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Regions of response transition of color-coded retinal units and an attempted analogy to behavioral response transition*

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Electrophysiological responses obtained from single color-coded red-green ganglion cells of the goldfish retina were analyzed in terms of the spectral region within which response transitions occur. The data showed that criteria for response transitions can be characterized by a frequency change with the stipulation that the same number of "on" and "off" spikes occur to the same wavelength(s). The overall spectral band within which response transition occurs is 570-620 nm. The physiological response ranges were compared to psychophysical unique-yellow responses and other "yellow" judgments. The former were displaced towards the longer wavelengths as predicted by the different pigment peaks. The response characteristics of sharp boundaries and relative invariance with intensity changes provided the basis of an analogy of the two response systems.

The manner by which the visible spectrum is divided psychophysically into identifiable units, by means of a verbal or a nonverbal response, and the techniques employed to obtain such responses continue to be of interest to color perception research. Beare (1963) and Beare and Siegel (1967) used a direct naming-of-wavelength procedure while varying luminance and instruction conditions. Boynton et al (1964) and Boynton and Gordon (1965) used a point-allocation method, similar to the constant-sum method employed in some scaling procedures. With nonverbal organisms such as the pigeon, an effective technique is exemplified in the work of Wright and Cumming (1971), where Ss are presented with center-key stimuli in a wavelength matching-to-sample paradigm.

Whatever the method employed, and from whichever species the responding organism is drawn, such experiments result in a set of frequency distributions exhibiting a certain degree of overlap between adjacent distributions. The point at which two adjacent distributions intersect is assumed to correspond to the psychophysical point of subjective equality (PSE)—a point along the spectrum at which either of two qualitatively different responses may occur with equal probability. The wavelength band in which the PSE is located is defined as the response transition range, the range within which the shift in response probability is located. Which variable, or set of variables, governs the location of such transition ranges along the visible spectrum is not yet entirely clear, nor is there any real indication that such determining parameters do, in fact, exist. If luminance, for instance, is proposed as one such parameter, one can show that a shift in transition range is merely part of an overall shift of the location of all distributions as a function of luminance (see especially Boynton & Gordon, 1965). One variable which has been shown by Beare and Siegel (1967) to be independent of the luminance parameter (at least for the luminance levels employed) is the particular set of response categories available to the S.

This finding permits the conclusion that in verbal and behavioral/manipulative color naming tasks, the location of the response transition range depends on decision or judgmental processes. These are assumed to depend, at least in part, on the learning or conditioning history of the respective S, the category context from which pertinent responses are elicited, and certainly the psychophysical methodology by which the data are obtained. Experiments dealing with the determination of unique hue seem to be less dependent on these parameters. The severely restricted stimulus-response context (relative to naming experiments utilizing broader spectral ranges and response categories) of such experiments keep them relatively free of interactions originating in conditioning history or available response categories. It is, therefore, of considerable interest to find a mechanism in the color-sensitive system which is equally free from these assumptions, and for which physical wavelength transition ranges can be demonstrated which can also be operationally defined in terms of changes in response. Such a mechanism is inherent in the dual-response, color-coded neural unit found in the visual pathway of many vertebrates.

The visual system of the goldfish (*Carassius auratus*), for example, contains retinal ganglion cells from which color-coded responses are fairly easily picked up and recorded. Units of opponent color responses most

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wavelengths, can some analogy be drawn between them and psychophysical response ranges, such as those determined for psychologically unique hues?

METHOD

The preparation used was the isolated retina of the goldfish (*Carassius auratus*). Prior to the experiment, the fish (20-25 cm long) was dark adapted in a covered tank. Eye excision and peeling of the retina were done under infrared illumination. The isolated retina was placed, receptor side up, in the recording chamber which was cooled by an adjustable water-circulating system. A moist mixture of gas (95% O_2 + 5% CO_2) at about the same temperature as the water-cooling system flowed over the preparation. The stimulating beam came from below so that it passed through the layers of the retina in the normal direction. The chamber containing the retina was covered by two blackened cover slips, leaving only enough of an opening for the electrode to enter. The electrode was vinyl-covered tungsten, as described by Hubel (1957), and was positioned on the preparation by means of a micromanipulator.

The optical stimulator was designed by E. F. MacNichol, Jr., and is described in detail by Daw (1967a). It provided two independently adjustable monochromatic beams, each consisting of a 6-V 18-A tungsten filament lamp, which passed light through a 50-mm square grating of 600 grooves/mm, and on to mirrors of 75 mm diam and 0.5 m focal length. The intensity of each beam could be varied by means of two Kodak circular neutral density wedges with Type M carbon coating. For the experiments described here, only one of the beams was used for stimulation. The other beam was adjusted to the same wavelength and intensity settings as the stimulating beam and focused elsewhere for visual checking on the part of the E at the beginning and again at various settings during the experimental determinations.

The stimulus plane contained a microscope stage with movement in two dimensions, marked in millimeter scales and verniers. A holder with a circular 3-in. hole was attached to a microscope stage, so that templates with varying size spots could be fitted into the stimulus plane and could be moved in the field of illumination to an accuracy of 0.1 mm. Energy readings at the plane of the retina were taken with a Reeder thermopile and Keithly Type 150A microvolt ammeter for the stimulating beam. The reference value, when the neutral density wedge was set at zero, was 3.8×10^{13} quanta/cm^2/sec at 630 nm. This energy value remained almost constant between about 590 and 650 nm, and intensity was therefore not varied as this area was traversed (see Daw, 1967a, Fig. 3).

The recording electronics were standard, action potentials being amplified through a low-noise, high-impedance amplifier whose bandpass was adjusted to maximize the signal-to-noise ratio.[1] Spike activity was read visually directly off a Tektronix Type Rm 561 four-beam oscilloscope, as equipment was not consistently available for automatic or photographic recording of spike activity or latency measures. When available, such equipment was used to corroborate the E's visual and auditory observational judgments.

The spot size chosen for any individual unit was the smallest to which that unit would respond. This turned out to be 1.78 mm for all but two units, which both responded to a 2.0-mm spot. Exposure time was 500-600 msec. After the electrode had made initial contact with the unit, the neutral density wedge was adjusted to that setting at which response was just audible and visible. That wedge setting was then kept constant for all determinations in that unit. Several units were tested at lower density settings (i.e., at higher intensity) to control for wavelength shifts in the criterion-response region. Each color-coded unit was tested in ascending and descending orders between its "on" and its "off" wavelengths in 10-nm steps to locate its region of response transition. Once this region was located, stimulus steps were decreased, and when band limits had been ascertained, the wavelength region was checked out repeatedly to make sure the transition response remained consistent. Response to each exposure was noted down before going on to the next exposure, while the preparation was kept in total darkness between exposures.

RESULTS

Goldfish retina potentially yields varying cell response types. The monophasic type is a cell which responds to all wavelengths. The biphasic type responds differentially to two opponent wavelengths, i.e., red and green, or yellow and blue. The triphasic type responds in one manner to one wavelength and differently to two other wavelengths (depolarizing to green, hyperpolarizing to blue and red). The majority of cell types encountered in these experiments were of the biphasic red-green variety and consequently only this type was sampled. A total of 18 RG units yielded the data presented below. Fourteen of these 18 units were "off" to red (−R) and "on" to green (+G); four units were −G+R. Since spot size was kept constant, no response reversal was found in any of the units.

Transition Response Criteria

When a color-coded cell responded to its specific "on" or "off" region, it typically was found to emit a burst of responses. As the wavelength transition region was approached from either end, the response in the majority of the units diminished in frequency so that spikes became identifiable and countable as single, discretely spaced spikes. This type of response is labeled here as "DS." When this type of response was found, that wavelength band within which it occurred was then checked repeatedly and that part of the band was accepted as a transition range within which the number of "on" DS equalled the number of "off" DS. This limitation, that number of "off" DS must equal number of "on" DS, represented the first criterion for delimiting a transition wavelength in terms of electrophysiological response.

Two other response types were identified, though not nearly for as many units as the DS criterion. One was complete silence in response to a wavelength band between the unit's "on" and the unit's "off" response band. Typically, as that region was approached, spike frequency diminished until a wavelength was reached at which no response occurred. Again, the band was bracketed for which silence was maintained, that is, the wavelength band between the last "on" response and the first "off" response. This band was then also accepted as a transition wavelength range and was labeled NS (no spike).

The second response type which was arbitrarily combined with the NS criterion was its converse. It represented an increase in frequency, indistinguishable between "on" and "off," similar to undifferentiated spontaneous baseline activity, which could, again, be

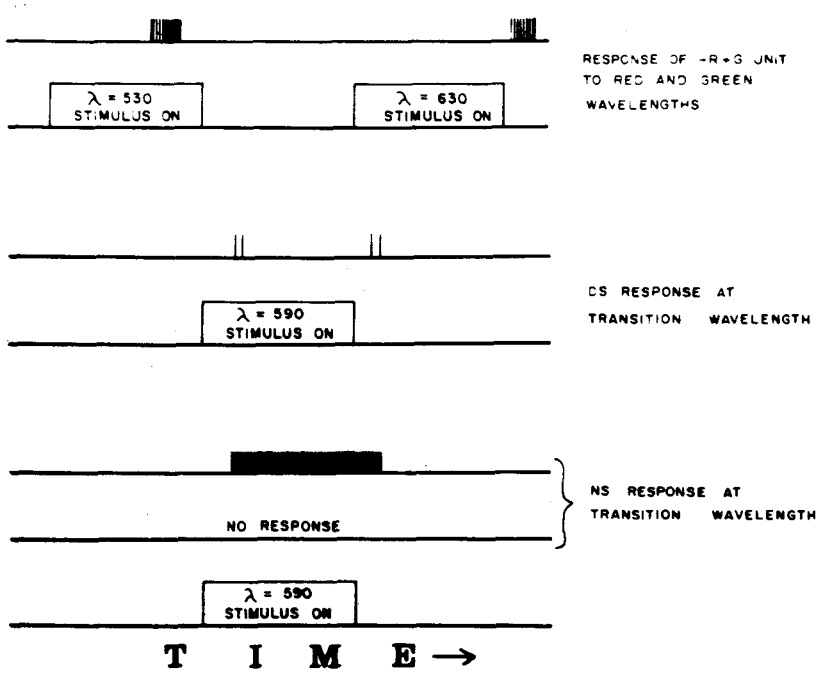

Fig. 1. Schematic presentation of −R+G unit firing pattern in response to wavelength. Top shows "on" response to green (λ = 530) and "off" response to red (λ = 630). Middle shows both the "on" and the "off" response occurring to the same (λ = 590) stimulus. This is the DS criterion response, and 590 nm would be the transition wavelength. Bottom shows the NS criterion response to the same transition wavelength. Both constant firing during and after stimulation, as well as "no response" during and after stimulation, are counted as NS criterion responses.

Table 1
Distribution of Cell Types and Their Criterion Transition Responses

	Cell Type			
	−R+G		−G+R	
	DS	NS	DS	NS
Total Recorded	14		4	
Transition Response	13	1	2	2
Total Transition Responses	DS = 15			
	NS = 3			

bracketed for specified wavelength bands between the last clearly distinguishable "on" response and the first clearly distinguishable "off" response.

To summarize, two separate response criteria were established to denote transition wavelength on the basis of electrophysiological response frequency. The first, DS, refers to wavelength bands which elicited an equal number of discrete "off" and "on" spikes. The second, NS, refers to wavelength bands which elicited either complete silence on the part of the cell or undifferentiated baseline-like spontaneous firing. Figure 1 gives a presentation of a typical −R+G unit (top), the DS response criterion of such a cell (middle), and both versions of the NS criterion (bottom). The figure is in schematic form since recording equipment was not available.

The breakdown by criterion response and cell types is provided in Table 1. Of the 18 units, 14 were used for further analysis since four did not last long enough for the complete measurement procedure. These 14 units are listed in Table 2 together with the intensity in log units at which measurements were made, and the type of response and wavelength range each gave at the transition. The intensities refer to the lowest luminance at which measurements could be made.

The data from Table 2 are presented graphically in Fig. 2, in which the response transition wavelength range is sketched for every cell as a function of the log intensity at which the cell was recorded. The upper part of Fig. 2 should be ignored and will be taken up in the discussion section below. The horizontal lines in Fig. 2

Table 2
Wavelengths at Which Criterion Response Transitions Were Obtained

Unit No.	Log I	Wavelength of Response Transition (nm)	Criterion Transition Response	DS Responses
		−R+G Cell Type		
1	−1.0	610-620	DS	1
2	−1.0	590-600	DS	1
3	−2.0	610-620	NS	
4	−2.0	590-600	DS	
5	−3.0	600-610	DS	
6	−3.7	590-600	DS	1
7	−4.0	570	DS	3
8	−4.0	580	DS	1
9	−4.0	600-610	DS	1
10	−4.2	590	DS	
		−G+R Cell Type		
11	−2.0	580	DS*	4
12	−2.0	550	DS*	2
13	−2.8	570	NS*	
14	−3.2	590-600	NS†	

**These three cells showed a center-surround organization.*
†NS here signifies that the unit responded with spontaneous (baseline) firing to the stimulus. This is treated as being equivalent to silence.

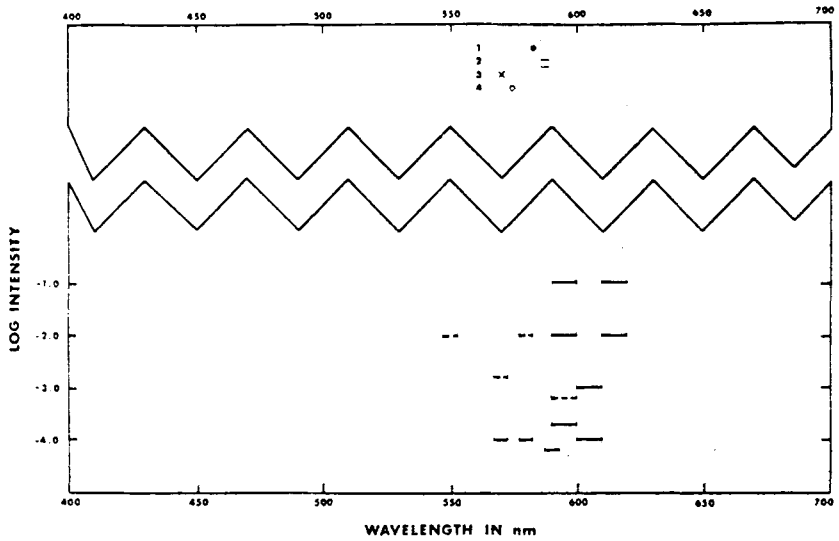

Fig. 2. (Lower portion) Wavelength regions to which criterion transition responses occurred. Solid lines show −R+G units, and broken lines are for −G+R units. (Upper portion) Symbols refer to psychophysically obtained "yellow" responses as a function of wavelength, as obtained by the four studies listed in Table 4, as follows: 1 = •, 2 = □, 3 = ×, 4 = ○.

delineate wavelength ranges which elicited transition responses. Short lines indicate instances where a single wavelength point only elicited the criterion response. Longer lines indicate that the criterion response occurred at both wavelengths spanned. Thus, Unit 9, for instance, gave the DS criterion response at 600 and 610 nm, but not below 600 or above 610. Solid lines denote −R+G units, broken lines denote −G+R units.

While units differed from one another in their criterion responses, no variation within a cell's response in the transition region was noted, with one exception. That is, a cell did not change from DS to NS, or vice versa. Each cell remained constant in its criterion response, even when checked out at a higher intensity level. The exception refers to Unit 6, which, at an increased intensity (−3.0 log I), changed its firing pattern and the transition range was characterized by spontaneous firing. Cells with the DS response criterion also showed no variation in the number of discrete spikes they emitted in response to the transition wavelength(s). For all DS cells, this number varied generally between one and four at the lowest intensities shown in Table 2. If a cell's DS response consisted of three spikes, this number remained constant in the course of repeated measurements. The general firing pattern of a cell was not observed to change in the course of measurement unless or until fatigue or damage became evident, at which point recording was terminated.

Since the data were recorded by auditory and visual counting, the precise number of DS responses was not recorded for all units. In most instances, the records merely indicate that wavelength at which = DS on = = DS off. It should be remembered that only those ranges were accepted as transition ranges for which the number of "off" responses equalled the number of "on" responses in the DS criterion. The information for recorded number of spikes available for eight of the units is provided in the last column of Table 2. While it was not always possible to maintain a unit over a long period of time, at least half the units of Table 2 were checked, in addition to the intensity shown, at intensities of up to one log unit above that tabulated. For these units, two points can be made: (1) The actual wavelength ranges in which the transition response occurred remained constant, even at the higher intensities. (2) The criterion response also remained qualitatively unchanged. In some instances, it changed quantitatively, i.e., yielding three DS responses for both "on" and "off" at the increased intensity instead of only one at the lower intensity.

DISCUSSION

While the data provide no conclusive answers as yet to the questions originally posed, they are indeed suggestive. Fifteen out of 18 units fell within the same criterion response, firing an equal number of discrete spikes to both onset and termination of a stimulus exposure within that range. If we subdivide the unit population further into −R+G and −G+R groups (Table 1), 13 of the 14 −R+G units gave a DS transition response. As a preliminary answer to the first question—whether a uniform and consistent electrophysiological criterion can be demonstrated which operationally defines a cell's transition wavelength—the data suggest that the DS criterion response is most likely to define that wavelength range within which the occurrence of an excitatory and an inhibitory response is equiprobable. Further work will have to determine whether other neural units, more of the −G+R type, as well as yellow-blue coded ones, will show a comparable criterion response. This transition response seems to be relatively independent of intensity level as long as that level does not fall below threshold.

The wavelength ranges delineated by the transition response remained invariant over an intensity range of at least 2 log units. A somewhat comparable finding was reported by Spekreijse and Norton (1970) for linearity in color-coded S-potentials in response to modulated

Table 3
Summary of Wavelengths Associated With the Response "Yellow" in Four Psychophysical Studies

Experimenter	Type of Determination	Wavelength (nm)	Symbol (in Fig. 2)
1 Dimmick & Hubbard (1939)	Determination of unique yellow	582.7	•
2 Beare (1963)	Color naming with six categories	587.0	□
3 Yager & Taylor (1970)	Determination of unique yellow (mean from four subject means)	571.0	×
4 Siegel & Siegel (1971)	Hue setting, estimation, naming, interpolated value at 1.0 fL from pointer setting of 25 (unique yellow)	574.0	○

light as long as adaptation level (and intensity-saturation effects) did not change. While the S-potential is qualitatively different and is thought to have a different origin, the similarity in the dynamics of the two types of responses in terms of intensity is of considerable interest.

Due to the numerical disparity between −R+G and −G+R cells sampled, the data do not permit conclusions about specific transition response ranges as a function of these two subclassifications of the R-G coded cell. They do, however, show a very definite response range for all the R-G units taken together. Thus, in answer to the second question concerning specific transition ranges associated with particular cell types, the data show that this range clearly and consistently spans the 570-620-nm band, with 590 nm as the modal wavelength.

The third question referred to the possibility of drawing an analogy between physiological response transition wavelengths and psychophysical response transitions. The emergence of a relatively homogeneous and invariant response transition range of the R-G coded retinal unit leads to a critical examination of psychophysical data with a possibly comparable response transition. The green-to-red transition is assumed here to be indicative of the underlying mechanism for judgments or determinations of the behavioral response of "yellow." For that reason, four representative studies concerning such judgments are summarized in Table 3, and their pertinent results sketched schematically into the upper portion of Fig. 2. The four schematic points represent two separate determinations of unique yellow, one data point summarizing three disparate color specification techniques and one involving naming of hue with conventional categories.

Comparison of the two sets of data—neurophysiological and psychophysical—show a greater degree of variability in wavelength ranges for the single units. In addition, the neurophysiological ranges clearly are displaced toward the long-wavelength end of the spectrum as compared to the (human) psychophysical data. This finding is consistent with the difference in pigment-peak displacement inherent in the two systems.

Studies concerned with the psychophysical determination of unique yellow, as well as other methods of obtaining judgments of "yellow," have been virtually unanimous in finding that the response is relatively independent of intensity. Yager and Taylor (1970) not only reconfirmed this invariance with intensity in their determination of unique yellow, but demonstrated that there also seems to be a real difference in thresholds between the two opponent color systems, the red-green and the blue-yellow, in terms of the power functions they obtained. An analogous intensity independence, spanning at least a 2 log interval, is demonstrated by the single unit transition range data, as well as by the findings of Spekreijse and Norton (1970) for color-coded S-potentials of biphasic receptors. This invariance with intensity seems to hold not just within receptor units tested at more than one intensity level, but between them as well. Figure 2 demonstrates that even where the lowest intensity at which responses were recorded differed from unit to unit, in some cases over an intensity interval of almost four log units, the response transition ranges greatly overlap for most units and are identical for others.

The inclusion of the data by Siegel and Siegel (1971) in the upper part of Fig. 2 is of some interest, as it represents three inherently different methods of obtaining hue judgments. These are naming, estimation, and setting. Calculations are all based on a priori unique hue settings. In the case of unique yellow (setting of 25 on the dial), the curves of all three methods are, to all intents and purposes, identical. Moreover, the point from Beare (1963), representing color naming data, falls within the same range as the points from Siegel and Siegel (1971) and the two unique-yellow points of Dimmick and Hubbard (1939) and Yager and Taylor (1971), respectively. Indeed, in ordinary color-naming experiments, unless categories are unnaturally restricted, the boundaries for "yellow" are extremely sharp, the curve rising and falling rapidly and steeply. The common explanation is that yellow occupies a very narrow wavelength band. The neurophysiological data lend weight to the assumption that these sharp boundaries may not be just an accompanying feature of the psychophysical context within which a judgment of yellow or unique yellow is obtained. Indeed, the boundaries shown by the firmness and relative invariance of the transition wavelengths of the retinal units may be both the necessary and sufficient conditions which

determine boundaries of psychophysical response.

The assumption has been made that an analogy can be drawn between red-green color-coded retinal unit responses and psychophysical judgments of unique yellow and, by extension, the judgment of yellow in broader psychophysical contexts. While an analogy between the goldfish retina and the primate eye may be open to question, the main difference between the two systems should concern displacement due to pigment peaks, and this is, in fact, the chief difference demonstrated by the data. The relative response and wavelength invariance with intensity demonstrated for both response systems for the transition range from green to red, as well as the equally sharp boundaries found in both systems, justifies the assumption that the psychophysical determination—for yellow at least—may be more fundamentally a function of the neural response mechanism than of judgmental variables. Such a conclusion must, however, await confirmation with additional data which also demonstrate analogous features in other types of neural codes. Specifically, examination is needed of blue-yellow transition ranges and their response characteristics and boundaries, together with a comparison to the relevant psychophysical data for that portion of the spectrum.

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NOTE

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