RESEARCH NOTE

EQUIVALENCE CLASSES OF VISUAL STIMULI

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INTRODUCTION

Physically different visual stimuli may be visually indistinguishable. Well-known examples of such equivalence are the Craik–O'Brien–Cornsweet effects and related phenomena (Craik, 1940, 1966; O'Brien, 1958; Cornsweet, 1970). In this note we formalize some old ideas on stimulus equivalence (some explicit in the earlier work, some implicit) and express them in terms of equivalence classes. We show that the concept of null stimuli is basic to a linear formulation and we demonstrate the dependence of one equivalence class on the relative strengths of excitation and inhibition in a model neural network.

MACH'S PRINCIPLE OF EQUIVALENCE

Mach (1865) stated: "every psychical event corresponds to a physical event and vice versa. Equal psychical processes correspond to equal physical processes, unequal to unequal ones". (The word physical, as used here by Mach, refers to the underlying neurophysiological processes rather than to the external stimuli). Thus Mach's principle of equivalence—as far as vision is concerned—is simply that equal neural responses in the visual system yield equal visual appearances, unequal responses, unequal appearances[2]. No correspondence between external stimuli and neural responses is implied in this principle. On the contrary, equal stimuli may yield unequal neural responses,[3] and unequal stimuli may yield equal neural responses. It is this lack of correspondence, particularly the latter case, with which this paper is concerned. See Ratliff (1965) for translations of Mach's papers on the retina.

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[2] Here, and in the following, we use "appearance" to signify a quantitative psychophysical measure. It is therefore also a response, which of course depends on certain other pre-determining responses. For a discussion of the use of matching observations to determine equivalence of stimuli in modern sensory experiments, see Brindley (1970).

[3] Stimuli for figure-ground illusions, Necker cubes and the like presumably elicit different neural responses at different times, for such stimuli change radically in appearance while remaining physically constant. This non-uniqueness points strongly to a non-linearity, and thus falls outside the scope of this note.

EQUIVALENCE CLASSES OF STIMULI

It is easy to understand why some unequal stimuli appear equal. For example, luminance patterns of very high temporal (or spatial) frequency appear the same as a steady (or uniform) light of the same mean luminance. Processes and structures which limit temporal (or spatial) resolution completely cut off the very high frequencies—thus, the apparent equality. At the other extreme, gently varying patterns in both time and space are also often indistinguishable from steady and uniform patterns. This latter equivalence, arising from very strong attenuation (or even cutoff) of low frequencies, is to be mainly due to the suppression of excitatory influences by antagonistic inhibitory influences. The restriction of such effects to fairly low frequencies is presumably a result of the relatively large temporal and spatial dimensions of inhibitory processes.

Actually, a richer variety of stimuli than those just mentioned can appear equal and it is useful to characterize these. If we use as a basis the criterion of equivalent neural responses (or equivalent visual appearances) then one can speak generally of equivalence classes of stimuli. Each member of such a class produces the same, or nearly the same neural response (and thus the same, or nearly the same appearance). For linear systems, the difference between any two equivalent stimuli produces a null response, and we term such stimuli "null stimuli". When dealing with real living systems or with realistic models in which noise and threshold effects are present, a somewhat forgiving definition of "null" must be used. For example, small non-zero responses that lie within the noise or are below threshold must be termed null. Also, according to a rigorous mathematical definition, equivalence is a transitive relation. This, however, must be relaxed since it is easy to envision a sequence of real stimuli, successive pairs of which yield "equivalent" responses within the range of experimental error, but the last and first of which do not. All of these ideas must figure in any practical working definition of equivalence classes.

Any stimulus composed of frequencies not passed by a system is a null stimulus for that system. In any real visual system, where there is always a high frequency cutoff and generally either a low frequency cutoff or a strong attenuation of low frequencies, null stimuli may contain both low and high frequency components of large amplitude. Null stimuli may also

contain significant contributions at intermediate frequencies. Their allowable amplitudes increase away from the peak response frequency, becoming quite large in regions of strong attenuation.

In summary, stimuli which differ objectively may produce equivalent neural responses (and visual appearances) simply because the visual system "filters out" those features of the stimuli which differ, and transmits some of those features which they share in common. Such stimuli form an equivalence class. For a linear system, the difference between any two members of the same equivalence class is a null stimulus. If the difference of two equivalent stimuli does not produce a null, the system is not linear. Thus the null provides a test of linearity.

LINEAR NETWORKS

The "filtering" or linear processing of visual information in the spatial domain is conveniently discussed in terms of the line-spread function or its Fourier transform, the modulation-transfer function[4] (Schade, 1956). This is depicted in a one-dimensional form in Figs 1 and 2. The line-spread function in the former—a narrow Gaussian—depicts a neural

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[4] Modulation transfer functions for the human visual system are usually determined at threshold, which is inherently non-linear. Whether such results can be safely extrapolated to more nearly linear suprathreshold operating points is questionable. However, suprathreshold electrophysiological experiments on single cells in the visual pathway do yield similar results (for a brief review see Heggelund and Krekling, 1976). The transfer functions for different cells differ widely; the transfer function of the visual system as a whole appears to be the envelope of the various transfer functions of the individual cells. Presumably, the loss of the opponent surrounds of many different members of a large ensemble of cells accounts for the loss of the opponent surround in the line-spread function of the visual system as a whole.

network with no inhibitory surround, its counterpart in the latter—a difference of two Gaussians—depicts a neural network with a totally compensatory inhibitory surround. In each figure the two columns represent Fourier transform pairs (e.g., f and $\bar{f}$) with the relationship between each function and its mate indicated by the double half-arrows. The left-hand column of each figure traces the passage of two dissimilar spatial stimulus patterns, f and g, through a model neural network represented by the line-spread function W. That is, f and g are convolved with W to obtain the two responses $W*f$ and $W*g$. The right hand column column shows the corresponding distribution of spatial frequencies, $\bar{f}$ and $\bar{g}$, and the corresponding modulation transfer function, $\bar{W}$. Here, $\bar{f}$ and $\bar{g}$ are multiplied by $\bar{W}$ to obtain the two responses $\bar{W}\cdot\bar{f}$ and $\bar{W}\cdot\bar{g}$. (In this particular case phase information is trivial as $\bar{W}$ is real and $\bar{f}$ imaginary, since W and f are respectively even and odd functions of space.) Note that the differences between the two stimuli (top row) lie mainly in the very low spatial frequency range. In case of the network with a strong inhibitory surround (Fig. 2), low spatial frequencies (predominantly in the stimulus pattern f) are suppressed. The high frequency components of the two stimuli are identical and both are cut off in the same way by the network. As a result, the dissimilar stimulus patterns of Fig. 2 produce nearly equal responses, as shown in the bottom row of this figure, and thus belong to the same equivalence class. (cf. Mach, 1865; Cornsweet, 1970; Campbell, Howell and Robson, 1971; Ratliff, 1971, 1972; Tolhurst, 1972; Shapley and Tolhurst, 1973.) In the absence of the inhibitory surround (Fig. 1, middle row), the dissimilar patterns (top row) pass through as dissimilar responses (bottom row), since low frequencies are passed in this case.

"FILLING IN" PROCESSES

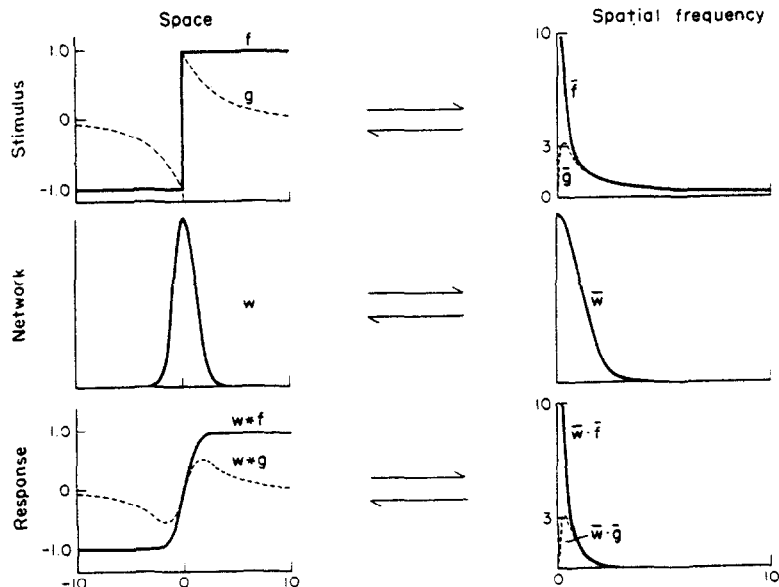We have made no assumptions about the relation of the form of a given response to the form of the

Fig. 1. Different responses to "step" and "exponential" stimuli by a model network with no opponent surround.
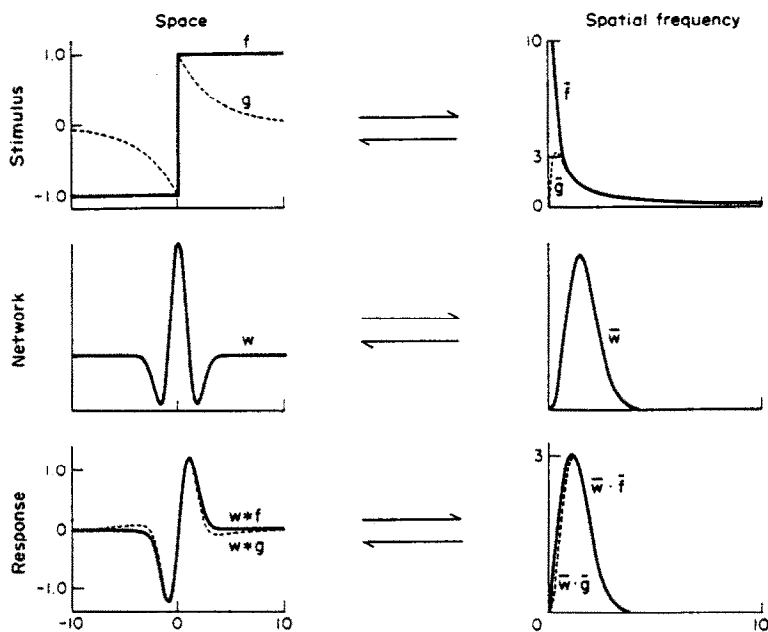
Fig. 2. Equivalent responses to "step" and "exponential" stimuli by a model network with an opponent surround equal in strength to the center.

corresponding visual appearance. In particular, no assumption has been made that they are or need be "isomorphic". But isomorphism has long been a central issue in the theoretical analysis of edge-dependent effects. And for this reason, the supposed neural mechanisms have generally been represented as a two-stage process (Fleischer, 1939; Fry, 1948; Walls, 1954; Hood and Whiteside, 1968; Gerrits and Vendrick, 1970; Ratliff, 1971; Shiffman and Crovitz, 1972). In the first stage, lateral inhibition accentuates rapid gradients (and eliminates slow gradients), and in the second, a "filling in" or "homogenization" of the pattern takes place. For example, Fry (1948) concluded that: "Although the mechanism of inhibition sharpens the contrast, it is necessary in addition to postulate a (nerve impulse) frequency-equalizing mechanism, which smooths out the (impulse) frequency differences on each side of the border..."

Our intuition may tell us that such a filling in process is necessary, but logic does not compel us to believe so. At least it is unnecessary to postulate filling in as an active process, as, for example, Fry does. Indeed, from the present point of view the second process is unnecessary, and its presence would not seem to be demonstrable. In our theoretical calculations the rectilinear step stimulus, as well as a wide range of other edge stimuli with curvilinear and rectilinear components (see Fig. 3), all belong to the same equivalence class; that is, they all result in effectively the same neural activity. According to this simple model, the perceived brightness distribution of each and every member of this equivalence class is the same.

We are all struck by the fact that Craik–O'Brien–Cornsweet stimuli (and other members of that equivalence class of stimuli) all "look like" rectilinear step stimuli, and many find this mysterious. But, conversely, it is equally true and equally mysterious that rectilinear step stimuli "look like" Craik–O'Brien–Cornsweet stimuli and also like all other members

of that equivalence class; that is, no one of the stimuli in this equivalence class is the "ideal" or "standard" stimulus. Some, it is true, may be more familiar, less complicated, more likely to occur in nature, or may have some other distinctive physical attribute. But no one is more effective as a visual stimulus than any other. All appear the same; all supposedly yield the same neural response.

The neural activity which underlies appearance must reach a final stage eventually. It may well be that marked neural activity adjacent to edges (as is postulated in this model and as is commonly observed in neurophysiological experiments) is, at some level of the visual system, that final stage and is itself the sought-for end process. Logically, nothing more is required. Nevertheless, we cannot by any reasoning eliminate a priori some higher-order stage or filling in process (whether it be the "frequency-equalizing" process of Fry or any of the manifold other possibilities one might imagine for this purpose). But parsimony demands that any such additional stage or process be considered only if neurophysiological evidence for it should appear.

EFFECTS OF ADAPTATION

The responses of the human visual system to various temporal and spatial frequencies depend on the state of adaptation (see, for example, Patel, 1966; Kelly, 1972; De Valois, Morgan and Snodderly, 1974). In particular, low frequency attenuation changes significantly with the level of adaptation. (Presumably, this results from changes in the dimensions of inhibitory processes). Such a transition is represented by the three line-spread functions shown on the top row of Fig. 3. These represent networks at three stages of adaptation: one with a totally compensatory inhibitory surround, one with a partially compensatory inhibitory surround, and one with no inhibitory sur-

round. As in Figs 1 and 2, these are superpositions of Gaussians. The first column contains seven different stimulus patterns and the associated rows show the transition of the responses at the three stages. As in Figs 1 and 2 the responses are the convolution product of the stimulus with the various line-spread functions shown.

For reference purposes we have designated each stimulus by name. Certain of the designations are self-evident; the others will be commented on briefly. Each of the stimulus patterns can be regarded as a combination of steps and exponentially falling functions. For example the "Cornsweet" pattern is the antisymmetric combination of two gently falling exponentials (each of which can be regarded as a separate "Craik" pattern); the "exp & step" stimulus is a step function with a sharply falling exponential subtracted on the left. The "O'Brien" pattern is also of this form but has a higher left starting point and contains a gently falling exponential. For obvious reasons the sixth pattern is given the name of "double O'Brien".
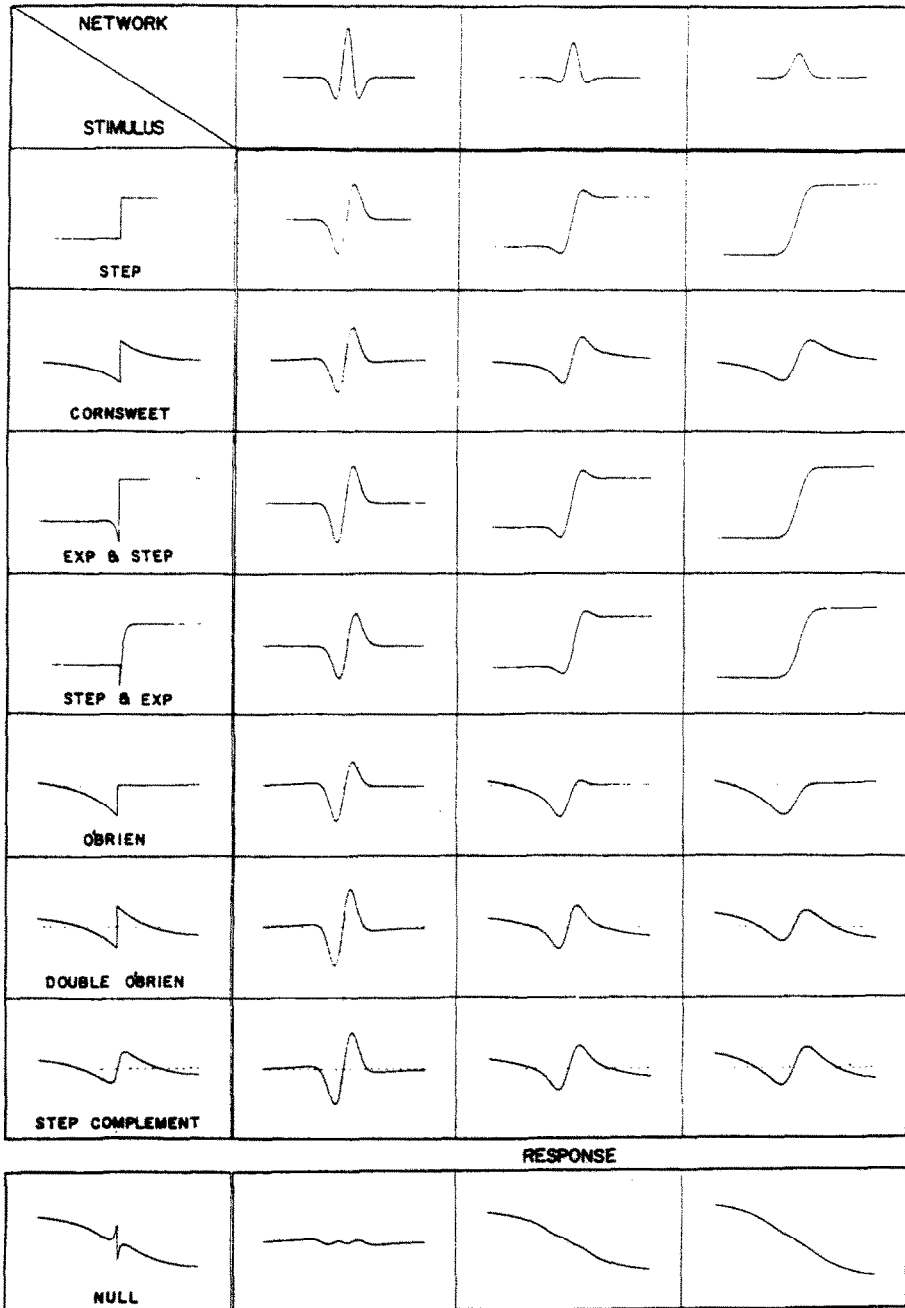

Fig. 3. Responses of model networks to a variety of edge stimuli. Effect of diminishing the strength of the inhibitory surround from totally compensatory to zero. To facilitate comparison the "network" amplitudes have been adjusted so that peak-to-peak response to the step is the same for all three networks.

The next column of this figure shows that, to good approximation, all seven stimuli produce very nearly the same response after passing through the first of these line-spread functions. In our earlier terminology, they all belong to the same equivalence class of stimuli, for the first line spread function. The O'Brien, double O'Brien, and step complement stimuli differ from all the others in that they exhibit a relative contrast exchange. That is, although the light intensity at the left is greater than at the right, the response under the first line-spread function is essentially the same as that of a step (first stimulus) with opposite relative intensity. (Note relationship to dotted lines.)

The next two columns show that equivalence classes are split under the loss of opponency. The second line-spread function (third column) has half as much inhibition as excitation and is therefore less able to produce pronounced edge responses. The third line-spread function (fourth column) has no inhibitory surround and hence merely results in a blurred copy of the stimulus. All three line-spread functions show high frequency suppression. This accounts for the stimulus equivalence of the "step", "exp & step" and "step & exp" stimuli under all three line-spread functions. For the same reason the "double O'Brien" and "step complement" stimuli also remain equivalent under all three line-spread functions.

For a given equivalence class of stimuli one may inquire as to what is the most dissimilar pair of stimuli giving rise to more or less the same response. Although this will not be considered here, the "step" and "step complement" stimuli provide an example of such a pair.[5] (Compare responses to them in the second column under the first line-spread function.) We reiterate that the difference of any two members of an equivalence class is a null stimulus, which gives rise to an effectively null response. This is illustrated in the bottom part of Fig. 3, where the null stimulus is the difference between the "step" and "step complement" stimuli in the upper part of Fig. 3. Passage of the null stimulus through the first line-spread function yields a nearly uniform (null) response. Actually, by further sculpturing the "null" pattern, a more nearly zero response can be obtained. We have deli-

berately avoided this to show the location of the vanishing response and to underline the notion that nearly zero responses appear as nulls as they enter the noise level.

We emphasize that the effects shown in Fig. 3 result from calculations using a model network. We do not mean to imply that equivalence classes of stimuli for this particular network would appear equal to a human observer. However, given a sufficiently exact measurement of the modulation transfer function—whether it be due to a single channel or is the envelope of many channels—one should be able to calculate equivalence classes of stimuli and null stimuli for the human observer, at least in the neighborhood of any operating point.[6]

Heggelund and Krekling (1976) found that one of the Craik–O'Brien–Cornsweet effects (Craik, 1940; 1966; O'Brien, 1958; Cornsweet, 1970) depends on adaptation level, and that it appears only in photopic vision.[7] They state that "the results...are...contrary to the model of Ratliff (1972) according to which level of adaptation should make no difference..." Heggelund and Krekling note that their results "might indicate that the effect only occurs under adaptational conditions where the retinal receptive fields have an antagonistic center-surround organization". However, in what they call the "Ratliff model", it is evident that if the opponent organization changes with adaptational level, as illustrated in Fig. 3, then, for example, so does the extent of the Craik–O'Brien–Cornsweet effect. Therefore, if such effects disappear at adaptation levels at which the opponent surround also disappears, as they suggest, then this is consistent with, rather than contrary to the "model" of Ratliff (1971, 1972).

As indicated in Fig. 3 total loss of surround is unnecessary for the breakdown of equivalence classes. Any significant change in the surround mechanism results in equivalence class modifications. Thus, according to this model, the loss of the Craik–O'Brien–Cornsweet effect implies a change but not necessarily a loss of the surround mechanism. In fact Maffei and Fiorentini (1972) have demonstrated contrast effects (and, by implication, the presence of a surround) at light levels significantly below that at which the Craik–O'Brien–Cornsweet effect is lost in the experiments of Heggelund and Krekling (1976). Furthermore, direct evidence of a surround mechanism, at extremely low light levels, has been shown in the cat (Enroth–Cugell and Lennie, 1975; Barlow and Levick, 1969) and in the monkey (Marrocco, 1972). None of these electrophysiological experiments was designed to bear directly on the problem of the possible physiological bases of the Craik–O'Brien–Cornsweet effects, however, and it would be premature to draw more than tentative conclusions from them at this time.

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[5] The demonstration of this assertion requires a mathematical discussion too lengthy for this note. In brief, one considers suitably normalized stimuli composed of frequencies lying in the bandwidth of the transfer function. The step and step compliment stimuli can then be shown to have the largest root-mean-square difference of any pair of stimuli taken from the equivalence class in which they lie.

[6] This neighborhood can be quite large. Dooley and Greenfield (1977) report that for wide Cornsweet edges with peak contrast of 20% or less the visual contrast is equivalent to that of the corresponding real step. Nonlinear effects are also considered in their paper.

[7] This contention has to be modified somewhat according to recent results of Sullivan and Georgeson (1977). They show that the "Missing Fundamental" version of the Craik–O'Brien illusion appears under scotopic conditions, but that the range of frequencies over which the illusion occurs becomes increasingly narrow at low luminances. Note that for suprathreshold effects at low frequencies, the fundamental in their experiments is somewhat analogous to our null stimuli.

CONCLUDING REMARKS

When properly defined, the idea of equivalence classes of stimuli is not limited to the effects discussed above. Evidence of stimulus equivalence occurs in all aspects of vision and may be observed at every level of the visual system and in every kind of vision research. Indeed, the equivalence class has long been

a fundamental, if implicit concept in vision research; for a hundred years or more it has been the basis for determining such fundamental functions as the human visibility curves and dark adaptation curves. Also, the concept of equivalence classes of stimuli was applied in early research on single optic nerve fibers. For example, intensity and duration of illumination may be interchanged over a wide range to produce large classes of equivalent stimuli that yield equal responses in the eye of *Limulus* (Hartline, 1934). The visibility curves of single ommatidia were measured by determining an equivalence class of stimuli (Graham and Hartline, 1935). More generally, equivalence is used to map out the spectral sensitivity of photopigments and is the underlying notion of the principle of univariance (Naka and Rushton, 1966; see also Sirovich and Abramov, 1977; Sirovich 1977). Another example is the mapping of a receptive field; here spots of light at different locations and of different intensities form equivalence classes which yield equal responses. Indeed, this is the basis of the very first mapping of a receptive field of a retinal ganglion cell (Hartline, 1940).

Although we have mainly discussed spatial patterns, a parallel treatment of temporal patterns also exists. To give one example, the responses of a *Limulus* optic nerve fiber to a spot of light on the retina modulated in time about the mean level with a square-wave and with properly chosen exponential waves (the temporal analogs of the spatial stimuli in Fig. 3) are almost indistinguishable; the unequal stimuli belong to the same equivalence class (Ratliff, 1977). Finally, as a last example, we mention color mixture experiments, where innumerable objectively different stimuli appear identical. In this case a continuum—the wavelengths of the visual spectrum—gives rise to responses in only a few different cell types—the cones. The net effect of this is to map an infinite dimensional space down to a relatively small finite dimensional space. Thus an infinite variety of different color mixtures can lead to identical responses. (We note in passing that in color mixture experiments the actual physical subtraction of stimuli is not possible. This is circumvented by formally using the operation of subtraction, including its use in defining null stimuli, and then, as a last step, arranging terms so that only additions appear.)

The study of equivalence classes provides a powerful tool for the study of structure and function. In examining any piece of neural network the graph (in the general sense) of response vs stimulus provides detailed information on the nature of the network. In the most extreme case of specialization (which is never realized) each response would correspond to a unique stimulus, and each equivalence class would contain but a single element. Occasionally one does find only one significant equivalence class and an underlying mechanism which can be completely characterized by that class alone. (An example of this is a single photoreceptor, where one equivalence class specifies the absorption function.) Generally, however, one finds many different equivalence classes with numerous elements contained in each one of them. This number and diversity reflects the complexity of the structure and function of the network being considered.

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