After-Effects and the Integration of Patterns of Neural Activity within a Channel

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After-effects and the integration of patterns of neural activity within a channel

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Prolonged inspection of an adapting stimulus changes the appearance of a subsequent test stimulus. There are five distinct viewing conditions under which such 'after-effects' may be generated. These are MON–MON (inspect with one eye, test same eye), BIN–BIN (inspect with both eyes, test both eyes), BIN–MON (inspect with both eyes, test only one eye), MON–BIN (inspect with one eye, test with both) and TRANSFER (inspect with one eye, test with the other eye).

A model based upon the assumption of the linearly additive effects of adaptation generated in 'dominance classes' of cortical units that are driven either by one eye, or the other eye, or by either eye or both eyes together, is described. This model generates predictions concerning the expected relative magnitudes of after-effects generated under the five viewing modes described above, and experiments are described that confirm these predictions.

The model can be extended to generate predictions about other experimental conditions. A more complex version of the model is consistent with electrophysiologically derived estimates of the proportion of cortical units in each dominance class.

1. Introduction

(*a*) *Background*

The electrophysiological discoveries of the past two decades, and particularly the results of recordings from single units in the visual cortex of cat, monkey and other animals, have had the most profound impact upon our thinking about the mechanisms of human vision. The most important single finding was undoubtedly the discovery of stimulus-specific neurons. Such units respond selectively to stimuli which have a particular orientation, or which move in a particular direction, or which generate a particular degree of binocular disparity, and so on. This discovery led directly to the notion that early processing of visual information in man, too, might be carried out by 'channels' consisting of subsets of neurons specializing in the encoding of particular stimulus attributes, and it is in establishing, elucidating and extending this notion that the role of the psychophysicist has been pre-eminent.

In this work many paradigms have been used, such as subthreshold summation, masking and simultaneous interaction. But by far the commonest has been the adaptation–after-effect paradigm. Typically, an observer is exposed for several minutes to a high contrast stimulus, and this exposure affects the subsequent appearance of similar stimuli in some measurable way. It is assumed that if the adapting stimulus is generating activity in some restricted subset of neurons, then prolonged exposure should lead to a reduction in the sensitivity of those neurons. This should then be made manifest by the changed appearance of subsequently presented test stimuli whose encoding involves the participation of at least some of the adapted units.

Within this tradition, two distinct streams of research activity may be discerned. First, there is the search for consistency between psychophysical observations on man and the electrophysiological findings from animal studies. For instance, if adaptation to a particular stimulus attribute can be demonstrated, a channel for the encoding of that attribute is assumed to exist. As John Mollon neatly put it: 'If it adapts, it's there' (Mollon 1974).

Secondly, there are models that are intended to elucidate the relation between sensations and their neural correlates. One example of this approach is the attempt to discover whether the detection of movement depends simply upon the amount of activity generated in neurons tuned to a particular direction of movement, or upon the ratio of activity in neurons tuned to movements in opposite directions (see, for example, Sutherland 1961; Moulden & Mather 1978).

The research described here has its roots in both of these fields of activity, and correspondingly has two main aims. The first is to discover a simple rule which would describe how diverse patterns of activity within a channel might be integrated to yield a unitary percept: are those diverse patterns independent and linearly additive in their effects, or is some more complex algorithm required? The second aim is to try to draw rough quantitative parallels between phenomenology and inferred cortical structure: can visual phenomena be related in some quantifiable way to our assumptions about the functional organization of the human visual system?

The adaptation–after-effect paradigm has one peculiarity that is of special value. Unlike any other manipulation, the technique of adaptation provides a unique opportunity to make a unitary stimulus have more than one sensory consequence at one time, so we can examine the way in which two (or more) patterns of neural activity are integrated into a unified sensation. Non-unitary responses to unitary stimuli may be generated in at least two ways. In the first, the subject may be adapted to two or more stimuli simultaneously, so that a subsequent test stimulus is applied to a neural substrate in which two adapted states coexist. Each of these adaptive states on its own would produce a specific perceptual distortion, and by examining their joint effect one may draw powerful inferences concerning the linearity and additivity of the integration process. Experiments of this kind are currently being carried out in this laboratory, and the results will be described elsewhere. In the second technique, it is arranged that an inspection stimulus adapts only some of the neurons tuned to its particular characteristics, leaving others unaffected. In such a case, if a subsequent test stimulus produces activity in the whole of the appropriately tuned subset, of which some respond normally and some respond abnormally, the question arises: how are the 'normal' and the 'abnormal' signals integrated to give a single percept?

We investigated the after-effects of movement (m.a.e.) and of tilt (t.a.e.). After prolonged inspection of a stimulus moving steadily in one direction, a truly stationary test stimulus appears, for a short time, to be moving in the opposite direction; this is the m.a.e. Similarly, after prolonged inspection of a line or grating tilted, say, 10° clockwise from vertical, a truly vertical test line or grating appears, for a short time, to be tilted a few degrees anticlockwise; this is the t.a.e.

(*b*) *Interocular transfer*

Our starting point was an apparently minor phenomenon associated with the m.a.e., the t.a.e. and with other similar after-effects. This is the phenomenon known as interocular transfer (i.o.t.). If, instead of viewing the adapting and test stimuli with the same eye (or eyes), one adapts with only one eye open and then views the test stimulus only with the *other* eye, an after-effect is still seen, although its magnitude is reduced to about 50–60 % of the monoptic (expose one eye, test same eye) effect. Now the existence of this interocular transfer immediately raises three questions of some theoretical importance. What is the mechanism underlying i.o.t.? Why is i.o.t. smaller than the monoptic effect? Why is the magnitude of i.o.t. a *particular proportion* (about 50–60 %) of the monoptic effect?

This paper is mainly concerned with the third of these questions. The first two questions can be answered fairly easily, and the logic underlying the answer is central to the approach to be developed here.

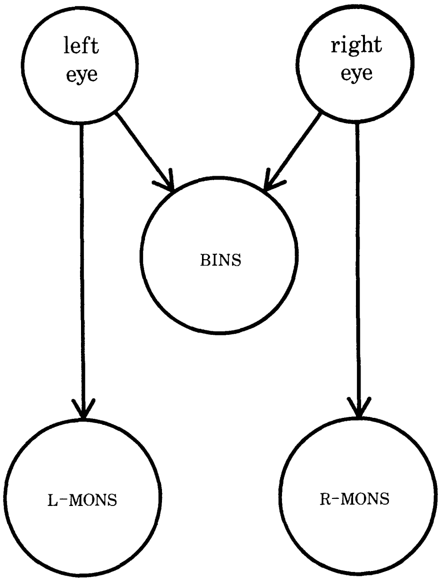

FIGURE 1. Scheme for the simplified three-unit model.

The key to the answers to the first two questions came from the electrophysiological discovery that in the cat and the monkey, cortical neurons could be classified into three broad groups. The neurons in one group could be driven only through the left eye (left monocular units, or L-MONS), those in the second group could be driven only through the right eye (right monocular units, or R-MONS), and those in the third group could be driven by either eye or by both eyes together (the binocular units, or BINS). These findings are schematized, albeit in a rather simplified manner, in the diagram in figure 1. Such a scheme can provide the basis of an explanation for i.o.t. Assume that the left eye only is adapted and the right eye only is tested. During the inspection phase the L-MONS and the BINS will become adapted; the R-MONS will not. During the test phase, the R-MONS and the BINS will be involved in signalling the test stimulus, and of these the BINS will be giving an 'abnormal' (adapted) signal while the R-MONS will give a 'normal' (unadapted) signal. As long as these two signals are integrated in some way, the resultant must be a signal that is neither 'normal' nor as 'abnormal' as if the R-MONS had also been adapted, as they would have been had the inspection phase involved the right eye and not the left.

Thus, our first two questions might be answered as follows: i.o.t. is mediated by adaptation of the BINS, and is smaller than the monoptic effect because only some of the units driven during the test phase are adapted.

(*c*) *The three-class model*

This model can in fact be extended, formalized and tested experimentally. The model can be extended by considering the monoptic and transfer conditions already described, and by adding three other possible viewing conditions. The five possible viewing modes are illustrated in figure 2. (It should be noted that for the four conditions that involve monocular viewing with the left or right eye in either the inspection or the test phase or both, there will be a symmetrical condition in which the other eye is used.) However, before predictions can be generated the notions employed in the explanation of i.o.t. must be formalized.

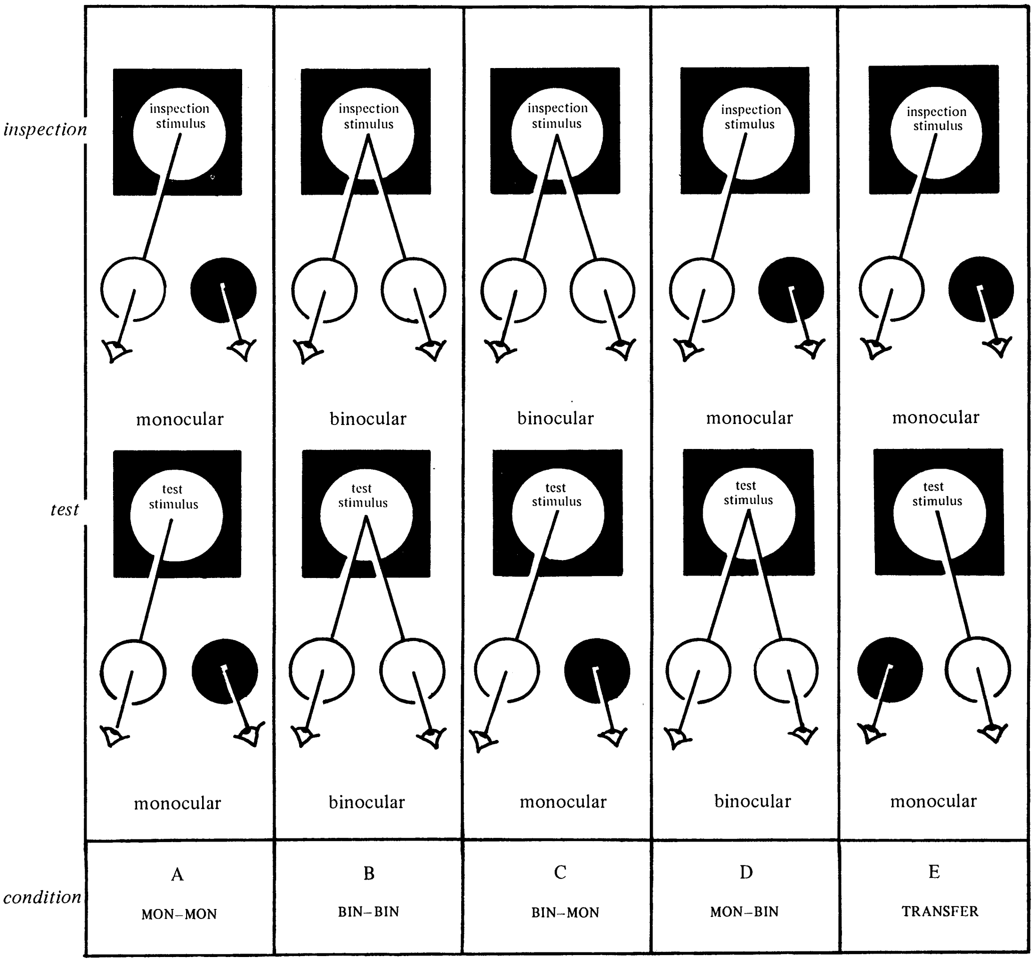

Figure 2. The five possible viewing modes involving inspection or test with either one eye, the other eye, or both eyes. For every case in which monocular viewing with the left eye was used for a condition, the symmetrical condition involving the right eye was also tested.

The formalization depends critically upon two key propositions, which are as follows:

(i) *The partitioning postulate*: the set of cortical units of which a channel is composed may be partitioned exhaustively into three mutually exclusive and independent subsets, namely the L-MONS, the R-MONS and the BINS.

(ii) *The ratio postulate*: the magnitude of an after-effect in a particular viewing mode depends upon the proportion of the units that are driven during the test phase that have previously been driven, and therefore adapted, during the inspection phase.

Two corollaries of the ratio postulate are that (1) units that are adapted during the inspection phase but that are not driven during the test phase do not contribute to the after-effect; and (2) units that are driven during the test phase but that have not been adapted during the inspection phase tend to reduce the after-effect.

The partitioning postulate is, of course, extremely naïve in electrophysiological terms. Electrophysiologists, following Hubel & Wiesel (1968), have generally classified cells into seven dominance classes. The units of class 1 are driven only by one eye, say the left; those of class 2 are driven by both eyes, but much more vigorously by the eye driving class 1; class 3 units are similar, but the dominance is less marked; class 4 contains units in which each eye is equipotential; and classes 5, 6 and 7 are symmetric with classes 3, 2 and 1, with the other eye dominating. Moreover, many binocular units are driven much more vigorously by both eyes together than by one eye alone (see, for example, Hubel & Wiesel 1968, p. 239). In fact, most of the objections that might be raised on these grounds are met by my five-unit model, involving three degrees of response vigour, which is described in § 3*a*, and which generates precisely the same predictions as the simple three-unit model. In view of the greater tractability of the three-unit model it will continue to be used here for ease of exposition.

The ratio postulate is a plausible one, but is by no means inevitable. Lehmkuhle & Fox (1975), for example, have suggested that after-effect magnitude might depend solely upon the *total number* of units both adapted and tested. The essential assumption underlying the ratio postulate is that if unadapted cells respond during the test phase, then their veridical signals will tend to dilute the distorting effect of the adapted units.

TABLE 1. THE PREDICTION OF ORDER RELATIONS, THREE-CLASS MODEL: THE DERIVATION OF THE EXPRESSIONS USED TO PREDICT THE ORDER RELATIONS BETWEEN THE MAGNITUDES OF AFTER-EFFECTS GENERATED UNDER THE FIVE VIEWING MODES

	A	B	C	D	E
condition	(MON–MON)	(BIN–BIN)	(BIN–MON)	(MON–BIN)	(TRANSFER)
units tested	$M+B$	$2M+B$	$M+B$	$2M+B$	$M+B$
of units tested, those that have been adapted	$M+B$	$2M+B$	$M+B$	$M+B$	B
expression for relative A–E magnitude	$\frac{M+B}{M+B}$	$\frac{2M+B}{2M+B}$	$\frac{M+B}{M+B}$	$\frac{M+B}{2M+B}$	$\frac{B}{M+B}$
relative magnitude	$A = 1$	$B = 1$	C = 1	D < 1	$E < D$

Hence order relations: $A = B = C > D > E$.

Table 1 shows how the partitioning postulate and the ratio postulate can be combined to predict the order relations between the after-effects generated in the five viewing modes. For example, in the condition MON–BIN (adapt monocularly, test binocularly), the units driven during the test phase are the L-MONS, the R-MONS and the BINS; of these only the L-MONS and the BINS (or the R-MONS and the BINS, according to the sub-condition involved) will have been adapted during the inspection phase. The predicted relative magnitude of the after-effect is thus indicated by the expression $(M+B)/(2M+B)$, which is less than unity. Simple algebra will show that the expression $B/(M+B)$, the expression which relates to the TRANSFER condition (condition E in table 1) must be smaller than the expression $(M+B)/(2M+B)$. The predicted order relations between the after-effects in the five viewing modes are thus $A = B = C > D > E$.

This predicted relation was tested in two experiments, one with the m.a.e. and the other with the t.a.e.

2. EXPERIMENTAL TESTS

The stimulus was a disk with eight black and eight white sectors, the Michelson contrast C being 0.84; the disk subtended 9.5° at the eye and was surrounded by a radically striped stationary annulus 5° in width. The disk rotated at 25 rev./min in the inspection phase and was stationary in the test phase. Subjects viewed the rotating disk for 1 min and then recorded the duration of their m.a.e. by holding down a Morse key. By means of shutters it was arranged that viewing was either with the left eye, with the right eye, or with both eyes.

There were seven naïve subjects, each of whom attended for four 1 h sessions. During the first session, subjects were given their first experience of the m.a.e. and were given practice in establishing their criterion for its cessation. They were also given experience of the various viewing modes so that they could become accustomed to the operation of the shutters. No record was taken of m.a.e. durations during this session.

During each of the three remaining 1 h sessions, each viewing mode was presented three times, so that for each of the five conditions each of the seven subjects gave nine m.a.e. durations. Each block of five conditions was presented in a different random order, with a recovery period of at least 2 min between each condition. The mean duration for each condition was thus based upon 63 observations, and these means are summarized in figure 3.

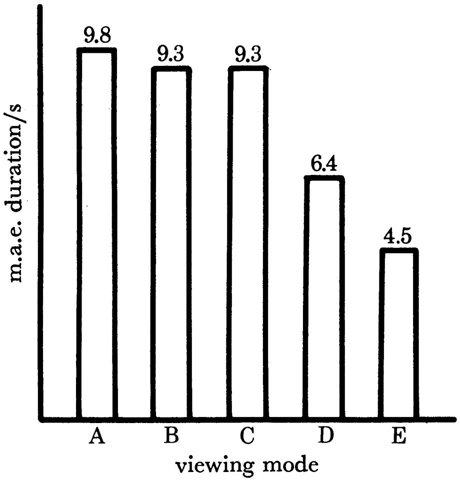

FIGURE 3. Mean m.a.e. durations in seconds for each viewing mode (N = 7, 63 observations per condition). A, MON–MON; B, BIN–BIN; C, BIN–MON; D, MON–BIN; E, TRANSFER. Standard errors: A, 2.38; B, 1.99; C, 2.13; D, 1.46; E, 1.60.

(*b*) *The t.a.e. experiment*

The inspection and test stimuli were back-projected square-wave gratings having a spatial frequency of 1.52 cycles/deg and a Michelson contrast of 0.9. There were three viewing fields each 8.0° in diameter; one field was to the right of the subject and was potentially visible only to the right eye via a half-silvered mirror; a similar field to the left of the subject was potentially visible only to the left eye via a second mirror. These were the inspection fields and contained gratings which, when viewed by the subject, were tilted 10° anticlockwise. These fields were illuminated only during the adaptation phase of the experiment. The third field was located straight ahead of the subject and was viewed through the half-silvered mirrors. This field was the test field and contained a grating whose orientation could be adjusted by the subject, and which was illuminated only during the test phase. By means of shutters it was arranged that during the inspection phase either the right eye only, or the left eye only, viewed its respective inspection field, or both eyes together viewed their respective, optically aligned, inspection fields. Similarly, in the test phase the test field could be made visible either to the right eye only, or to the left eye only, or to both eyes together. There were 15 subjects in all, each of whom was experienced in the use of this apparatus. Each subject attended for a total of about 2 h, and each yielded two data points for each condition (one based upon the use of the right eye and one based upon the use of the left eye in each condition involving monocular viewing; the BIN–BIN condition was also presented twice). These data were each based upon five settings, as described below, and were pooled to give a single measure for each of the five conditions. The mean t.a.e. for each condition was thus based upon 15 (subjects) × 2 (eyes) × 5 (settings) = 150 settings in all.

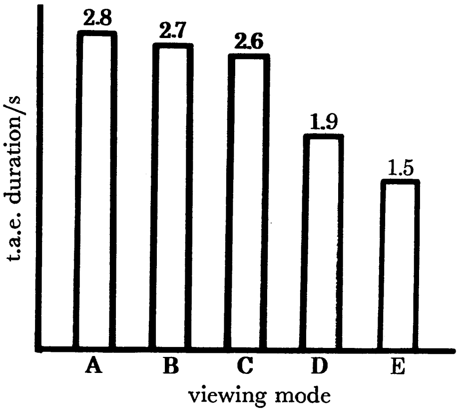

FIGURE 4. Mean t.a.e. magnitudes in degrees for each viewing mode ($N = 15$, 150 observations per condition). Symbols as for figure 3. Standard errors: A, 0.29; B, 0.28; C, 0.21; D, 0.20; E, 0.19.

The procedure in any one condition was as follows. Before adapting, and using the eye or eyes to be used in the later test phase, the subject set the movable grating to appear vertical; he made five such settings in succession, and the mean of these settings was taken as the baseline for that condition. He then viewed the tilted inspection stimulus with one eye or with both eyes, as appropriate, for 60 s. At the end of that time the test field was presented for 4 s, followed by the inspection field for 6 s and so on, with the shutters changing in synchrony with the illumination of the fields to give the appropriate viewing conditions in each phase. The alternating presentation of inspection and test fields was repeated until the subject had adjusted the test field to appear vertical. Five such adapted settings were made in succession; the difference between the mean of these settings and the mean of the baseline settings was taken as the measure of t.a.e. for that subject in that sub-condition.

The mean t.a.e. over all 15 subjects in each of the five conditions is shown in figure 4.

(*c*) *Results*

In the m.a.e. experiment (see figure 3), conditions A, B and C were not significantly different (Friedman's analysis of variance by ranks gave a χ_r^2 of 0.85; for $N = 7$, $k = 3$ a value of $\chi_r^2 = 6.00$ is required for significance at the 0.052 level). The smallest of these three (condition B) was compared with condition D; in all of the matched pairs for each subject the value for condition D was smaller than that for condition B. Similarly, each value for condition E was smaller than that for condition D. In the t.a.e. experiment (see figure 4), conditions A, B and C were again not significantly different (Friedman's test, $\chi_r^2 = 2.8$, $0.1 > p > 0.05$). On Wilcoxon's test, condition D was significantly ($0.005 > p$) smaller than condition B, the smallest of conditions A, B and C. Similarly, condition E was significantly ($0.025 > p > 0.01$) smaller than condition D.

A similar pattern of results was obtained from an experiment on the simultaneous tilt illusion, in which the inducing and test stimuli were presented simultaneously instead of successively. (In this experiment the condition equivalent to TRANSFER was a dichoptic condition in which one eye viewed the tilted inducing grating while the other eye viewed the test grating). The results, in degrees of induced tilt, were: condition A, 0.96°; B, 1.12°; C, 1.12°; D, 0.69°; E, 0.42°.

It is worth mentioning that an attempt was made to measure the eye dominance of the 15 subjects used in the t.a.e. experiment and to compare the magnitude of interocular transfer from the dominant to the non-dominant eye with the reverse condition. No consistent effect was found, but this may well have been due to an inadequate measure of dominance. Other workers (see Wade (1976) for a discussion of this point) have shown that there is an effect of eye dominance. Such an effect could very easily be incorporated into the model offered here by the simple addition of weighting functions, and cannot have been a source of systematic bias in the experiments described above because in every condition involving monocular inspection both the left and the right eye were used in separate sessions.

It will be recalled that the model based upon the combination of the partitioning and ratio postulate led to the prediction that the order relations between the magnitudes of after-effects generated under the five viewing conditions was A = B = C > D > E. This prediction has been confirmed. The notion that sensations depend upon the linearly additive effects of the activity of independent groups of detectors within a channel appears to be well founded.

(*d*) *A further prediction*

The simple algebraic expressions shown in table 1 allow a further quantitative prediction of the precise relative magnitudes of the MON–BIN (D) and TRANSFER (E) effects where 'relative magnitude' means the magnitude of the after-effect generated under conditions D and E expressed as a proportion of the after-effects generated under conditions A, B and C. If $D = (M+B)/(2M+B)$ and $E = B/(M+B)$, it can be shown by simple substitution that $D = 1/(2-E)$. In other words, the structure of the model requires that there should be a fixed and specifiable relation between the relative magnitude of the MON–BIN effect and that of TRANSFER. Table 2 shows the obtained and predicted magnitudes based upon the findings from the two experiments described earlier and upon an earlier m.a.e. experiment similar to that described above. Figure 5 shows the function $D = 1/(2-E)$ for all values of D, together with the individual subject data on which the means of table 2 are based. The straight line is the best linear fit for the data. The agreement is good, and this, together with the correct prediction of the order relations between the five viewing modes, lends considerable support to the model.

Table 2. Predicting mon–bin from transfer: the relation between the mon–bin (D) after-effect and the transfer (E) after-effect, when both are expressed as proportions of the mon–mon, bin–bin and mon–bin effects, is described by the expression $D = 1/(2-E)$

	obtained value of E (transfer)	if	predicted value of D (mon–bin)	obtained value of D (mon–bin)
m.a.e. experiment I	0.47	$D = 1/(2-\mathrm{E})$	0.65	0.67
m.a.e. experiment II	0.43		0.64	0.65
t.a.e. experiment	0.56		0.69	0.70

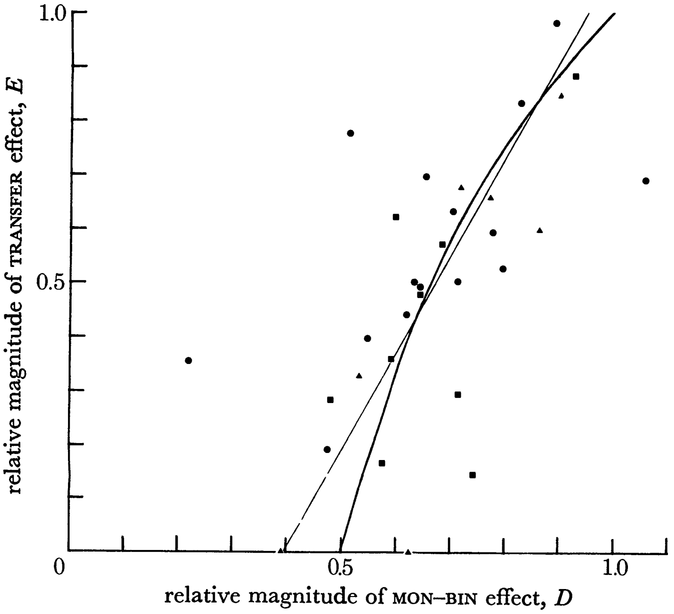

Figure 5. Function showing the predicted relation (curved line) between the relative magnitude of the mon–bin condition (D) and that of the transfer condition (E), according to the expression $D = 1/(2-E)$. Data points are individual subjects' measures from experiment 1 (m.a.e.), experiment 2 (t.a.e.) and a similar m.a.e. experiment not described here. The straight line is the line of best fit to the data determined by the method of least squares.

(*e*) *A further experimental manipulation: the r.a. experiment*

The use of a novel technique developed in our laboratory permits a further manipulation: this technique permits one to vary the magnitude of an after-effect generated in particular subsets of detectors in response to a constant adapting stimulus. Consider the effects of adapting, either alternately or simultaneously, to two identical stimuli moving in opposite directions. This will produce, of course, no *differential* state of adaptation in the detectors tuned to those directions of movement, and consequently no m.a.e. However, *both* sets of detectors will be adapted to some degree, and the differential adaptive effect of a subsequent unidirectional stimulus will be less than it would have been had that stimulus been applied to an unadapted system. In short, the effects of 30 s of adaptation should be less after a period of 'repeated alternations' (r.a.) than it would have been before it. Now if r.a. is applied to only some of the detectors involved in a particular viewing mode, it should be possible to predict the relative magnitudes of the after-effects so generated by considering the altered relative contributions of the sets of detectors involved.

The scheme of such an experiment is illustrated in figure 6. Conditions A and B are baseline MON–MON and TRANSFER conditions respectively. Condition *C* is a MON–MON condition preceded by r.a.; the predicted magnitude of the after-effect from this condition should be less than for condition A. Condition D is also a MON–MON condition, but one that is preceded by a period of r.a. applied to the eye *not* involved in the main adapt–test procedure. This procedure involves one set of MONS and the BINS; of these, the BINS will have been affected by r.a. and their contribution to the after-effect will be thereby reduced.

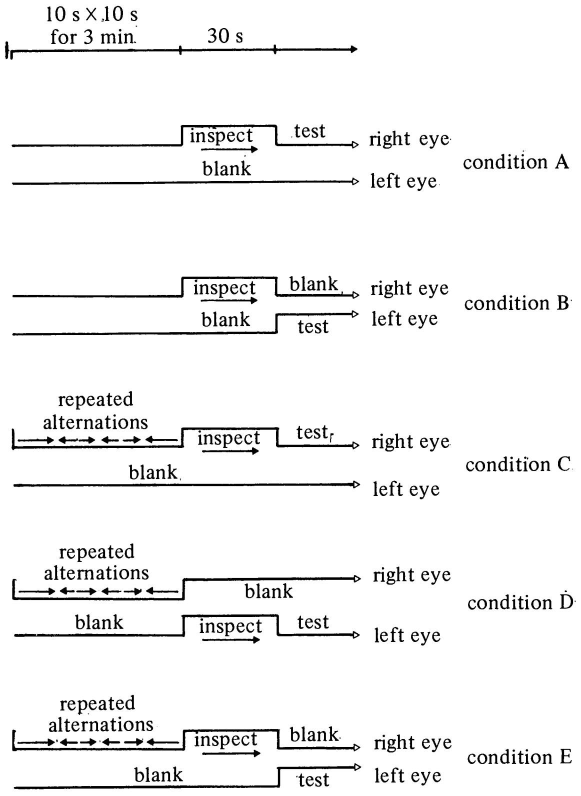

FIGURE 6. The procedure employed in each of the five conditions of experiment 3.

The after-effect from D should be less than that from A, but greater than that from C, in which *all* of the units contributing to the after-effect will have been affected by r.a. Condition E is a TRANSFER condition with the eye used in the inspection phase being exposed to r.a. beforehand. This should reduce the magnitude of the differential adaptation generated in the MONS and BINS that are driven during the inspection phase; of these, the BINS mediate the transferred effect, which should therefore be less than that in the baseline condition, condition D. The predicted size of the after-effect in the five conditions is thus $A > D > C$ and $A > B > E$.

The details of the experiment were precisely the same as those for the m.a.e. experiment described earlier, with the following exceptions. There were ten subjects, each of whom received a brief period of training to establish their criterion for the cessation of m.a.e. Whenever an r.a. condition was administered, the temporal sequence was as follows. For 3 min the subject viewed with only one eye (left or right according to the condition) a disk whose direction of rotation reversed every 10 s. At the end of this period, he viewed unidirectional rotation for 30 s again with the appropriate eye, and then viewed the stationary disk through the eye appropriate to the test phase, holding down a Morse key for as long as he could see an m.a.e. There was a 5 min recovery period after every condition involving repeated alterations, and a 2 min recovery period after other conditions. Each subject attended for two $1\frac{1}{4}$ h sessions, and during each session he experienced each of the five experimental runs twice, the ten conditions within a run being presented in a different random order for each subject. Each mean m.a.e. duration is thus based on 40 observations. The results are shown in table 3.

TABLE 3. RESULTS OF REPEATED-ALTERNATION EXPERIMENT

(Mean after-effect durations in seconds generated under the conditions represented in figure 6 and described in the text. $N = 10$.)

condition	A	B	C	D	E
mean m.a.e. duration/s	9.90	5.91	4.21	6.34	2.09
s.e.	1.19	0.83	0.67	0.82	0.43

The first set of predictions was that $A > D > C$; ideally, then, the rank order of these conditions should be 1, 2, 3 for each subject. Eight of the ten subjects showed this pattern of results. The probability of such a result occurring by chance is given by the binomial expansion for $N = 10$, $x = 8$, $p = \frac{1}{6}$, $q = \frac{5}{6}$. The associated p value is very much less than 0.001, and the first set of predictions is confirmed. The second set of predictions was that $A > B > E$; this was true for all ten subjects, and no statistical analysis is necessary. The experimental predictions are, therefore, all confirmed.

(*f*) *Summary*

So far, then, it has been possible to account for the existence of i.o.t., to account for the fact that it is smaller than the monoptic effect, to predict the rank order of the magnitudes of the after-effects in all five viewing modes, both with and without r.a., and to predict the precise relative magnitude of the MON–BIN and TRANSFER effects.

All of this, however, has been achieved within the framework of a three-class model, and it remains to be demonstrated that the predictions derived from this simple model may also be derived from a five-class model based upon more plausible assumptions, particularly with regard to the relative responsivity of binocular units to input either from one eye only or from both eyes together.

3. EXTENDING THE MODEL

(*a*) *The five-class model*

The units in the five classes of this extended model are assumed to have the following properties. Units in classes 1 and 5 are purely monocular. Units in class 3 may be driven equally by either eye but more strongly by both eyes together. Classes 2 and 4 contain units that are similar to those in class 3 except that one eye is more effective than the other. Assume for simplicity that a maximum of four different relative firing rates may be produced in a unit, depending upon the viewing conditions, and that the degree of adaptation generated in a class of units (and therefore the contribution of that class to the after-effect) is proportional to the relative firing rate. Let the maximum possible firing rate be unity, the minimum zero, and let two intermediate values be $1-x$ and $1-y$, where $y > x$. Let purely monocular units, those in classes 1 and 5, have only two possible levels of firing: zero or unity according to the input mode (ignoring other possible determinants of firing rate such as stimulus contrast). Let equipotential binocular units, those in class 3, have three possible relative firing rates: zero, $1-x$ (when driven by one eye only) and unity (when driven by both eyes together). Let unequal-dominance binocular units, those in classes 2 and 4, have four possible firing rates: zero, $1-y$ (when driven by the non-dominant eye), $1-x$ (when driven by the dominant eye) and unity (when driven by both eyes together). Let the degree of adaptation generated in each class of unit in a particular condition be directly proportional to the firing rate, so that after adaptation a unit will have either unit gain (if it has not been driven during the adaptation phase); a high gain, H, if it has been driven at the relative rate of $1-y$; a medium gain, M, if it has been driven at the relative rate of $1-x$; or a low gain, L, if it has been driven at its maximum (relative firing rate of unity).

Table 4. Firing rates and subsequent gains, five-class model: the relative firing rates assumed to be generated in each dominance class by each of the three input modes, together with the gains of the classes after adaptation

dominance class ...	1	2	3	4	5	
L–MON						
firing rate	1	$1-x$	$1-x$	$1-y$	0	1
subsequent gain	L	M	M	H	1	2
R–MON						
firing rate	0	$1-y$	$1-x$	$1-x$	1	3
subsequent gain	1	H	M	M	L	4
BIN						
firing rate	1	1	1	1	1	5
subsequent gain	L	L	L	L	L	6

This argument is summarized in table 4, which shows the dominance classes (classes 1–5), the various potential firing rates (unity, $1-x$, $1-y$, zero) for each class in each possible viewing condition (right monocular, left moncular or binocular), and the various gains (unity, H, M of L) resulting from these firing rates. The relative firing rate in a unit after adaptation in a particular condition will be given by the product of its potential relative firing rate in that condition and the gain of the unit after adaptation. For example, in a left monocular adaptation phase, a class 4 unit will have been driven at a relative firing rate of $1-y$ (see line 1 of table 4); its gain will subsequently be H (line 2). If the unit is now driven in a right monocular test phase, which would normally drive the unit at a relative firing rate of $1-x$ (see line 3), the post-adaptation relative firing rate will be $H(1-x)$. In this way it is possible to describe the post-adaptation relative firing rates of the units driven in a particular test phase. If the magnitude of an after-effect in any condition is proportional to the ratio (in terms now of *relative firing rates*) of units driven in both adapt and test phase to units driven in test phase, then the relative magnitudes of the after-effects will be reflected by the ratios in table 5. The first three ratios are obviously unity, since of the units driven during the test phase, all are adapted during the inspection phase. D is clearly less than unity, and it can be demonstrated quite simply that E must be smaller than D. It is clear that the predictions from this five-class model are identical with those from the three-class model, but it is not open to the objections to the latter described in § 1*c*.

Table 5. The prediction of order relations, five-class model: the expressions, derived from the assumptions represented in table 4 and described in the text, that can be used to predict the order relations between the magnitudes of after-effects generated under the five viewing modes

adaptation condition	test condition		
L–MON	L–MON	$\dfrac{L+M(1-x)+M(1-x)+H(1-y)}{L+M(1-x)+M(1-x)+H(1-y)}=1$	A
BIN	BIN	$\dfrac{L+L+L+L+L}{L+L+L+L+L}=1$	B
BIN	L–MON	$\dfrac{L+L(1-x)+L(1-x)+L(1-y)}{L+L(1-x)+L(1-x)+L(1-y)}=1$	C
L–MON	BIN	$\dfrac{L+M+M+H}{L+M+M+H+1}<1$	D
L—MON	R–MON	$\dfrac{M(1-y)+M(1-x)+H(1-x)}{M(1-y)+M(1-x)+H(1-x)+1}<D$	E

(*b*) *The proportion of units in each class*

Up to this point, the issue of the relative proportions of units in each dominance class has been ignored, because the prediction of order relations between the magnitudes of after-effects generated by the five viewing modes is quite independent of this factor, with two constraints. First, if a subject had no BINS, then the mechanism for the mediation of transfer would not exist; TRANSFER would be zero. (It is: subjects with a history of strabismus, who are stereoblind, and who by inference have failed to develop binocular units, do not show transfer; see, for example, Movshon *et al.* (1972) and the cautionary note by Hess (1978).) If equal numbers of monocular units were associated with each eye, the MON–BIN effect should be exactly 50 % of the MON–MON, BIN–BIN and BIN–MON effects. Secondly, if *all* of the units in a channel were binocularly driven, transfer would be 100 % and so would the MON–BIN effect.

Nevertheless, although the order relations are independent of the proportions of units in each class, it is obvious that the *precise relative magnitudes* of the TRANSFER and MON–BIN effects must be dependent upon this factor. This consideration raises the question of whether it might be possible to estimate those proportions given the exact relative magnitude of these effects. It is, but only at some cost in terms of the plausibility of the assumptions adopted. It is necessary to assume that class 3 units are driven equally strongly by either eye alone or by both eyes together, and that class 2 and class 4 units are driven as strongly by their dominant eye as both eyes together. Given these assumptions, the argument may be developed as follows.

It is assumed that the magnitude of the after-effect generated in a particular condition is a linearly additive function of the 'contribution' of each class of unit driven during the test phase. It is further assumed that the contribution of a class of unit depends first on the proportion of units in a particular class, and secondly upon the degree to which the units in that class have been adapted during the inspection phase, this in turn being directly proportional to the degree to which those units have been driven during the inspection phase.

In figure 7, the five classes of unit described above are represented along the abscissa, and the ordinate represents the proportion of units in each class; this proportion is of course unspecified, so that the overall shape of the distribution is entirely hypothetical. The width, again unspecified, of each column represents the maximum firing rate and hence the maximum potential degree of adaptation for each class of unit. The shaded areas represent the amount of firing in each class as a function of the three types of presentation mode, left monocular, binocular, or right monocular. The width of the shaded areas may take one of three values: zero, unity, and some unknown value k. This value k represents the degree to which units in classes 2 and 4 are driven by the non-dominant eye; consequently $1-k$ represents the degree (as a function of maximal firing rate) to which a unit in that class is *not* driven by input from the non-dominant eye.

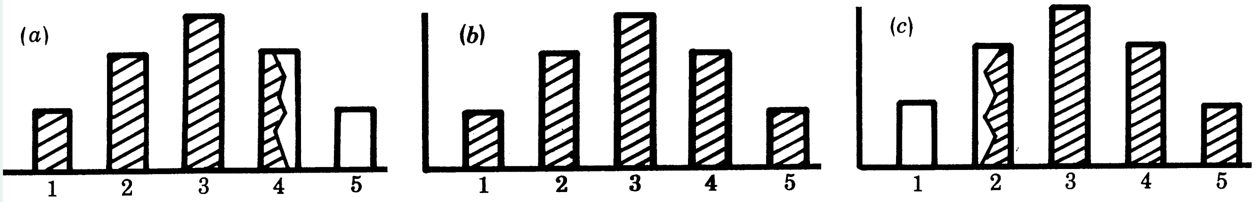

FIGURE 7. Illustrating the concept of the area $1 > k$. On the abscissa are the five classes of eye dominance described in the text; the ordinate represents the (purely imaginary) proportion of units in each class; the hatching represents the degree to which a class of units is driven (and therefore adapted) by a particular viewing mode. The unhatched area in classes 2 and 4 represents the quantity $1 > k$, being the degree to which a class of units is not driven by monocular exposure through its non-dominant eye. (*a*) L-MON presentation; (*b*) BIN presentation; (*c*) R-MON presentation.

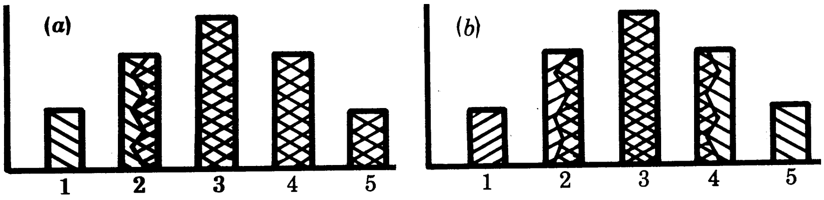

FIGURE 8. Conventions as for figure 7. The figure shows the degrees of overlap between the amounts of firing generated in the inspection phase and in the test phase in the various dominance classes. (*a*) The overlap in the condition R-MON–BIN; (*b*) the overlap in the condition TRANSFER.

The magnitude of an after-effect is a function of the extent to which the area representing the amount of adaptation generated during the inspection phase overlaps the area representing the amount of firing generated during the test phase. (This 'degree of overlap' is simply a spatial representation of the ratio postulate described in § 1*c*.) The three possible extents of overlap are, first, *complete* (as in MON–MON, BIN–BIN and BIN–MON, when all of the tested cells have previously been adapted); secondly, *intermediate* (as in MON–BIN, where the whole of the area in class 1 and the area $(1-k)$ in class 2 is non-overlapping); and thirdly, *small* (as in TRANSFER, where the whole of the areas in classes 1 and 5, and the two areas $(1-k)$ in classes 2 and 4, are non-overlapping). The overlap in the MON–BIN and the TRANSFER cases are illustrated in figure 8. Let the sum of the area in class 1 (or 5) and the area $(1-k)$ in class 2 (or 4) be called W. Then the overlap in MON–MON, BIN–BIN and BIN–MON is unity; the overlap in MON–BIN is $1-W$; and the overlap in the case of TRANSFER is $1-2W$. If the sum of the areas taken over all classes is unity, than a quantity $V = 1-2W$ may be defined. A set of expressions representing the relative magnitude of the after-effect in each condition may now be derived; these expressions are in terms of areas V and W, and are given in table 6. These ratios are obviously isomorphic with the expressions derived from the three-class model (see table 1), and differ only in that the symbols

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V and W, representing areas derived from the five-class model, replace the symbols M and B, representing class types in the three-class model.

V and W are in terms of proportional areas; the after-effects are expressed as proportions of the maximal after-effect, so the expressions may be treated as true equations. In the expression for the MON–BIN after-effect,

$$D = (V+W)/(V+2W); \quad V+2 = 1; \quad D = V+W; \tag{1}$$

similarly $E = V/(V+W)$; from (1),

$$E = V/D; \quad V = DE. \tag{2}$$

Therefore, from (1) and (2),

$$D = DE+W, \text{ or } W = D-DE. \tag{3}$$

Now let the proportion of units in class 1 (and class 5) be a; let the proportion of units in class 3 be b; then the proportion of units in class 2 (and class 4) must be $\frac{1}{2}(1-2a-b)$. In the L–MON–BIN paradigm, class 1 is driven at its maximum; its contribution to the after-effect is therefore simply equal to the proportion of units in that class, namely a. Similarly, the contributions of class 2 and class 3 are respectively $\frac{1}{2}(1-2a-b)$ and b. The contribution of class 4 is equal to that part of area W that is not accounted for by the proportion of units in class 5, which is a; class 4 therefore contributes $(W-a)$. But $W = D-DE$ (equation (3) above), so the contribution of class 4 is $(D-DE-a)$. All of these contributions are hypothesized to be linearly additive, so that the relative magnitude of the after-effect in the MON–BIN condition (D) may be expressed as

Table 6. The prediction of order relations in terms of the quantities V and W

(Note the isomorphism of this set of expressions with the set shown in table 1.)

BIN–BIN	MON–MON	BIN–MON	MON–BIN	TRANSFER
$\frac{V+2W}{V+2W}$	$\frac{V+W}{V+W}$	$\frac{V+W}{V+W}$	$\frac{V+W}{V+2W}$	$\frac{V}{V+W}$

$$D = a+\tfrac{1}{2}(1-2a-b)+b+(D-DE-a).$$

Making this explicit for b, we obtain

$$b = 2DE+2a-1. \tag{4}$$

In other words, given only an estimate of the proportion of units in class 1 (that is, of a) and an estimate of E (the TRANSFER effect), it is possible first to calculate a value for D (since $D = 1/(2-\mathrm{E})$) and then a value for b, the proportion of units in class 3. Since the sum of the proportions in each class must be unity it is simple to derive an estimate for classes 2 and 4 by subtraction.

The data of Hubel & Wiesel (1968) provide a means of testing this model. They classified monkey cortical cells into seven dominance classes and their text-figure 14 shows how their sample of 177 units were distributed among these classes. These data, however, describe dominance classes in terms of whether the dominant eye was ipsilateral or contralateral to the hemisphere from which the recordings were made, rather in terms of their being left-eye or right-eye dominant. Assume that all of these recordings were taken from the left hemisphere; then units described as contralaterally driven would be driven by the right eye, and units described as ipsilaterally driven would be driven by the left eye. Now assume that a similar distribution could be found in the right hemisphere: 'contralateral' would mean left-eye driven and 'ipsilateral' right-eye driven. To obtain an estimate of the proportions of cells, in both hemispheres taken together, that are driven by a particular eye, it would be necessary to take the two hypothetical identical distributions described above and to fold one on to the other. In this way the so-called ispilateral units from the left hemisphere (left eye driven) would be added to the so-called contralateral units from the right hemisphere (also left-eye driven), so that the classes are added as follows: 1+7, 2+6, 3+5, 4+4, 5+3, 6+2, 7+1. If the distributions resulting from this 'foldover' transform are then collapsed so that the new classes 2 and 3, and 5 and 6 are combined, a five-class categorization results in which the characteristics of the units in each class matches those of the units in the five-class model described above.

Table 7. Estimating the proportion of units in each dominance class

(The upper row shows the data from Hubel & Wiesel (1968), text-figure 14, transformed as described in the text. The lower row shows the distribution estimated from the model given the value of 17.3% for *a*, the proportion of units in class 1 and class 5, and the value of 52.4% for the relative magnitude of the TRANSFER (E) effect, based upon expression (4) in the text: $b = 2DE+2a-1$.)

dominance class...	1	2	3	4	5
distribution from Hubel & Wiesel	17.3%	30.2%	5%	30.2%	17.3%
estimated distribution	(17.3%)	29.9%	5.6%	29.9%	(17.3%)

The proportion of units in class 1 and in class 5 computed in this way is 0.173 (17.3%). From three m.a.e. experiments and one t.a.e. experiment (a total of 41 subjects and 289 observations) an average value for the TRANSFER effect (E) of 0.524 (52.4%) was obtained. (The data from these experiments are given in full in Moulden (1974).) The derived value for the MON–BIN effect (D), from the expression $D = 1/(2-\mathrm{E})$, is 0.678 (67.8%). These values may be substituted in (4) to give $b = 2(0.678)(0.524)+2(0.173)-1 = 0.056$. The estimated proportion of units in class 3 is thus 5.6%, and by subtraction the proportions in class 2 and in class 4 are 29.9%. In table 7 these estimates are compared with the observed values from Hubel & Wiesel (1968).

The agreement is at first sight very impressive, but a number of qualifying factors must be borne in mind. The predicted distribution is actually derived from the prediction of only one value, that for the proportion of units in class 3 (5.6%). While the difference between this figure and the observed value of 5% is apparently small, the discrepancy of 0.6%, when expressed as a proportion of the predicted value, actually represents an error in prediction of 12%. Moreover, the statistical reliability of the Hubel & Wiesel estimates is indeterminate; the estimates derived above are based upon the implausible assumption that binocular units fire as strongly to one eye as to both together; and the obtained values depend critically upon the obtained value of transfer (here 52.4%), and a difference of a small percentage in this value makes a dramatic difference to the predictions. The agreement in this case should perhaps be taken as indicating only that the model outlined here is not inconsistent with electrophysiologically derived dominance distributions.

4. Conclusion

The model described here is based upon the assumptions that sets of cortical units making up a channel in the human visual system may be partitioned exhaustively into five mutually exclusive subsets of specified dominance, and that effects generated within these subsets are independent and linearly additive. An after-effect generated in a particular viewing mode thus depends upon the ratio between the number of tested units that have previously been adapted and the total number of units tested.

A few details remain to be settled. First, several workers (see, for example, Henry *et al.* 1969; Creutzfeldt *et al.* 1971; Noda *et al.* 1971) have described a very few binocular units for which stimulation via one eye was excitatory while stimulation via the other eye was inhibitory; it is difficult to assess the impact of this discovery upon the plausibility of the model described here. Secondly, Lehmkuhle & Fox (1976) have shown that interocular transfer is increased in magnitude if the non-adapted eye, rather than being occluded (as it was in the experiments described here), views a homogeneous bright field during the inspection phase. The present model can offer no explanation for this phenomenon. Finally, Wade & Wenderoth (1978), using a homogeneous field rather than occlusion for the unadapted eye during the inspection phase, failed to confirm that the condition MON–BIN results in a smaller tilt after-effect than either MON–MON, BIN–BIN or BIN–MON. The reason for this discrepancy is unclear.

Nevertheless, the broad features of the model appear to be well established, and it has two particular merits, namely simplicity and explicitness, which make it easy to test. One particularly intriguing possibility concerns the use of cyclopean stimuli, which would permit one to drive the binocular units without involving the monocular units. By using purely cyclopean stimuli in the inspection (or test) phases and monocular or binocular stimuli in the test (or inspection) phases, it would be possible to derive an independent estimate of the contribution of binocular units to an after-effect; this should agree with the estimates put forward in this paper.

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