

## The Effect of Two Wave-Lengths of Light upon the Same Retinal Element.

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The problem raised in this work concerns the interaction of two lights of different wave-lengths which simultaneously stimulate a retinal element which has been investigated in the eye of the decerebrate cat by means of the micro-electrode technique. Only large, well isolated spikes have been used and the animal has been dark adapted for not less than two hours with the micro-electrode inserted. This is our standard technique (see *e. g.* GRANIT, 1947).

In a way then we are dealing with the effects of colour mixture upon a single element. But the aim of such work on animals must be stated in terms of wave-length and impulse activity: here the question can be put very precisely with the aid of the schematic figure 1. We know that an element in the cat's eye may be excited by receptors of different colour sensitivities (GRANIT 1945, 1948, GRANIT and TANSLEY 1948, GERNANDT 1947, 1949). If two receptors overlap in spectral sensitivity in the manner illustrated by fig. 1 and we are stimulating by a single wave-length in the region of the

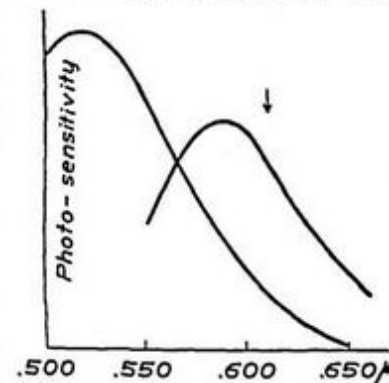


Fig. 1. Diagram showing the overlapping hypothetical absorption curves of two photosensitive substances in the retina (see text).

arrow in the figure, do we then always obtain merely a photochemical summation of the effects due to the addition of the two ordinates in the figure or is it, for instance, possible for either of the two responses so to 'canalize' the path that the other is wholly or partially suppressed?

The situation may be compared with the reflex effects of two different nerves upon the same motoneurone. When the impulses from these two sources enter the motoneurone, what happens? Is the output frequency of the motoneurone augmented or diminished? The photochemical overlap in the equivalent retinal experiment is a complication that always means addition of energy to both receptors but which can be minimized by selecting wave-lengths rather far apart.

The significance of possessing decisive information on this point is readily understood. Such information has been obtained in this work.

### The Technical Problem.

In order to give differentially sensitive receptors a good chance of interacting it is necessary to use supra-threshold stimuli which means that spike frequencies must be counted at onset and cessation of illumination. This being so it becomes imperative to know the result immediately both to be able to plan the experiment according to the properties of the element isolated and in order to find out whether the frequencies per unit time are stable enough for quantitative work. For these reasons automatic frequency counting was introduced and combined with an electronic shutter limiting the counting time to a duration of 1 or 2 seconds after respectively onset and cessation of a 3 or 5 sec. illumination. The total number of impulses during the counting period was directly and immediately read off during the experiment. Depending upon the stability of the preparation, from 3 to 8 illuminations were considered necessary to establish the count with an accuracy of within 10 %. If, owing to respiratory movements or other changes, the spike varied too much to render an accuracy of this order possible the result was rejected.

In the first version of this apparatus the calculator of a Geiger-Müller counter was connected to the condenser coupled amplifier from the micro-electrode over a relatively simple electronic shutter limiting the duration of the counting period. Later a clock-work counter, designed by Mr. B. AURELIUS of the Nobel Institute for Physics, was used. This ingenious mechanical device can easily follow up to 300 impulses/per sec. which proved satisfactory. An electronic delay and shutter, built by Mr. K. O. DONNER and E. ÅSTRÖM in this laboratory, was started by the amplified current of a photocell, placed in a de-

flected part of the stimulus beam of our Wright spectrometer (WRIGHT, 1946). Onset and cessation of illumination were led to separate channels of electronic delays and shutters adjustable so that the spikes at respectively 'on' and 'off' could be counted by two separate Aurelius clock-works delayed to any time after the action of the photocell, from about a few milliseconds to 5 seconds, and counting for durations which also could be selected within fairly wide limits. This convenient apparatus was necessary for some work of DONNER (1949) tracing time-frequency curves in detail. In my experiments it was set without use of the delay for instantaneous counting during 1 sec. after respectively onset and cessation of illumination, the eye in this case being exposed to the light only for 3 sec.

With all the wave-lengths and the full intensity range of the spectrum available the number of possible combinations of stimuli is legion. By means of the Wright colorimeter 2—3 wave-lengths can be applied singly or together onto the same retinal area in proportions selected by calibrated wedges. Clearly it becomes a most fundamental question how to select the particular stimuli and intensities to be tested, singly and together, in order to study the problem formulated in the introduction.

### The Theoretical Problem.

Since the spectral distribution of sensitivity of all elements, so far isolated in dark adapted retinae of cats (GRANIT, 1947) shows the influence of visual purple (VP) it is necessary to know the VP-curve of this retina with a high degree of accuracy. It has been shown that the pure on-elements are likely to be the purest VP-elements (GRANIT, 1947, GRANIT and TANSLEY, 1948, DONNER and GRANIT, 1949) whilst a considerable number of the on/off-elements, despite full dark-adaptation, have humps deviating from the smooth VP-distribution of sensitivity. The pure scotopic dominator which is the VP-curve of the on-elements, needed for this work, was carefully measured by DONNER and GRANIT (1949). This curve is slightly narrower than the VP-curve of extracts in solution. In comparing the effects of any two wave-lengths in the dark adapted eye we can measure the ordinates of energy of the two stimuli in the visual purple units obtained from the curve of DONNER and GRANIT (here called DG-ordinates) and thus know where we are in terms of the dominating photochemical substance in the dark adapted eye. The DG-ordinates thus represent reciprocals of the DG-curve, the latter being a plot of sensitivity (= reciprocal of energy) whilst for this work we have to return to the corresponding energy values in the spectrum.

If two wave-lengths are tested separately on a pure on-element and both are adjusted to equal DG-ordinates of energy, their responses, in terms of spike frequency, should be equal at all intensity levels if the receptors of the element concerned are pure visual purple receptors (also if other types of receptors are present but too few to influence the response or if actively inhibited). If this rule holds good, it also means that on/off-elements which behave in this fashion are dominated by visual purple to such an extent that they cannot be used to solve the problem we wish to solve.

*Experiment 1.* Inasmuch as one desires to use spike frequency as an index of colour effects it is imperative to know whether the statement just made is true or not. It has been repeatedly tested and found to hold good, in fact, I have never seen any deviations from this rule for pure on-elements. Now the range of spike frequencies in relation to stimulus intensity is, on an average, smaller for the on-elements than for the on/off-elements and this makes the test in experiment 1 less stringent than otherwise would be the case.

*Experiment 2.* This showed that the rule, tested in experiment 1, also held good for several on/off-elements. The test was generally carried out in either or both of two ways: (a) with a neutral filter interposed the frequencies were counted in a number of wave-lengths for equal DG-ordinates of energy. Then the filter was removed or further filters added. Again the rule was found to hold good both for 'on' or 'off' frequencies at all the wave-lengths selected. (b) two wave-lengths in the spectrum, generally  $0.520 \mu$  green and  $0.640 \mu$  red, were adjusted to equal DG-values, some multiple of unity for which the spike frequencies were identical on the counter. Then, adding the red and green and, simultaneously dividing the intensity for each of them by 2 so that the energy sum of the two remained equal to that of the individual stimuli, the frequencies should be constant. Several on/off-elements actually behaved in this way. The spike frequency for the sum of the halves was found equal to the spike frequency of the individual stimuli when our rule held good. This is a very sensitive test and therefore it became the standard method by means of which those on/off-elements were weeded out that to all appearance behaved according to the rule, *i. e.* as if they had been pure on-elements merely reflecting the properties of the homogeneous visual purple channel of reception.

Since full understanding of this argument is essential let us repeat it in slightly different terms: if only VP-receptors are involved the superposition of red and green (equated in energy for visual purple), each at half their former energy levels, will produce exactly the same photochemical effect as either full light alone. Therefore the response should be unchanged by this procedure. The on/off-elements that behaved in this way thus declared themselves to be unsuitable for the present investigation.

*Conclusion:* For pure on-elements and a considerable number of on/off-elements the curves relating impulse frequency to log stimulus intensity in the fully dark adapted eye must be independent of wave-length, provided that such curves are plotted in DG-units representing the visual purple distribution of sensitivity. This conclusion is simply a corollary of the experiments 1 and 2. This corollary, besides, was sometimes directly tested by plotting the appropriate curves from the data. But experiment 2 (b) gave the same result far more quickly and was just as reliable if a few more wave-lengths were added from the other end of the spectrum. It did not prove necessary to measure a large number of curves in different wave-lengths.

The DG-ordinates of energy are thus accurate enough to represent stimulation of an element by those receptors that contain visual purple. It is, of course, impossible to neglect this highly sensitive photochemical substance and we therefore have to proceed along the course laid out above which implied elaboration of methods by means of which the VP-contribution to the stimulus frequency could be assessed. The safest way is clearly to make the two stimuli equal in terms of DG-ordinates knowing, as we do, from the experiments just reported, that if the frequency responses to these wave-lengths then are equal they will remain equal at all levels of intensity available in the spectrum.

If the responses differ in spike frequency for two stimuli of equal DG-ordinates then something else has been stimulated besides visual purple and the experiment becomes a great deal more interesting. To these cases we shall now turn our attention. All of them refer to on/off-elements.

### Spike Frequency and Stimulus Intensity.

The spike frequency-log intensity curves of the on/off-element in fig. 2 are plotted on DG-energy units as abscissae for  $0.620 \mu$

(red) and  $0.520 \mu$  (green), on-components in full, off-components in broken lines and it is clear that it is impossible to find a red on/off-response identical with a green one for any point on the abscissa barring the extremes. By sliding a vertically placed ruler along the abscissa this will immediately become evident. Here then is a case in which, despite equal DG-energy values, one

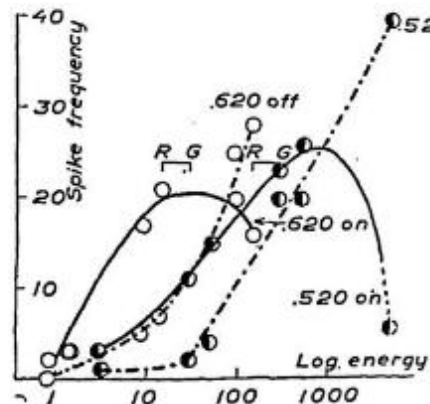


Fig. 2. Spike frequency-log intensity curves for on- and off-components of a red  $0.620 \mu$  and a green  $0.520 \mu$  stimulus. The logarithmic abscissae are in terms of multiples of energy necessary for visual purple threshold response.

The two places marked R and G in the middle of the figure show the energy levels at which the red and green were combined for simultaneous stimulation. The energies are obtained by projecting the vertical lines for R and G on to the abscissa.

wave-lengths and that, in general, the types of curve are similar though not superimposable by appropriate shifts along the abscissa. This, too, is characteristic of the cat's retina. Such curves can only be measured accurately by alternating between the wave-lengths selected so as to maintain the retina in the same state for the wave-lengths to be compared. Actually the curves illustrated are of a considerable degree of accuracy, 112 counts, representing 56 illuminations (counts doubled because of 'on' and 'off') averaged into 24 values. The high intensity inhibition for the green 'on' was observed on the screen and found to be almost complete but it could not be measured accurately because a high-threshold spike from another element with smaller spikes interfered in the counting machine. (Both loudspeaker

Table 1.

Energy ratio R/B	Red alone	Blue alone	Red + Blue
1400 .....	- 14	- 5	- 13
270 .....	- 8	- 6	- 10
180 .....	- 4	- 6	- 8
71 .....	- 3	- 6	- 9

and screen were always used to control the isolation of the spike as well as the response. Thus the spikes were both seen, heard and counted.)

The combinations R(ed) and G(reen), marked in the figure, were selected for simultaneous stimulation, the red being about one half the energy of the green. At the lower intensity-level red gave 21-7 for respectively 'on' and 'off', green 11-2. The sum of R + G gave 19-9. At the higher intensity level the red gave 16-28, the green 23-20. The sum R + G was 16-31. The interesting point here is that at the lower level of intensity, the absolute frequency of the red was higher at 'on' than that of the green and, vice versa, lower at the higher level of intensity. It is therefore clear that it was not the higher frequency as such that, as it were, took charge of the element when R and G were added but the *properties of the 'red'* that dominated over the *properties of the 'green'*. In both cases the "red reaction" determined the response of the element in the sum, both at 'on' and 'off'. It succeeded, so to speak, in dominating the path. The green was then made 150 times stronger than the red and now succeeded in impressing its value upon the sum.

It is difficult to evaluate inhibition quantitatively. It can only be done in cases where there is a high spontaneous frequency depressed by the light. This depression can be measured and the minus sign, used below, means the number of impulses subtracted per unit time from the spontaneous frequency owing to the inhibitory effect of the stimulus. Above is a case combining  $0.650 \mu$  (Red) and  $0.460 \mu$  (Blue) in which the latter was kept at a constant intensity and the former decreased in steps. Table 1 presents to the left the energy ratios Red/Blue. It is a case of inhibition of the on-component of an on/off-element. The spontaneous frequency was 16 per sec. and the decrease of this rhythm at the onset of illumination is tabulated.

The blue light is always kept the same, and the inhibition due

to it varies but little. As the red is weakened so the inhibition by it alone weakens but that of the sum  $R + B$  is practically constant in the last three horizontal rows. In these the inhibition for the sum exceeds that of the singles. Only the strongest red of the uppermost row was of the relative order of magnitude necessitated by the DG-scale. In all the other rows the red was far too weak relative to the blue so that red receptors must have contributed heavily to the element, in every case reinforcing the inhibition of the blue.

One generally tries to avoid the elements with heavy spontaneous frequency because the rhythm rarely keeps constant and for this reason I have comparatively few cases in which inhibition could be expressed quantitatively. I shall take another very striking case of inhibition of the on-component. Wave-length  $0.640 \mu$  (R) on the DG-ordinates gave an inhibition of  $-20$ . When pitted against the equivalent DG-values for  $0.420$ ,  $0.500$  and  $0.520 \mu$  the inhibition at "on" were respectively  $-16$ ,  $-14$  and  $-14$  whilst each of the three individual stimuli had given respectively  $-5$ ,  $+5$  and  $-3$ , all on the DG-ordinates. There was a progressive change in this experiment because  $0.520 \mu$  later gave  $+5$ . A number of other intermediate wave-lengths also gave values of that order. All these, when pitted against each other, gave values around zero or slightly positive values suggesting VP-dominance from  $0.600$  to  $0.420 \mu$ . But the extreme red in  $0.640 \mu$  always had this remarkably strong inhibitory component, clearly due to special receptors, that maintained their preponderance in any combination.

### Dominant Wave-Lengths in Mixtures.

*The theoretical problem.* I shall now proceed to another type of experiment in which all spectral stimuli always are at the same constant multiple of the visual purple curve in DG-units. For all wave-lengths the wedges are set for the DG-curve and the spectrum is used without additional filters. This means, about 200—500 times the threshold strength depending upon the sensitivity of the element. For the sum of red and green we use the half filter in the beam so as to keep the energy sum constant in terms of visual purple. It is clear that red and green enter into the energy sum, each with their half values, because of the half-filter interposed. If there is complete mixture the mean value might be obtained. If either of the two dominates in the response the value of the dominant wave-length at half intensity will show up unless the spectral curves of the substances represented in the two wave-lengths have a zone of overlap adding something to the

Table 2.

	G, full	G, half	R, full	R, half	Half R + G
On—off .....	27—16	21—9	25—30	21—16	23—18
Off/on-ratio .....	0.6	0.4	1.2	0.8	0.8

effect of the dominant wave-length. In any case it is clear that for a detailed analysis it is necessary to know the full values of the singles, their half values and the sum of the latter. With only visual purple present the sum of the half values will equal either full value and this is the situation already discussed above (Experiment 2) on p. 284.

*Experiment.* These schematic deductions are easily translated into an experiment which, accordingly, consists in determining the spike frequencies for  $R = 1$ ,  $R/2$ ,  $G = 1$ ,  $G/2$  and  $\frac{R + G}{2}$ . Above are tabulated the results of an actual experiment with R ( $0.640 \mu$ ) and G ( $0.520 \mu$ ), on an average 7.4 counts (= illuminations) for each figure. Counting period is 1 sec.

Within the limits of accuracy obtainable in such experiments it is clear that half the sum of the red and the green has reproduced the half-red value. The off/on-ratios show this very strikingly. They are identical and twice the value of the green off/on-ratio for the half value.

If the red path in this manner 'canalizes' the element when pitted against some other path it is often possible to stimulate the dominant path by some fraction of the energy required for the DG-ordinates and yet to obtain dominance in the sum. In another element the red ( $0.640 \mu$ ) full value for on-off, counted during 1 sec., was 44—37, its half value 39—32. The green ( $0.520 \mu$ ) full value 42—24, its half value 41—15 and the sum of the half values 44—33. There were on an average, 7.4 counts for each value and the accuracy was about 10 %. The on-component thus did not change much and behaved as if it had been dominated by visual purple but the red half value for the off-component came out in the sum. Then the experiment was repeated with the red stimulus reduced in strength to one quarter of its earlier DG-value. The result was: for the new red full value 44—29, its half value 45—20, G full value 43—25, G half value 41—15, and the sum of  $\frac{R + G}{2}$  gave 43—29. Into this sum red entered

with 1/8 of its original strength and yet it not only dominated the result for the off-component but this component (29) actually was greater than the amount (20) which the red half value could have contributed alone, not to mention the green half value that was only 15. In combination with 1/2 G the 1/8 R actually produced an off-effect corresponding to 1/4 R. This probably signifies that in this element the red modulator also to some extent was stimulated by the green stimulus. By reducing the strength of the red stimulus its frequency-intensity curve reached a portion of steeper rise (as can be seen by plotting the red off-values given above) so that it became a more sensitive index for red than at the higher intensity level.

*Conclusion.* By these experiments the principle has been established that in a combination of two wave-lengths one of the two may be prepotent and impress its particular distribution of on- and off-frequencies upon the sum. Such facts can, of course, only be established when the two wave-lengths differ in their individual effects so as to provide us with an index for measuring the dominant and the suppressed wave-length.

### Tests with Other Wave-Lengths.

We proceed to observations with elements in which various wave-lengths were used at their DG-values at the maximum intensity of the spectrum and the half filter employed for the sum so as to keep the energy sum constant in terms of visual purple. The first spike to be mentioned is one with post-excitatory inhibition in the green at 0.520  $\mu$  for which the on-off values were 8—1, *i. e.* a slight suppression of the spontaneous activity at 'off'. The 0.640  $\mu$  red gave 11—+1 the sum  $\frac{R+G}{2}$  7—1, *i. e.* the value of the green. In the same experiment the violet 0.420 alone gave 8—+1 and combined with the green 10—1 perhaps summation at 'on' but preponderance of the green post-excitatory inhibition at 'off'.

A very perfect experiment is illustrated by Table 3. There was practically no spontaneous rhythm. The green 0.520 varied between on-off-values 18—4 and 19—5 during a couple of hours while it was combined with lights in a number of other wave-lengths, all values adjusted to the DG-curve, the sums obtained

Table 3.

Wave-length in $\mu$	0.640	0.620	0.600	0.580	0.520	0.460	0.440	0.420
Singles on .....	25	24	24	19	18—19	26	16	23
off .....	11	10	7	5	4—5	5	4	7
Combined with 0.520 $\mu$ on .....	19	20	20	20		18	20	20
off .....	7	7	5	4		3	5	6

with the half filter. There were 5—6 counts for each value, 2 sec. counting period.

From 0.640 to 0.600  $\mu$  the off-effect diminishes towards the middle of the spectrum. The combination with 0.520 regularly brings out the value of the green on-component whilst the red off-component maintains itself somewhat better and approaches a mean value between the constant green and its own wave-length. In 0.600 and 0.580  $\mu$  the green 0.520 already dominates in the sum. In the short wave-lengths there is a sudden rise of the on-component in 0.460  $\mu$  but this is suppressed in the combination with the green. The same happens to the drop of the on-component in 0.440 and the new rise in 0.420. The green 0.520 maintains itself as the dominant wave-length in every match, and there is a measurable sign of something else at 'off' only in combinations with the extreme red and violet. Increased off-effects in the short wave-lengths are quite common. Sometimes they are maintained against a low off-value in the green (0.520  $\mu$ ) but more often than not the green is relatively more dominant in combinations with blue and violet than in combinations with red.

It is perhaps not necessary to present further examples. Suffice it to mention that in an experiment similar to the one of Table 3 the green (0.520  $\mu$ ) again was combined with the same short and long wave-lengths and that the value for the off-effects fell practically on the mid point between the low green off-effect (19) and the others which varied from 42 to 21 with maxima in 0.640 (42) and 0.440  $\mu$  (30). In this case there was no dominance but perfect mixture of the two effects. The on-component varied but little from wave-length to wave-length.

Red modulators are common and by several methods easy to demonstrate and were therefore well suited for the demonstration of the principle that has been established. I often tested the violet in 0.440 or 0.420  $\mu$  in the cases where experiments were performed with the combination red and green and noted that, if the off-

effect was stronger for red than for green (DG-units), then it nearly always had a small rise in the violet too. This observation is merely mentioned in passing and I do not intend to discuss alternative explanations of it.

### Discussion.

The results obtained are, of course, dependent upon the use of the DG-ordinates as units of energy. Despite this uniform scale there have been qualitative differences in interaction from case to case although red dominance has been easier to demonstrate than prepotency of other wave-lengths. Activation of red modulators is favoured by the increase of energy necessary to compensate for the low sensitivity of visual purple in the extreme red. Nevertheless green dominance has been seen from time to time (Table 3) and, also, if, in red dominance, the red stimulus is shifted in steps from  $0.640 \mu$  towards the green at  $0.520 \mu$  it is but rarely that in  $0.580 \mu$  the red component succeeds in showing up against the green component of the stimulus whatever the nature of the latter. To maintain prepotency the red modulator generally must be stimulated within  $0.640$  to  $0.600 \mu$ . The best effects have been obtained with the red at  $0.640 \mu$ .

Once more I want to draw attention to the interesting fact that, when the red end is characterized by an increased off-response, so also is the violet at  $0.420 \mu$  though in this region the increase generally is somewhat smaller. GERNANDT (1948) determined the off/on-ratios at the threshold of the dark adapted eye for 72 elements and in this material found the probability for maximum off/on-ratios to be only 0.18 in the green as against 0.47 in the red and 0.39 in the blue. The off/on-ratio in his work was calculated on threshold sensitivity, *i. e.* reciprocal of threshold energy. In a later set of experiments of the same type GERNANDT (1949) measured the off/on-ratios of a number of elements in the whole spectrum and found some for which the values increased towards the two ends.

The animal may or may not discriminate with the aid of the off/on-ratio as such. The significant point in our measurements is that the variations in relative spike frequency at 'on' and 'off' serve to indicate differences in the rates of rise and fall of the frequency-log intensity curves for different wave-lengths. When an

animal turns its eye towards the coloured light these differences will emerge in the pulsations of frequency set up by the stimulus.

The demonstration that two wave-lengths may interact in such a fashion that, to judge by the frequency pattern, one is prepotent and the other one suppressed is of particular interest against the far less striking evidence for the opposite process, a facilitation leading to pooling of the effects of the two wave-lengths at 'on' and 'off'. Within a considerable range of relative intensities the elements are thus easily triggered in favour of either of two wave-lengths in a most interesting alternative fashion. The explanation may be that the wave-lengths used in this work have been rather far apart and that for this reason we have struck the effects which psychophysically are known as contrast phenomena. These are characterized by that same aspect of exclusion of one alternative in favour of another. We shall proceed to test this proposition by successive illuminations. The selection of wave-lengths in this work has been determined by the desire to create a situation that could be analyzed. Phenomena of summation would provide greater difficulties if, as seems probable, they would require wave-lengths that did not differ by specific signs.

These experiments, as far as they go, are not without interest for our ideas about colour mixture. The final mixing of colours may well be a central process but the retina itself has here been shown to deliver a message determined by synaptic interference with consequent suppression or enhancement of one part of the spectrum. There are therefore interesting retinal problems of interaction involved in colour mixture. For this reason negative coefficients in work on colour mixture as well as deviations from Abney's law seem perfectly reasonable.

### Summary.

Well isolated elements picked out by the micro-electrode technique from the dark adapted retina of the cat have been stimulated with one or two wave-lengths of a spectrum and the discharge of spikes counted at 'on' and 'off'.

In many isolated elements the log intensity—spike frequency curves have been shown to run a different course for different wave-lengths. When this is so two wave-lengths can be shown to elicit different relative frequencies at 'on' and 'off' within a large

range of variation in the energy ratio of the two wave-lengths. The pure on-elements and a considerable number of on/off-elements do not have these properties; wave-lengths equated for equal visual purple activation at one energy level then remain equated at all intensity levels.

When two wave-lengths, which *can* be differentiated by their relative spike frequencies at 'on' and 'off', are acting simultaneously on the same element it is generally found that either of the two is prepotent and succeeds in maintaining its off/on-ratio in the sum whilst the properties of the other one are suppressed.

By making such comparisons in equal retinal visual purple units the contribution of visual purple stimulation can be kept constant for all wave-lengths to be combined. By these means contributions from other types of receptors to the interaction patterns of two wave-lengths can be distinguished.

Several examples of interaction between the effects of two wave-lengths upon the same element are given. They substantiate the conclusion that interaction can take place when one wave-length simultaneously stimulates two photochemical substances with ordinates overlapping the same spectral region.

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