varying stimulus area and luminance, presented twenty degrees in the peripheral retina. In Experiment I, stimulus areas subtending 1.0, 1.69, 2.84, 4.79, 8.08, 13.6, 23.0, 38.7, 65.2, and 110.0 minutes of visual angle with a luminance value of 0.55 foot lamberts were employed. In Experiment II luminances of 0.05 and 0.005 foot lamberts were presented, with each of seven stimulus areas subtending, in minutes of visual angle: 1.69, 2.84, 4.79, 8.08, 13.6, 23.0 and 38.7.

Mean reaction times were plotted as a function of stimulus area for each subject as well as for all subjects pooled for Experiment I. Mean reaction times were also plotted as a function of stimulus area for each of the two luminance conditions for each subject for the tests of Experiment II. The curves for the high luminance value show that as stimulus area increased from one minute of visual angle, reaction times for both stimulus onset and cessation decreases. Onset-cessation reaction time differences gradually decreased as a function of increasing stimulus area until the largest stimulus areas (i.e.,

65.2 and 110.0 min) are involved. For such sizes there were no obvious differences.

The curves for the medium and low luminance conditions of Experiment II show that reaction time decreased as a function of increased stimulus area. Differences between reaction time to the onset and cessation of stimulation increased as a function of reduced luminance.

An analysis of variance for Experiment I indicated that the main effects of stimulus area and onset-cessation were highly significant. The interaction of the two parameters was also statistically significant. The analyses of variance computed on the conditions of Experiment II shows that the main effects of stimulus area and onset-cessation to be significant. The main effect of luminance was not significant.

INTRODUCTION

Long ago, Aubert, according to Brown and Mueller (1965), reported variation in the visual differential threshold with changes in the size of the test stimulus. Over the years, in subsequent experiments, various empirical formulations for the dependence of threshold luminance on the area of the stimulus were developed. Most prominent of these is Ricco's law which states that the relationship between an increase in the area of the retinal image is similar to the effect of an increase in intensity of the stimulus, or the product of stimulus area A, times the luminance L is a constant for threshold (AL=C). With small stimulus areas the applicability of Ricco's law is certain. Lohle (1929) has shown that the law holds in both the periphery and fovea if the visual angle subtended by the threshold object is less than 10 minutes. For larger areas, Piper's equation (the product of the square root of area and luminance is a constant) gives an adequate description. For very large stimulus areas covering substantial regions of the retina the contribution of size becomes negligible and threshold is dependent on luminance alone.

For peripheral excitation Piper's law holds for visual angles between the limits of 2 degrees and 7 degrees. Deviations from both Piper's and Ricco's laws have been reported by several investigators (Abney, 1897; Abney and Watson, 1915) and it is apparent that the empirical relationship obtained depends upon the range of areas examined.

Graham, Brown and Mote (1939) examined these previous investigations and found much of the methodology to be questionable. They proceeded to cite four major shortcomings. First, the data were not extensive enough. Few experiments utilized a large range of areas and in other experiments where the range of stimulus areas was large, the measurements were not sufficiently numerous. Secondly, variation in the size of the retinal image was often accomplished by moving the subject away from or toward the stimulus display. Freeman (1932) has demonstrated that this procedure introduces anomalous results. Thirdly, in several experiments heterogeneous parts of the retina were stimulated. This defect brings the prospect of contaminating foveal data with peripheral elements and vice versa. Finally, fixation conditions were usually inadequate.

Cognizant of these limitations, Graham et al. (1939) performed their experiments, using a large range of

stimulus areas with diameters covering a range of 1.86 minutes to 1 degree of visual angle in the fovea. In the periphery they employed a range of 1.86 minutes to 25.5 degrees. They also maintained the observing distance constant in any given series of experiments with the areas in the retina so stimulated that they activated relatively homogeneous regions. Finally, fixation was maintained constant for both the peripheral and foveal conditions.

Under these conditions, the authors found that the relationship obtained between the intensity threshold and visual area of the stimulus for the fovea and the periphery to be similar in general outline to those which had been presented in earlier experiments. With a small area a high intensity is required to produce threshold and as the area increases the intensity requirement decreases. The curves for both the fovea and periphery are not linear but decrease in slope as one progresses from the smallest stimulus area to the largest stimulus area.

In the foveal data, the first four data points, corresponding to the areas subtending 0.93, 1.24, 2.10, and 3.03 minutes of visual angle, may be roughly fitted to Ricco's law, $AL=C$. In the periphery, the same law may be used as a description of the smallest areas used. However, beyond these ranges both curves tend to have smaller slopes, and over the medium range of peripheral areas

Piper's law, I A=Constant, might be considered to hold. With the largest areas used intensity finally becomes independent of area. These results indicate, in support of earlier investigations, that all of these descriptions or laws are empirical and have little validity for describing the data for a large range of stimulus area.

An early investigation of the effect of stimulus area on threshold response was that of Abney's (1897). He measured the extinction thresholds for stimulus fields of various sizes and found that the greatest excitation occurs in the center of an area illuminated near threshold. Graham et al. (1939) followed this reasoning and suggested that when an area of the retina is illuminated, the excitation in the associated nerve fibers varies depending on their location relative to the illuminated field. They reasoned that there is a gradient of effect in an illuminated retinal region from the margin inward, with the greatest effect at the center. Thus, if the illumination is roughly uniform over the area, the greater excitation would be in the center, such as was reported by Abney (1897), and could come only from some interaction yielding a peak effect at that center. More specifically, they assumed that the contribution of each elemental area to the effect at the center was inversely proportional to some power of the distance of the element from the center.

They investigated the area-intensity function in both the fovea and periphery, and from this formulation adequately described their foveal data and peripheral data for stimulus areas of diameter greater than about 20 minutes. However, with small areas (i.e., areas less than 20 minutes) there was a consistent deviation from the theory.

In a succeeding study, Graham and Bartlett (1939) examined these systematic deviations found with small peripheral areas. In this study a greater number of stimulus areas were used and the wave band of the test flash was restricted to minimize any phenomena from light scattering that might contaminate these foveal data. In order to assess whether cone activity was involved in the peripheral determinations, two wave bands were chosen on the basis that if cones come into action with the higher intensities required for small areas, they should, because of the smaller photochromatic interval in the red, be activated more noticeably with red light than with violet. Specifically, a transition from rod to cone function would be evident at lower relative intensities of red than of violet. However, the functions relating intensity to area, with these two wave bands, were parallel and thus it is doubtful if any cones were appreciably involved.

A possible explanation of these deviations was offered by Graham and Bartlett. They asserted that the

receptive unit of the periphery is not the single sense receptor, but rather the ganglion cell with its many converging fibers. Twenty minutes of visual angle is approximately the diameter of the retinal area served by a ganglion cell with all its associated connections in the part of the retina in which these investigators were working. The integration with large stimulus areas may involve a summation effect with the ganglion cells as the primary units; the more nearly complete integration for small areas may reflect the activity of the rods feeding into the ganglia. Ricco's law is a satisfactory description for areas small enough to be served by a single ganglion cell. However, the theoretical formulation of Graham, Brown, and Mote (1939), is adequate both for the spatial limits ordinarily encountered and for wider ranges of area than any of the well-known empirical laws (e.g., Ricco's or Piper's).

Graham et al. (1939) assumed that not only does an increase over a homogeneous retinal area permit a greater number of individual receptors to come into play, but that through physiological summation, each receptor also contributes an element of excitation proportional to some power of the distance from the center of the region excited.

Proponents of simple probability theory such as Wald (1938), and Pirenne, and Marriott (1959) ignore retinal interaction and suggest that decrease in over-all intensity demands for a threshold response with larger area is attributable solely to the fact that with greater stimulus area, more retinal receptors with varying degrees of sensitivity are involved and, thus, the probability for an earlier response is enhanced.

Wald (1938), in his hypothesis, described threshold data for areas of intermediate size by assuming a statistical distribution of the various thresholds of receptive units. Increase of the stimulus area results in the stimulation of a greater number of units with low thresholds to respond. If the total available number of units corresponds roughly to the area $\underline{A}$, $\underline{n}$ is the number of excitatory units active, and $\underline{L}$ is the luminance, then as an approximation,

$$KL = \frac{n^p}{(A-n)^q}$$

where $\underline{K}$, $\underline{p}$, and $\underline{q}$ are constants; $\underline{p}$ applies to the number of activated elements for threshold, and $\underline{q}$ to those not yet excited. If a constant number of elements n_t is required for threshold, the equation becomes

$$(A-n_t)\ q_L = \frac{n_t p}{K}$$

Wald (1938) did not apply this equation to very large or to very small stimulus areas. He reasoned that since very small stimulus fields require intense light for stimulation, the responses of the elements might involve a nervous discharge at supraliminal frequencies. Therefore, the threshold might be modulated by a constant frequency of discharge rather than by a constant number of retinal elements contributing to the discharge.

In addition to those studies employing threshold as the response index, there has been some rather elegant electrophysiological work on the question of the merits of simple probability theory vs some form of retinal interaction.

Hartline (1938, 1940b) completed a series of experiments on the receptive fields of single nerve fibers of frogs. For moderate intensities and small points of light, he found that the strongest response from the marginal region was typically of the threshold type. The fibers Hartline examined were third order neurons; the receptive field for each was presumably the area served by the sense receptors associated with the ganglion cell.

Important electrophysiological evidence for retinal interaction was presented by Adrian and Matthews (1928) in their investigation on the Conger eel. These investigators recorded the gross electrical activity in the whole

optic nerve and indicated that as stimulus area increased, with luminance constant, amplitude increased and latency decreased. They concluded that summation in the synaptic layers of the retina was responsible for this dramatic effect.

These same investigators demonstrated a reduction in latency with four stimulus spots as compared with the latency for each stimulus spot alone. Thus, spots not too widely separated resulted in a decrease in latency in a manner comparable to an increase in area. Another demonstration of neural interaction at the retinal level was provided by Adrian and Matthews with the aid of strychnine, which has the property of facilitating synaptic conduction. This chemical was placed on the retina and was found to increase the minimum separation between spots that resulted in a reduction in latency. Therefore, by manipulating conditions of synaptic conduction, they were able to produce a reduction in latency similar to that found for increasing the area of a stimulus. Presumably, strychnine had extended the area over which retinal neural interaction was possible.

Ratliff and Hartline (1958) reported an inhibition of the activity of a single ommatidium in the lateral eye of Limulus when other ommatidia in surrounding regions of the eye were stimulated. This experiment, along with

others, shows that excitement of one region of the retina has an effect on immediately adjacent responding regions. Increase in stimulus area, therefore, not only allows a greater statistical opportunity for reacting; there may also be a change in the excitability of one part of an illuminated region when responses occur in an adjacent area.

In addition to the electrophysiological studies directed at the nature of the retinal response to variation in stimulus area, there have been many psychophysical studies bearing on this question.

Beitel (1934) wished to determine the extent of interaction between two sites of stimulation in both the fovea and the periphery, and employed the absolute visual threshold as the response measure. In his method, the threshold was first calculated for two areas separated by varying spatial intervals (from 0 to 150 minutes separation) and then for either area alone. His results gave pointed evidence for interaction between spatially separated, subliminally stimulated areas in both the peripheral and foveal systems. In the peripheral system this interacting process obtains until the stimulus patches are separated by a visual angle of 2½ degrees and in the fovea until the separation reaches 10 minutes.

In another threshold study, Brown (1947) determined the limits within which complete spatial summation occurs in the peripheral retina of the human eye. Using monocular intensity thresholds measured by a modified method of limits for 12 circular areas illuminated by white light and varying in diameter from 0.64 to 51 minutes of visual angle, Brown presented the stimuli in the temporal periphery approximately 30 degrees from the fovea. In each case, as area increased, threshold intensity decreased. Brown reported no lower limit in the peripheral retina to perfect spatial summation, not withstanding the smallness of the stimulus. The upper limit for complete summation was reached when the diameter exceeded 10 to 25 minutes of visual angle. As area is increased beyond this, the change is less effective. This limit is in agreement with previous studies (Graham, et al., 1939; Graham and Bartlett, 1939) and with estimates of the convergence of receptors on a single ganglion cell.

With a different method Riopelle (1951) examined an increased dispersion of stimulus sub-areas and the scotopic threshold. He stimulated at 20 degrees in the periphery of the temporal retina with three dispersion conditions. First, the stimulus array consisted of 64 one-eighth inch diameter holes. Second, there were 16 one-fourth inch diameter holes. Finally, there were four

sub-areas, each one-half inch in diameter. In the first two conditions the sub-areas were uniformly distributed within circles of 1½, 2, 3, 4, 5, and 6 inch diameters. In the third phase the four sub-areas were placed just inside these limiting diameters. Total area was constant throughout.

His data demonstrate that the more widely the sub-areas are separated, the more the threshold rises. The extent of this elevation in threshold is a function of the size of the sub-areas. The threshold intensity of the most widely separated small spots was eight times as great as that for the one inch solid spot. However, the threshold for the dispersed large spots was only one and one-half times as great as the control area. Riopelle interpreted his results as supportive of retinal interaction theory.

In a very similar study, Hufford (1964) examined the effects of stimulus dispersion on reaction time (RT). He employed two stimulus conditions. In the first condition, five equal circles were presented. Each circle subtended very nearly nine minutes and was centered on the corners and centers of squares whose diagonals subtended seven angles in geometrical progression from 44 minutes 28 seconds to 3 degrees 10 minutes. The second stimulus was a pattern of single circles subtending eight angles in geometrical progression from 20 minutes to 3 degrees 10

minutes, the first of which had the same area as the total area of the five circles in each pattern of the first type. Hufford projected the stimulus flash on the temporal region of the retina 18 degrees peripheral to the fovea. Several levels of luminance were employed and RT to the onset of the flash was his response measure.

This investigator discovered that RT increased as stimulus dispersion increased. However, this result occurred only with the dim stimulus luminance values. At higher luminance values the dispersion of the stimulus field (up to 3 degrees 10 minutes in this experiment) had no effect on the speed of a response. The author suggested that, "it is possible that at higher luminances there is sufficient energy to excite enough of the faster elements of the visual system so that reaction time is comparable over the stimulus dispersion range used in this study" (Hufford, 1964, p. 1372).

This study suggests that areal summation is effective only to a critical dispersion distance (about 2 degrees 46 minutes of visual angle) beyond which summation ceases and RT becomes constant.

Research into the mechanisms of the sensory processing system was launched by Hartline (1938) with his report of differential unit responses to the onset and cessation of visual stimulation in the retina. He found that only about 20% of the optic nerve fibers of the frog

responded with an initial burst followed by a continued discharge. Nearly 50% showed an initial burst when the light appeared and a final burst after the light went off--with no discharge appearing during steady illumination. The remaining 30% of the optic fibers did not respond at all to the stimulation of the light but gave an active and prolonged discharge after the light disappeared.

Several other investigators have examined the nature of these "on" and "off" unit responses (Kuffler, 1953; Granit, 1955; Barlow, Fitzhugh and Kuffler, 1957; Wolbarsht, Wagner, and MacNichol, 1961; Ratliff, 1962, 1965). They suggest that "on" and "off" responses may perhaps act to signal significant aspects of the visual field such as patterns of intensity, specific contours, and movements. They further assert that "on" and "off" neural activity is a complex phenomenon highly dependent upon stimulus characteristics such as luminance, wavelength, and area.

The electroretinogram (ERG) has provided a fruitful avenue for the investigation of the role of "on" and "off" activity in the visual system. Granit (1955), as a result of his ERG investigations, has reported that the "off" effect is more noticeable in cone than in rod ERG's. ERG's from pure rod eyes have a less developed off component, while the converse is true for pure cone eyes. These

results lead one to expect that the unit "on" and "off" responses may be related to the different functions of the peripheral and foveal systems.

"On-off" differences have been studied not only with electrophysiological techniques, but also an increasing number of investigators have subjected them to psychophysical study. Reaction time (RT) has been commonly employed as the psychophysical response measure. RT has been demonstrated to be a sensitive and reliable index of neural activity in the visual system, provided that the subjects (Ss) have had prior experience and training on the RT task and have reached their assymptotic level with minimal variability (Bartlett and MacLeod, 1954; Rains, 1961; Hufford, 1964; Pease, 1964). Another critical rule in any RT experiment is to establish, before the experiment is initiated, explicit and consistent criteria for the S to employ in data rejection. In the experiments described in this dissertation, rejection of RT data is based on S's detection of mechanical failures such as improper fixation or blinking at the time of stimulus presentation. Additionally, data were disqualified if the S articulated great discomfiture in the execution of a particular RT. With well over 6,000 RTs recorded, less than 2 per cent were rejected as a result of the aforementioned criteria.

Jenkins (1926) and, according to Pease and Sticht (1965), Pieron in 1927 found significant differences between the onset and cessation of stimulation. Both reported RT to cessation of luminous stimulation in the fovea as faster than that to stimulus onset.

Steinman (1944) presented further evidence that there were, indeed, significant differences between the two types of reaction. She measured RT to an increase or decrease in prevailing luminance and reported that RTs to decreases were faster than to corresponding increases for the fovea.

More recently, Rains (1961) examined the RT to the onset and to the cessation of a bright, large flash against a dark field. Onset and cessation RTs were obtained for the onset or cessation of a large ($12^{o}44'$), long duration, bright (344 ml) stimulus at various retinal locations with a dark background. He concluded that no difference exists for these conditions. He added, however, "preliminary exploration suggests that differences may be apparent when a small, dim, peripheral flash is employed" (p. 267).

Following this suggestion, Pease and Sticht (1965) investigated RT as a function of the onset or cessation of a visual stimulus covering a wide range of intensities. The stimulus subtended 20 minutes of visual angle at the eye. With these small stimulus areas, the authors concluded

that in the periphery cessation RTs are longer than onset RTs. They discovered, however, that these differences decrease as luminance increases. The authors further speculated that RT differences in onset and cessation reactions may be due to a number of things such as "intensity, area, wavelength of the stimulus, the state of the adaptation of the eye, and the presence or absence of other stimuli."

Bartlett, Sticht, and Pease (1968) studied RT differences in RTs to onset and cessation stimuli for different wavebands and intensities. The wavebands were selected with the purpose of isolating the foveal and peripheral systems. Two retinal positions were stimulated, one in the center of the fovea, and the other 12 degrees in the periphery of the temporal retina of the right eye. Cognizant of the photochromatic interval and having made adjustments for it, these investigators clearly revealed that the relationship of onset and cessation RTs to luminance is related to the different functions of the foveal and peripheral systems. Wavelength was not the crucial variable, but the manipulation of wavelength enabled the authors to investigate the retinal mechanisms involved. Bartlett et al. concluded that there were no significant differences between foveal onset and cessation stimuli with respect to RT for either waveband. However, they

found that RTs in the peripheral system for the onset of light were consistently and significantly faster than for the cessation of the same light. These results were interpreted as a demonstration of a difference in response between the foveal and peripheral systems.

The effects of a surround upon onset and cessation reactions in the fovea were examined by Pease (ms. in preparation). In this study, in the onset condition, the S viewed a surround, in the center of which appeared a test flash that was turned on or terminated independently of the surround. In the termination condition, S viewed a uniformly illuminated disc, the center of which could be turned off, thus preserving a constant state of adaptation in the surround at the time of the cessation condition. Three Ss highly trained in RT tasks responded to four luminances of surround test flash. The luminance of the flash and surround were identical in every test. Results showed no statistically significant differences between onset and cessation RTs with these parameters.

Pursuing the suggestion that differences in onset-cessation reactions might be due to the presence or absence of other stimuli in the visual field. Versteeg (1970) investigated the effect of proximity to a border on foveal onset and cessation RTs. In this experiment, the visual field comprised two continuous regions of different

illumination with an abrupt transition between them that provided a "border" contrast effect. The purpose of the investigation was to examine RT to a stimulus probe as it moved across this field and to assess further the effect of the border on the resulting onset and cessation RTs. This was done foveally as the stimulus flash was of high luminance. Under these conditions Versteeg reported no significant onset-cessation differences, although a border effect on RT reported earlier by Payne and White (1967) was verified.

Manipulation of the area of the stimulus has been an important parameter for visual scientists. A number of salient facts may be elicited from their investigations. First, the decrease in absolute visual threshold is not attributable solely to the fact that with a greater stimulus area, more sense receptors, with varying degrees of sensitivity, are involved, yielding an increased probability of a lower threshold. Second, the visual system is composed of retinal elements that interact at the neural level. Finally, differential neural interactive effects in both the peripheral and foveal systems are presumably due to differences in anatomical convergence.

Research concerned with the nature and locus of onset-cessation differences has also produced certain generalizations. (1) RT, as a response measure for studying

onset-cessation differences, is a sensitive psychophysical index of visual behavior under specified conditions (Bartlett and MacLeod, 1954; Hufford, 1964; Pease and Sticht, 1965; Versteeg, 1970). (2) In the peripheral system, there are consistent differences, apparently dependent upon luminance, between onset and cessation RTs. The onset of stimulation elicits faster RTs than the cessation of stimulation (Pease and Sticht, 1965; Bartlett et al., 1968; Hansteen, 1968). (3) These onset-cessation RT differences appear to be independent of wavelength, but are presumably related to the different functions of the foveal and peripheral systems (Bartlett et al., 1968). (4) Experiments using the fovea as the locus of stimulation have produced no clear evidence concerning any differences in onset-cessation effects (Pease, manuscript in preparation; Versteeg, 1970). (5) Electrophysiological findings from single unit studies (Hartline, 1938; Granit, 1955; Kuffler, 1953; Wolbarsht, Wagner and MacNichol, 1961; Werblin and Dowling, 1969a and 1969b) have demonstrated that various retinal and higher order ganglia in the visual system respond selectively to the onset and cessation of stimulation. In addition, those who have studied onset-cessation differences employing RT as the response measure (Pease and Sticht, 1965; Versteeg, 1970) attribute these on-off differences to some type of

inhibitory and excitatory process which is dependent upon such stimulus characteristics as area, wavelength and luminance.

Several experiments have been conducted to study the effects of various parameters on the RT to the onset and cessation of visual stimulation. The present experiment was designed to assess the parameter of stimulus area on the RT to the onset and cessation of stimulation in the periphery. The effects of stimulus area upon simple RT to brief flashes are known (Hufford, 1964), but the effects of stimulus area upon RTs to cessation and the differences between onset and cessation RTs are not known. Additionally, no investigation of differential onset-cessation RT effects has had stimuli of very small retinal subtense (i.e., less than 20 minutes) in its design. The present investigation employs a large range of retinal stimulus areas--from small (1 minute) to large (110 minutes).

The periphery was chosen as the locus of stimulation for several reasons. (1) With low luminance levels, on-off differences in the periphery have been conclusively demonstrated (Pease and Sticht, 1965; Bartlett et al., 1968; Hansteen, 1968). (2) Neural interaction effects are potentially greater due to the greater anatomical convergence evidenced in the periphery. In the fovea the relation of outer nuclei (sense receptors) to ganglion

cells shows a ratio of 1.9 to 1. At approximately 20 degrees in the periphery, however, the ratio is approximately 42 to 1 (Polyak, 1957).

The luminance values of the stimulus source were suprathreshold, but sufficiently dim to avoid exciting the faster elements of the visual system. At high luminance levels onset-cessation differences attenuate and, indeed, show a tendency to reverse (Pease and Sticht, 1965). This suggests a more complex mechanism than simply the functioning of "on" and "off" and "on-off" fibers. Three luminance levels were employed in the present study. Experiment I was the high luminance condition. Experiment II incorporated two additional luminance levels, medium and low.

METHOD

Apparatus

The visual display board was a 65 by 108 cm black backdrop. Attached to it was a small 10 cm by 10 cm masonite box containing 16 argon bulbs (Type AR-3) which served as sources of illumination for the stimuli. The front of the visual display box was fitted with white, translucent plexiglass and was mounted on the backdrop so that the transmitting surface was flush with the front of the backdrop.

Directly in line with the visual display box was mounted a small, 5.35 cm metal frame in which field stops and neutral density filters were inserted. Field stops that restricted the area of stimulation were constructed from lightweight aluminum and sprayed flat black. They provided 10 different areas of stimulation: 1.0, 1.69, 2.84, 4.79, 8.08, 13.6, 23.0, 38.7, 65.2, and 110.0 in minutes of visual angle.

A fixation cross was placed 43 cm to the right of the stimulus display so that the light stimulated the peripheral retina 20 degrees from the fovea. The cross was also flush with the anterior of the backdrop and a neon bulb (Type NE-2H) served as its stimulus source.

A Heathkit regulated power supply (Model W-PS-4) was used to energize both the sources of illumination for the stimuli and the fixation cross. The luminance value of the stimulus source was adjusted with the aid of Wratten Neutral Density Filters mounted in "B" glass. In Experiment I, the highest luminance condition, the luminance value of the stimulus source, after such filtering, was 0.55 foot lamberts. In Experiment II the luminance values of the stimulus source were 0.05 ft L and 0.005 ft L respectively. The luminance value of the fixation cross was maintained at 0.65 ft L throughout both Experiments I and II. All luminance values were calibrated with a Gamma Scientific Log-Linear Photometer (Model #700M).

The S sat with his head in a head-rest stand and rested his right arm on a shelf and placed his middle finger on a microswitch key (B2ZBW80). The microswitch key was adjusted so as to be activated when depressed by a weight of 1/2 gram. Activation entailed a travel distance of 8 cm for the finger. Mounted on the floor to the S's right was a foot switch. RTs were recorded, in msec., on a Hewlett-Packard Digital Recorder (Model 560A) and were printed on a Hewlett-Packard Digital Printer (Model 560A).

Two Hunter Decade Interval Timers (Model 100C) controlled the foreperiods, described later. A white

noise generator with accompanying earphones masked auditory cues from the equipment.

Subjects

S's were three male students in attendance at The University of Arizona. Each S had emmetropic vision. All Ss had at least 25 hours of practice in this RT task prior to the tests of this study.

Procedure

Prior to each session, S dark adapted for 30 minutes. After this period, S adapted 5 additional minutes in the experimental room. With earphones on, S placed his head in a head rest which restricted vision to the right eye and ensured that steady posture and an appropriate viewing position were maintained.

S was seated 125 cm from the stimulus source and was instructed to fixate on the fixation cross. With the aid of the cross, S was able to prepare himself readily for the peripheral stimulus onset or cessation. To initiate a reaction, S held the microswitch lever against the metal stop and depressed and released the footswitch until he detected the appearance or disappearance of the stimulus. Then he removed his finger as rapidly as possible.

Each stimulus presentation was preceded by a variable foreperiod which was initiated by the footswitch. The

duration of the foreperiod was randomly varied by E from trial to trial, ranging from 2.5 secs to 4.5 secs, in 0.1 sec steps. For the onset condition the light appeared at the end of the foreperiod; in the cessation condition, the light was on and S reacted to its disappearance at the end of the foreperiod.

Prior to each session, each S was instructed to signal E if an RT was to be disqualified on the basis of some malfunction of the apparatus or some problem in fixation, such as blinking during the stimulus presentation, the finger slipping off the reaction key, etc. S was additionally advised to signal E if he felt some discomfort in the execution of an RT.

Experiment I

Three Ss reacted to the onset or cessation of visual stimuli of varying area. Ten stimulus areas were employed; they were, in minutes of visual angle: (1) 1.0, (2) 1.69, (3) 2.84, (4) 4.79, (5) 8.08, (6) 13.6, (7) 23.0, (8) 38.7, (9) 65.2, (10) 110.0. Luminance was held constant throughout the experiment at 0.55 ft L. The tests of this experiment comprised the high luminance condition.

Trials were administered in blocks of 10 presentations. Each block was preceded by a practice trial; also within each block a "catch" trial was randomly incorporated

in which the stimulus either appeared or in the case of the cessation condition, disappeared. This trial was inserted to maintain a high level of alertness on the part of S. Each block was identified by one of the 10 stimulus areas and either an onset or cessation condition. The order of each stimulus area as it was paired with the onset-cessation condition is given in Table 1.

Ten RTs were collected for 5 stimulus areas and onset/cessation condition in every session. Data were collected for 10 consecutive days and 50 RTs were obtained for each stimulus area/onset-cessation condition. Each session lasted approximately one and a half hours. A total of 1,000 RTs were executed by each S during the tests of this experiment.

Experiment II

Two Ss reacted to the onset or cessation of visual stimuli of varying area and luminance. In the medium luminance condition (0.05 ft L), the stimulus areas employed, in minutes of visual angle, were: (1) 1.69, (2) 2.84, (3) 4.79, (4) 4.79, (5) 8.08, (6) 13.6, (7) 23.0, (8) 38.7. In the low luminance condition (0.005 ft L) the same stimulus areas were used with the exception of the smallest area (1.69 min) which was not detectable.

Table 1. Experimental Design 1

Onset-cessation conditions are represented by capital letters (A for onset, B for cessations), and stimulus areas are represented by their value in minutes of visual angle.

Day	Conditions			
1	A	1.0, 1.69, 2.84, 4.79, 8.08;	B	8.08, 4.79, 2.84, 1.69, 1.0;
2	B	13.6, 23.0, 38.7, 65.2, 110.0;	A	110.0, 65.2, 38.7, 23.0, 13.6;
3	A	1.69, 2.84, 4.79, 8.08, 1.0;	B	4.79, 2.84, 1.69, 1.0, 8.08;
4	B	23.0, 38.7, 65.2, 110.0, 13.6;	A	65.2, 38.7, 23.0, 13.6, 110.0;
5	A	2.84, 4.79, 8.08, 1.0, 1.69;	B	2.84, 1.69, 1.0, 8.08, 4.79;
6	B	38.7, 65.2, 110.0, 13.6, 23.0;	A	38.7, 23.0, 13.6, 110.0, 65.2;
7	A	4.79, 8.08, 1.0, 1.69, 2.84;	B	1.69, 1.0, 8.08, 4.79, 2.84;
8	B	65.2, 110.0, 13.6, 23.0, 38.7;	A	23.0, 13.6, 110.0, 65.2, 38.7;
9	A	8.08, 1.0, 1.69, 2.84, 4.79;	B	1.0, 8.08, 4.79, 2.84, 1.69;
10	B	110.0, 65.2, 38.7, 23.0, 13.6;	A	13.6, 23.0, 38.7, 65.2, 110.0;

Trials were administered in blocks of 10 presentations, each block preceded by a practice trial and containing a "catch" trial, as described on page 27. Foreperiods were randomized, as before, within blocks. The order of each stimulus area as it was paired with the luminance and onset-cessation conditions is given in Table 2.

Ten RTs were collected for each of the 8 (7) stimulus areas, onset-cessation and luminance conditions. Data collection continued for 4 consecutive days and provided 40 RTs for each stimulus area/onset-cessation/luminance conditions. An experimental session lasted for 2 hours. A total of 1,040 RTs were executed by each S during the tests of this second experiment.

Table 2. Experimental Design 2

Onset-cessation conditions are represented by capital letters (A for onset, B for cessation), luminance conditions are represented by Roman Numerals (II for medium, III for low) and stimulus areas are represented by their value in minutes of visual angle.

Day	Conditions	
1	A II 1.69, 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;	A III 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;
	B II 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;	B II 1.69, 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;
2	B II 38.7, 23.0, 13.6, 8.08, 4.79, 2.84, 1.69;	B III 38.7, 23.0, 13.6, 8.08, 4.79, 2.84;
	A III 38.7, 23.0, 13.6, 8.08, 4.79, 2.84;	A II 38.7, 23.0, 13.6, 8.08, 4.79, 2.84, 1.69;
3	A II 1.69, 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;	A III 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;
	B III 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;	B II 1.69, 2.84, 4.79, 8.08, 13.6, 23.0, 38.7;

Table 2. (Continued)

Day	Conditions		
4	B II	38.7, 23.0, 13.6, 8.08, 4.79, 2.84, 1.69;	B III 38.7, 23.0, 13.6, 8.08, 4.79, 2.84;
	A III	38.7, 23.0, 13.6, 8.08, 4.79, 2.84;	A II 38.7, 23.0, 13.6, 8.08, 4.79, 2.84, 1.69;

RESULTS

Tables 3 and 4 show the means and standard deviations for each of the experimental conditions for each S. These data demonstrate that for all Ss there is great consistency in responding (i.e., low RT variability) and further suggest that each S was responding at his asymptotic level. The only apparent exception to this patterned consistency occurred with the employment of the smallest stimulus areas. This was the case in both Experiment I and II.

A treatment-by-treatment-by-subjects analysis of variance (ANOVA) was performed on the data of Experiment I. The effects of stimulus area and stimulus onset-cessation, and stimulus area/onset-cessation interaction were tested. Table 5 presents the critical values of the analysis of variance.

The main effects of stimulus area and stimulus onset-cessation were highly significant. The effect of interaction of the two parameters was also statistically significant.

Figures 1, 2, and 3 present mean RTs to onset and to cessation plotted as a function of stimulus area for each of the three Ss.

Table 3. Means and Standard Deviations for Experiment I for Each Subject, in Milliseconds

Subject	Condition	Index	Stimulus Area (in minutes of visual angle) 1.0	1.69	2.84	4.79	8.08	13.6	23.0	38.7	65.2	110.0
B	On	Mean	494	387	370	357	343	328	323	311	307	296
		S.D.	75	23	11	14	26	9	10	12	12	10
	Off	Mean	512	447	423	424	408	387	371	349	325	313
		S.D.	37	20	8	13	14	43	13	14	7	18
G	On	Mean	455	360	337	321	313	307	292	288	273	265
		S.D.	30	10	8	14	4	15	16	13	13	9
	Off	Mean	462	432	400	381	367	358	338	321	294	282
		S.D.	31	20	31	19	9	7	20	20	18	20
A	On	Mean	506	346	315	302	288	280	277	262	252	252
		S.D.	80	13	5	7	6	6	12	5	5	11
	Off	Mean	572	381	357	357	341	316	304	278	270	257
		S.D.	38	20	8	16	10	16	12	3	15	5

Table 4. Means and Standard Deviations for Experiment II for Each Subject, in Milliseconds

Subject	Condition	Index	Stimulus Area (in minutes of visual angle) 1.69	2.84	4.79	8.08	13.6	23.0	38.7
		Medium Luminance (0.05 Foot Lambert)							
G	On	Mean	397	335	304	292	265	258	255
		S.D.	71	27	21	20	15	23	18
	Off	Mean	398	371	356	347	342	327	317
		S.D.	17	38	20	20	20	17	26
A	On	Mean	382	335	309	296	283	275	272
		S.D.	25	10	9	11	10	19	6
	Off	Mean	434	373	377	371	334	326	317
		S.D.	12	6	20	10	8	13	15
		Low Luminance (0.005 Foot Lambert)							
G	On	Mean		504	425	352	339	314	307
		S.D.		58	21	19	33	12	23
	Off	Mean		579	449	410	375	361	352
		S.D.		51	25	10	22	12	22
A	On	Mean		452	378	339	327	305	296
		S.D.		23	19	7	8	9	14
	Off	Mean		439	410	384	379	367	373
		S.D.		9	19	36	19	14	13

Table 5. Analysis of Variance for Reaction Time Data for Experiment I

Source	df	MS	F	P
Stimulus Area (A)	9	25,143.974	35.362	<.005
Onset-Cessation (B)	1	24,806.701	220.543	<.001
Subjects (S)	2	11,933.151		
AXB	9	431.411	4.408	<.005
AXS	2	112.541		
BXS	18	711.614		
AXBXS	18	97.858		

Inspection of these curves reveals, in general, that as stimulus area increased from 1 minute of visual angle to 110 minutes, RT for both stimulus onset and cessation decreased. RT decreased most dramatically from the 1 minute stimulus area to the 1.69 minute area. Onset-cessation RT differences gradually decreased as a function of increasing stimulus area up to the largest areas (65.2 and 11.0 min) where they became virtually identical. Figure 4 presents curves based on the pooled mean RT data for all Ss for Experiment I.

Experiment II was designed so that the additional variable of luminance on stimulus area/onset-cessation

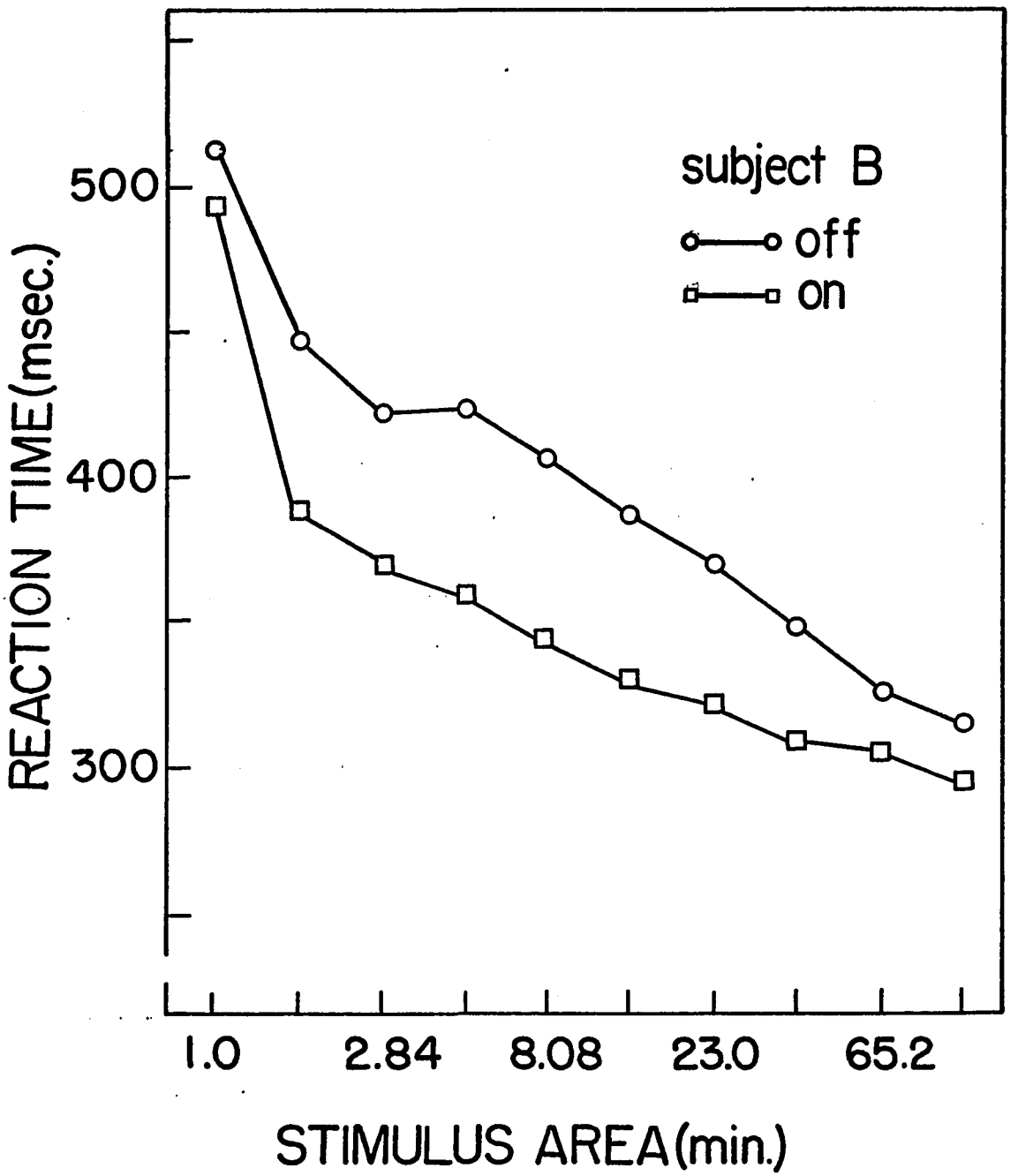

Figure 1. Mean reaction time as a function of stimulus area in minutes of visual angle for the high luminance condition for Subject B, in milliseconds.

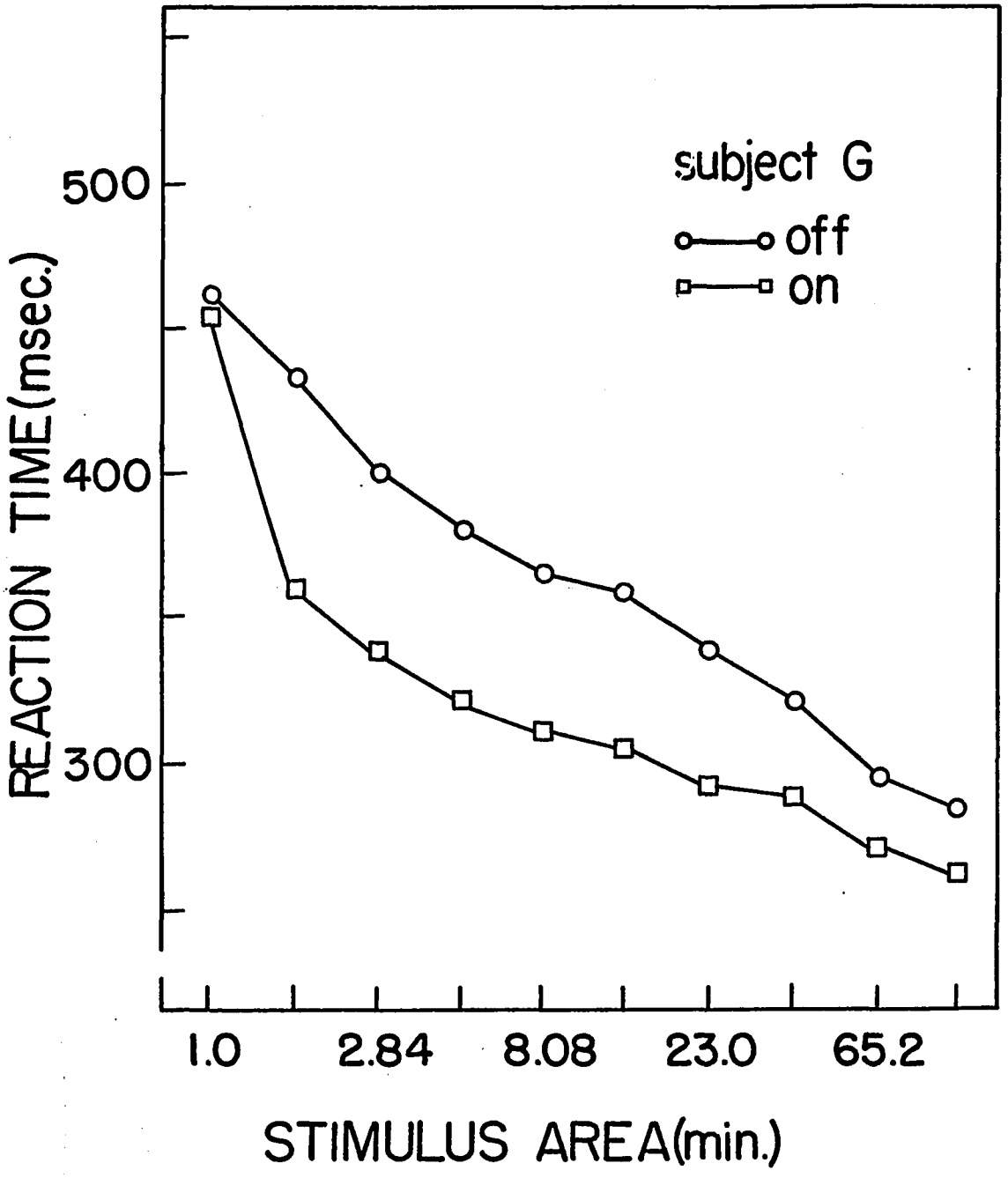

Figure 2. Mean reaction time as a function of stimulus area in minutes of visual angle for the high luminance condition for Subject G, in milliseconds.

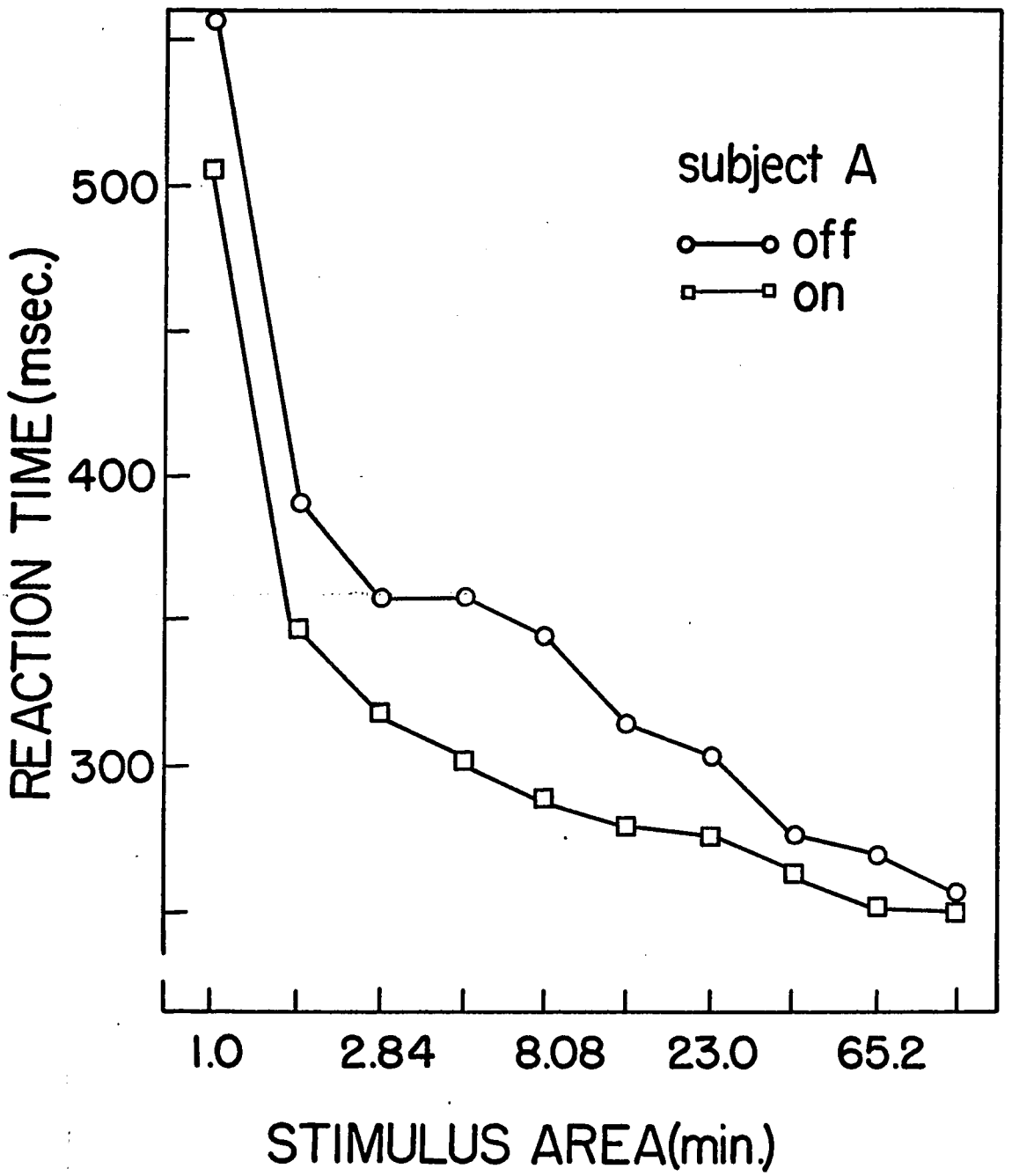

Figure 3. Mean reaction time as a function of stimulus area in minutes of visual angle for the high luminance condition for Subject A, in milliseconds.

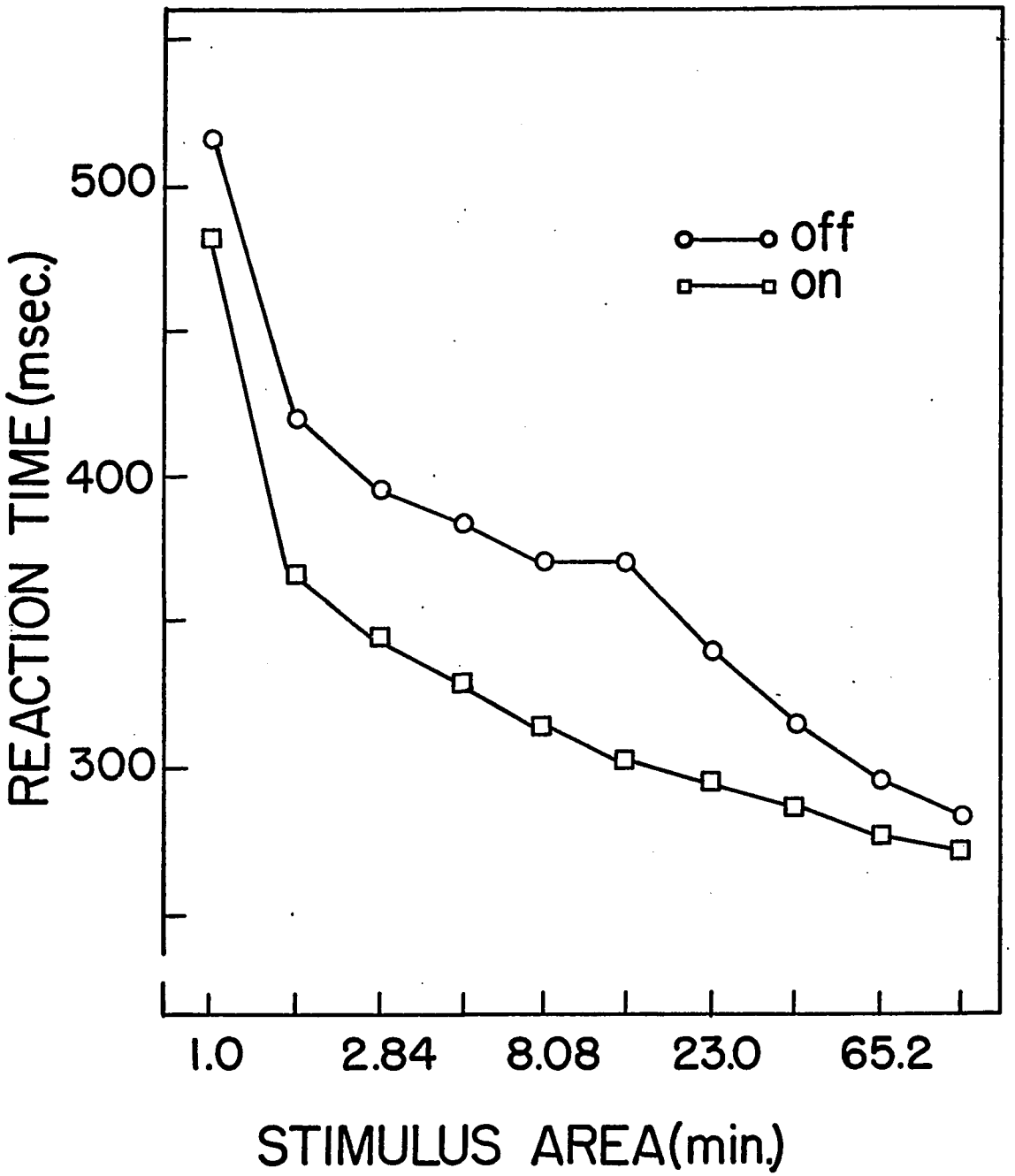

Figure 4. The means of the mean reaction times as functions of stimulus area in minutes of visual angle for the high luminance condition for all subjects, in milliseconds.

could be ascertained. Two luminance levels were employed; .05 ft L (medium luminance condition) and .005 ft L (low luminance condition). Table 4 presents the means and standard deviations for both luminance conditions of Experiment II for both Ss.

The F ratio for the analysis of variance was tested at both the $P < 0.05$ and $P < 0.01$ per cent levels of confidence. The main effects of stimulus area, stimulus onset-cessation, and luminance were tested. In addition, the area onset-cessation, luminance onset-cessation, and area luminance interactions were tested. Table 6 presents the critical values of the analysis of variance.

The main effects of stimulus area and onset-cessation were significant at the $P < 0,005$ and $P < 0.025$ per cent levels respectively. The main effect of luminance was not significant. Furthermore, none of the interaction effects were significant.

Figures 5 and 6 present mean onset and cessation RTs plotted as a function of stimulus area for the medium luminance condition for both Ss.

Inspection of these curves indicates that the differences between RT to onset and RT to cessation stimuli increased when luminance is reduced (cf. Figure 4).

Table 6. Analysis of Variance for Reaction Time Data for Experiment II

Source	df	MS	F	P
Area (A)	5	14,743.231	24.204	< .005
On-Off (B)	1	29,700.754	1,391.785	< .025
Luminance (C)	1	14,743.231	68.357	NS*
Subjects (S)	1			
AXB	5	187.954	.341	NS
AXC	5	2,983.637	3.398	NS
BXC	1	271.141	17.013	NS
AXBXC	5	84.275	.673	NS

*Not significant

Figures 7 and 8 give mean onset and cessation RTs plotted as a function of stimulus area for the low luminance condition for both Ss.

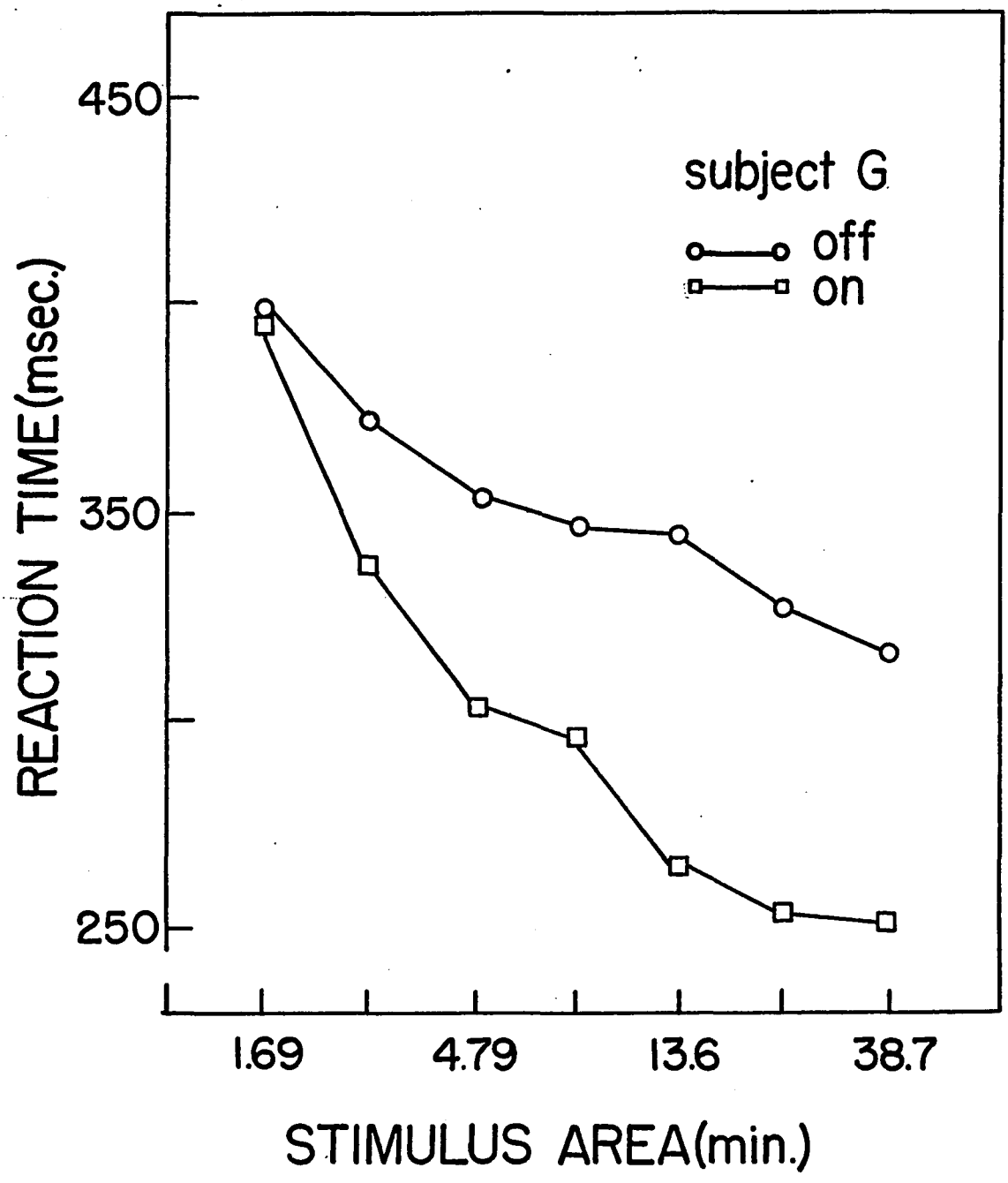

Figure 5. Mean reaction time as a function of stimulus area in minutes of visual angle for the medium luminance condition for Subject G, in milliseconds.

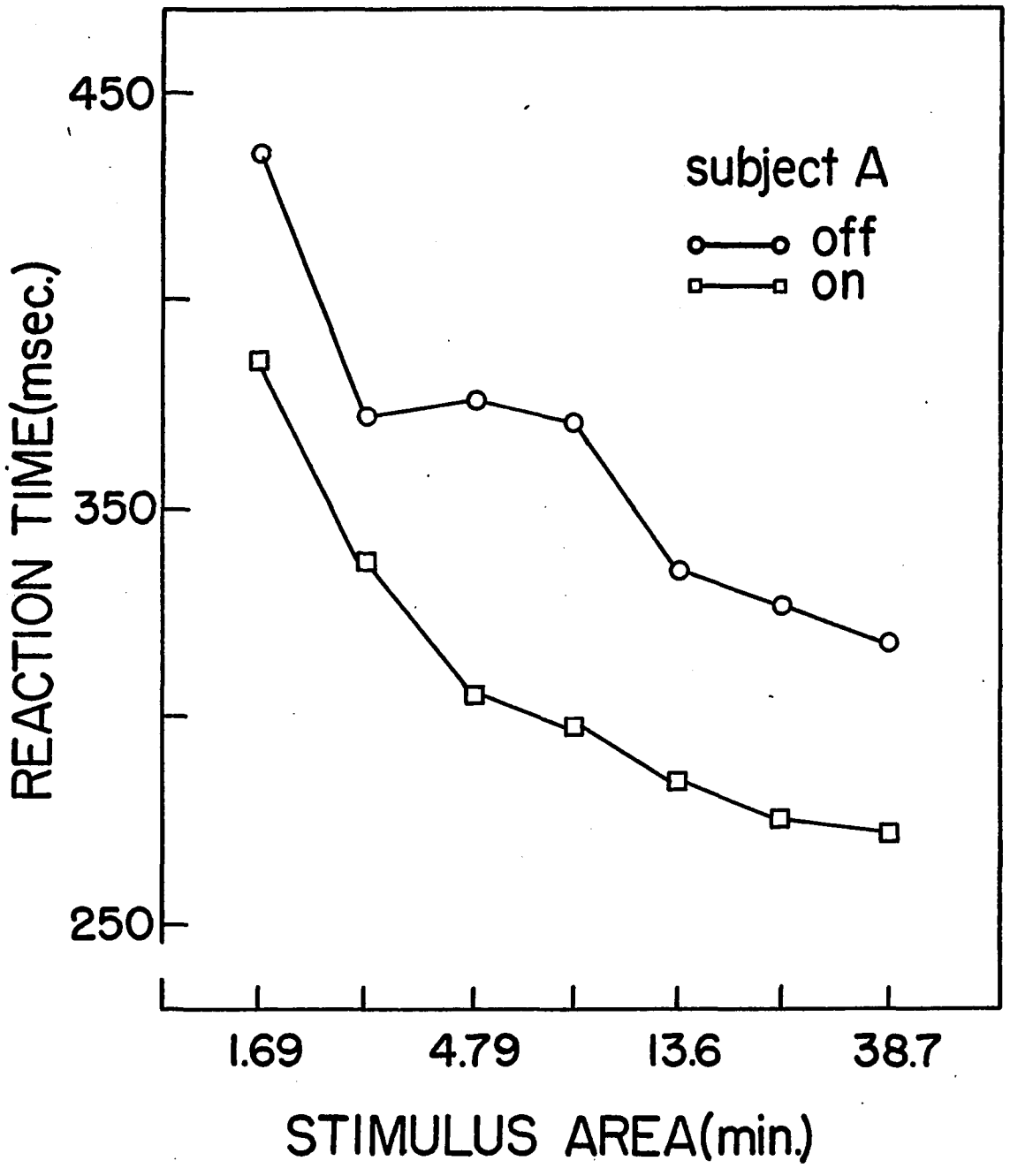

Figure 6. Mean reaction times as a function of stimulus area in minutes of visual angle for the medium luminance condition for Subject A, in milliseconds.

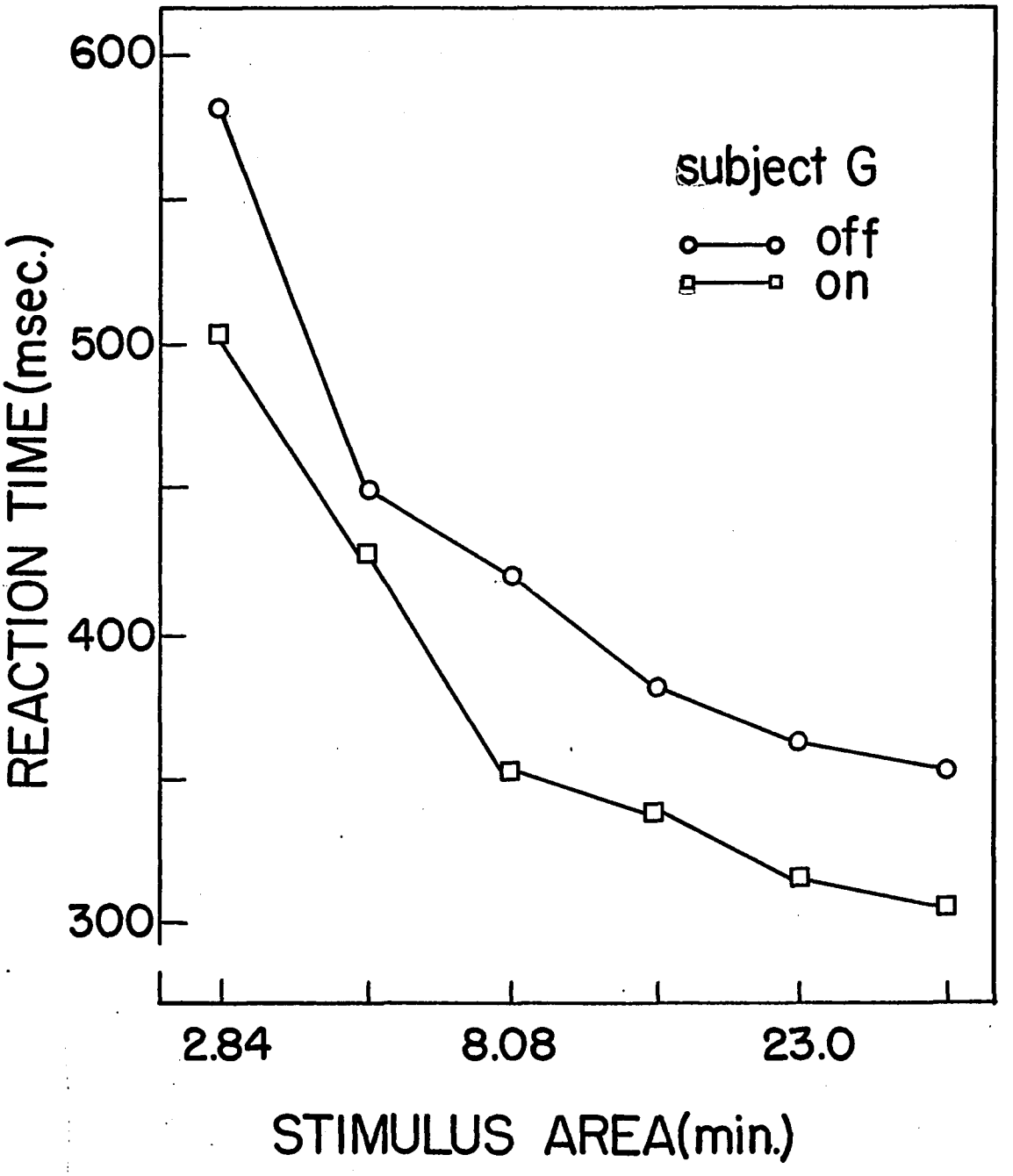

Figure 7. Mean reaction times as a function of stimulus area in minutes of visual angle for the low luminance condition for Subject G, in milliseconds.

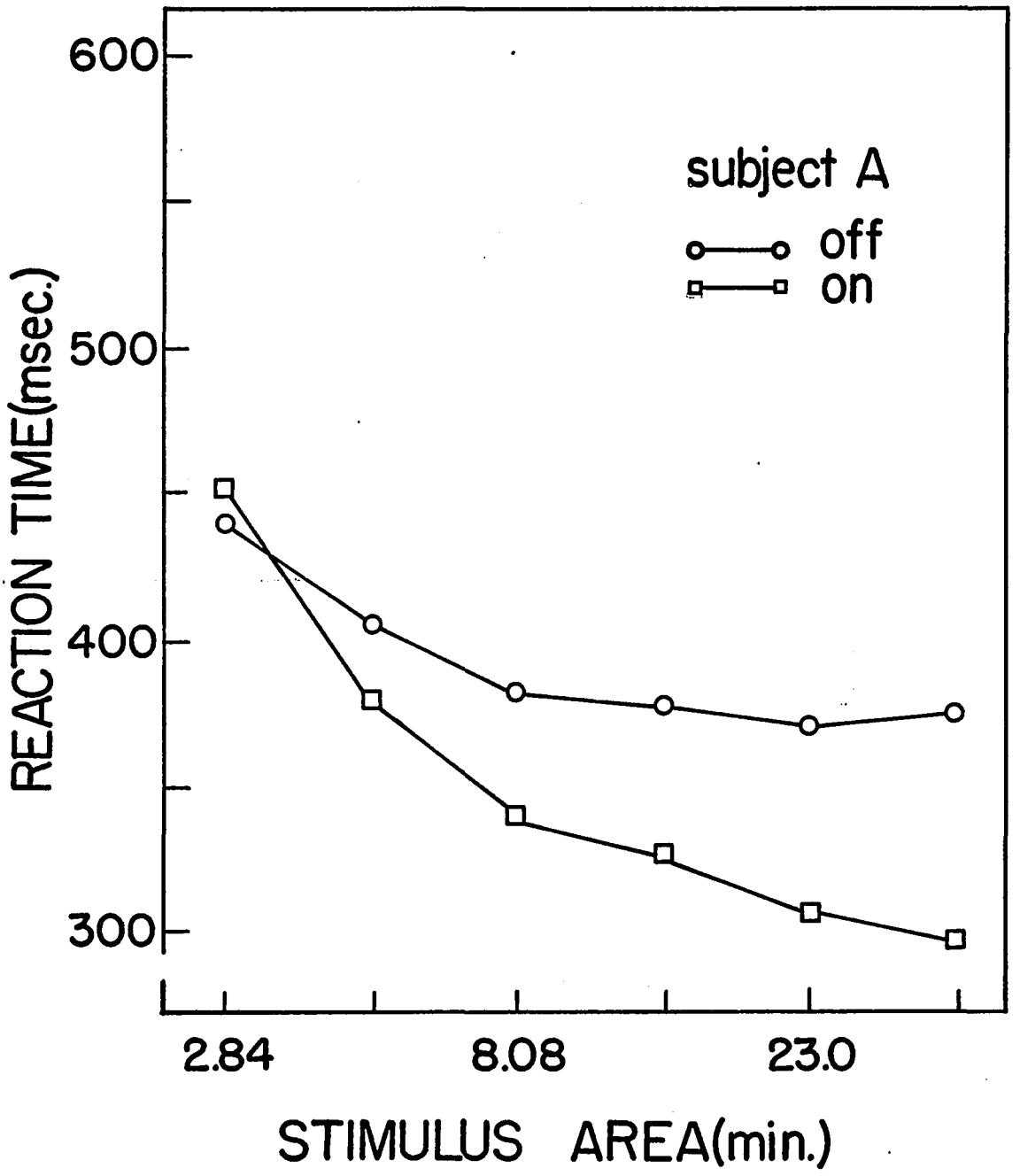

Figure 8. Mean reaction times as a function of stimulus area in minutes of visual angle for the low luminance condition for Subject A, in milliseconds.

DISCUSSION

In support of earlier investigations (Pease and Sticht, 1965; Bartlett, Sticht, and Pease, 1968; Hansteen, 1968), the several conditions of this experiment demonstrated that RT to the onset of visual stimulation is faster than the RT to the cessation of stimulation in the peripheral system. All RTs decreased as luminance increased--again consistent with the historical literature. However, the onset-cessation differences did not dissipate as a function of increased luminance. Inspection of the appropriate graphs (Figures 1-8) reveals these onset-cessation RT differences to be present in the high luminance conditions as with the medium and low luminance levels. But no high levels were, of course, tested.

Pease and Sticht (1965), Bartlett et al. (1968), and Hansteen (1968), among others, have reported that onset-cessation differences tend to attenuate as a function of increased luminance. Luminance did not have a statistically significant effect on RT to the onset and cessation of stimulation in the present study. Upon cursory examination the data of the present investigation may appear to conflict with those of the historical literature; however, methodological differences adequately

account for the disparity. The aforementioned investigators typically employed a wide range of luminance levels--from very high to very low (e.g., Pease and Sticht, 1965; 31,400 ml, 314 ml, 3.14 ml, and 1.98 ml). This study had a rather restricted range of luminance values (i.e., 0.55 ft L, 0.05 ft L, and 0.005 ft L). Additionally, the effect of luminance could only be ascertained from the data of Experiment II. It appears certain that luminance would have a critical effect on the difference between onset-cessation RTs if relatively high luminance stimuli were employed. Exploratory data gathered previous to the tests of this experiment support this.

The main effect of stimulus area was statistically significant in both Experiments I and II. As stimulus area increased reactions to both the onset and cessation of stimulation were faster. With the employment of the smallest areas, for all luminance conditions, RTs were very large and somewhat unreliable (cf. Tables 3, 4). RT variability, indicated by the large standard deviations, to these small areas was presumably due to problems of detection and it is unlikely that any representative sampling of specific units in the receptor field was tapped. Reactions to these smallest stimulus areas showed little consistent onset-cessation differences.

This lack of onset-cessation differentiation is also evident with the employment of the largest areas (65.0 and 110.0 min) in the high luminance condition (Experiment I). This loss of differentiation may have been due to the fact that with larger stimulus areas a greater number of units with varying degrees of sensitivity are stimulated.

In any event, RTs from these initial small areas and reactions from the largest stimulus areas account for the significant interaction of stimulus area/onset-cessation in Experiment I.

The data of the several conditions tested in this study suggest an interesting relationship between luminance and onset-cessation RTs. Apparently as luminance decreased, the point of maximal onset-cessation differentiation increased in a fairly regular fashion. In Experiment I the point of optimal onset-cessation differentiation was reached at approximately 5 min. In the medium luminance condition of Experiment II, luminance was reduced by 1 log unit and consequently the point of maximal onset-cessation differentiation was reached at approximately 10-13 minutes. When luminance was reduced by 2 log units from the high luminance condition, maximal onset-cessation differences were noted at about 20 minutes.

In addition to this suggested relationship between luminance and onset-cessation RTs, this study revealed that onset-cessation RT differences obtained (excepting the smallest stimulus area) although the area of retinal stimulation was extremely small. Typically, the origin of these on-off retinal responses is attributed to the integrated effects of excitatory and inhibitory influences exerted over retinal structures interposed between the ganglion cells and the photoreceptors, rather than to the special properties of the photoreceptors themselves. Most experiments on retinal ganglion cells, the third-order neurons, provide evidence to support the view that complex patterns of response observed in these cells result from the integrative action of the retinal network. Hartline (1938) suggested that the integrative response resulting from the stimulation of different portions of the receptive field (the ganglion cell with all its converging fibers) is not a mere summation of identical influences converging on a final common pathway because the influences from neighboring regions often oppose one another.

Barlow, Fitzhugh, and Kuffler's (1957) experimental results support the view that the different parts of a receptive field not only share in common the final pathway through the ganglion cell, but suggest that they also probably share numerous intermediate structures as well.

The experiments, reported herein, do not negate the possibility that the receptors may possess special properties, which allow for differential responses to the onset-cessation stimuli. Indeed the data suggest that the photoreceptors should not be ruled out as partially responsible for these changes in sensitivity.

The results of the present study provide no conclusive evidence with respect to the question of the relative contributions of the photoreceptors and the neural structures interposing between the photoreceptors and the ganglion cell in the generation of on-off responses. It may be noted that with extremely small retinal areas stimulated--significant on-off differences emerge. With the stimulation of small retinal areas (e.g., 1.69 min) neural interactions among the convering fibers in the receptive field are severely attenuated. If the on-off response to retinal stimulation is due solely to the interplay of the interposing neural structures, this interaction process is highly efficient and requires the activation of only a small number of photoreceptors and second-order neurons.

SUMMARY

Visual RT data were recorded to the onset and cessation of stimulation varying in area and luminance. RT became faster as a function of increased area. The well established luminance function was found where RT becomes longer as luminance is decreased. This was the case for both onset and cessation reactions.

RTs to the onset of visual stimulation in the periphery were significantly faster than to the cessation of stimulation.

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