Overprediction and blocking in the McCollough aftereffect

MICHAEL E. SLOANE, JOHN W. P. OST, DEBORAH B. ETHERIEDGE,
and STEPHEN E. HENDERLITE

University of Alabama at Birmingham, Birmingham, Alabama

The Rescorla-Wagner theory (Rescorla & Wagner, 1972) of associative learning offers specific predictions about the associative strength of CS-US pairs when two or more CSs are conditioned to the same US separately and subsequently paired in a compound with the same US. The magnitude of orientation-contingent color aftereffects (AEs) was used as an index of associative strength in this study. The results of experiments using an "overprediction" (Rescorla, 1970) and a "blocking" (Kamin, 1969) paradigm conformed to the predictions of the Rescorla-Wagner theory. In Experiment 1, AEs were established simultaneously for horizontal-vertical and diagonal patterns. When observers subsequently viewed compound induction patterns, AE magnitude was found to be significantly decreased, relative to a condition in which observers did not view such an induction pattern. In Experiment 2, AE magnitude for a given test pattern following inspection of compound induction stimuli was significantly reduced by inspection of the other component prior to viewing the compound induction stimuli. The applicability of associative learning and feature-adaptation models of the McCollough effect is discussed.

In 1965, McCollough described an orientation-contingent color aftereffect (AE). A typical way to generate such an AE is to present an observer with magenta and black vertical stripes alternating every few seconds with black and green horizontal stripes. After inspecting these alternating chromatic gratings for several minutes, the observer, on viewing an achromatic test pattern composed of vertical and horizontal stripes, will see weakly saturated colors approximately complementary to those formerly paired with each orientation. The initial report of the McCollough effect (ME) gave rise to a large body of research, which has shown the original orientation-contingent color AE to be just one member of a large class of contingent AEs (see Anstis, 1975, and Stromeyer, 1978, for reviews).

While there is currently no comprehensive explanation for MEs, the literature is divided between neural adaptation and associative learning models (see Harris, 1980, and Skowbo, 1984, for detailed discussion of these alternatives). There has been an ongoing debate about the adequacy of each model to explain the wealth of empirical data on the ME (Allan & Siegel, 1986; McCarter & Silver, 1977; Murch, 1976; Skowbo, 1984, 1986). The neural model attributes MEs to the adaptation of units in the visual system that are assumed to be tuned for both color and orientation. The details of these neural models have

varied (see Grossberg, 1980; Harris & Gibson, 1968; Kruger, 1979; McCollough, 1965; Stromeyer, 1978), but all have in common the adaptation of feature-specific neurons. More global elements such as the vectorfields postulated by Hoffman's Lie transformation group model of neuropsychology (Dodwell, 1983; Hoffman, 1966, 1978) have recently been suggested as potential mediators of contingent AEs (see, Cavill & Robinson, 1976; Dodwell, 1984; Dodwell & O'Shea, 1987; Emerson, Humphrey, & Dodwell, 1985; Humphrey, Dodwell, & Emerson, 1985).

As research on the ME expanded, it was noticed that certain ME characteristics were similar to those of an associative learning paradigm. These included generalization, extinction, spontaneous recovery, and reconditioning (Bonnet, 1975; Murch, 1976; Westbrook & Harrison, 1984); long-term persistence (Jones & Holding, 1975); and findings that AE magnitude varied in a manner consistent with well-established CS-US interval effects in conditioning (Murch, 1976; Schmidt, Pinette, & Finke, 1978). Promoters of associative models have also argued that, given the wide variety of contingent AEs, it is unlikely that the visual system has compound detectors sensitive to both color and a variety of other stimulus dimensions. Simply stated, the associative learning explanation of MEs is that the lined grid presented in the inspection period serves as the CS, while the color serves as the UCS, which gives rise to UCR—namely, a negative color AE. As a result of the pairing of the CS and UCS, a CR develops. The CR is in the form of a negative color AE, which can be elicited by subsequent presentation of the CS (achromatic test pattern) alone. It is important to bear in mind, as Skowbo (1986) pointed out, that although certain characteristics of MEs may be similar to those of con-

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ditioning, this does not imply that MEs are actually CRs. This same caveat about functional similarity is equally applicable to neural adaptation models.

While Murch (1976) proposed the first formal associative model of the ME, couched in traditional Pavlovian terminology, more recent studies advocating a learning model have focused on more parametrically precise models of Pavlovian conditioning, such as the Rescorla-Wagner theory (Rescorla & Wagner, 1972). This theory holds that the mere pairing of the CS and US is a necessary, but not a sufficient, condition for altering associative strength. The theory provides specific predictions about the associative strength of CS-US pairs when two or more CSs are conditioned to the same US separately, and subsequently paired with the same US. For example, a CS paired with a US that is already well-predicted by another CS will not gain associative strength when the two CSs are presented in compound conditioning. The basic equation for a two-component (A,B) condition experiment is:

$$\Delta V = \alpha\beta(\lambda - V_i) \quad (1)$$

Delta V is the change in associative strength (V) for a given stimulus component present on that trial. Alpha is a learning rate parameter associated with a given CS component. Beta is a learning rate parameter associated with a given US. Lambda is the theoretical asymptote associated with a given US. V_i is the sum of associative strength of all components present on the trial. The theory assumes that all stimulus components compete for a share of the total amount of associative strength available for a given US.

In Experiment 1 in the present study, we test predictions of the Rescorla-Wagner theory for the ME by using an "overprediction" paradigm (Rescorla, 1970); in Experiment 2, we test predictions of the Rescorla-Wagner theory by using a "blocking" paradigm (Kamin, 1969). In both cases, the magnitude of ME is an index of associative strength. Overprediction occurs when two components are separately conditioned until each one is close to its asymptotic response level. Then the components are presented in a compound, paired with the same US as before. Following the compound conditioning, the associative strength is measured for each component separately and is found to be reduced relative to precompound levels. Blocking occurs when prior conditioning to one component impairs the subsequent conditioning of a second component presented in compound with the first (Kamin, 1969). Both paradigms predict seemingly counterintuitive results, in light of the literature on visual adaptation. In the case of overprediction, the theory suggests that the magnitude of an AE will decrease, despite the continued presence of the adapting stimulus in the compound. In the case of blocking, the theory suggests that AE magnitude, measured for one component of a compound adapting stimulus, will be less if there has been prior adaptation to the other component, even though the two components are processed by supposedly independent sets of neurons.

It was our intention to design experimental conditions for generating MEs that allowed us to examine the specific predictions of the Rescorla-Wagner theory for the overprediction and blocking paradigms.

EXPERIMENT 1

In the overprediction paradigm each component (CS) is initially conditioned separately to a single US. A reduction in associative strength for each component is predicted to follow pairing of the compound with the US. Couched in terms of the parameters set out in Equation 1, each component is initially conditioned separately, such that the V for each is close to λ . Thus, when the components are later presented in compound, V_i (i.e., $V_a + V_b$) will be much larger than λ , yielding a decrement in associative strength. (For example, if both components have reached asymptote, V_i will be twice λ .) The theory therefore predicts that there will be a loss in associative strength, even though the CSs continue to be paired with the US. Both Rescorla (1970) and Kremer (1978) have provided strong evidence for such a loss in associative strength, though St. Clair-Smith and Mackintosh (1974) failed to replicate the results of the earlier report.

We established the conditions for overprediction in terms of generating MEs as follows. The first component (CS₁) was composed of the traditional horizontal and vertical gratings, paired with magenta and green, respectively. The second component (CS₂) was composed of right-diagonal and left-diagonal gratings, paired with magenta and green, respectively. The compound stimuli (CS₁/CS₂) were superimpositions of vertical and left-diagonal gratings paired with green, and horizontal and right-diagonal gratings paired with magenta. A reduction in AE magnitude is predicted for both diagonal and horizontal-vertical test patterns when they are measured separately after inspection of the compound stimuli.

Method

Subjects. Forty undergraduate students (16 male, 24 female) volunteered to participate in this experiment in order to satisfy a course research requirement. The subjects had no prior knowledge of, or experience with, the ME. All subjects were screened for color vision deficiencies using the Dvorine pseudo-isochromatic color plates. Error-free performance on this test served as the inclusion criterion.

Apparatus and Stimuli. The inspection patterns subtended a visual angle of 7.96° at the 213-cm viewing distance. They consisted of high contrast square-wave gratings of 4.61 cpd. They were displayed on a white screen, using two Kodak Ektagraphic projectors (Model III AT). The orientation of the gratings was 0°, 45°, 90°, or 135°, which will henceforth be described as horizontal (H), right-diagonal (RD), Vertical (V), and left-diagonal (LD), respectively. In addition, there were two compound patterns, one composed of the superimposition of H and RD gratings (H/RD), and the other composed of V and LD gratings (V/LD). The compound stimuli were not optical superimpositions of the constituent gratings; they were made by combining photographic gratings in a single slide. This method was chosen for practical reasons, although it is theoretically less desirable because new two-dimensional Fou-

rier fundamentals of lower spatial frequency are introduced at orientations of 22.5° and 112.5° . The V, LD, and V/LD stimuli were projected through a green filter (Kodak Wratten No. 53), which was affixed to the zoom lens of one projector [henceforth V_g , LD_g , and $(V/LD)_g$]. The H, RD, and H/RD inspection stimuli were projected through a magenta filter (Kodak Wratten No. 32) attached to the zoom lens of the second projector [henceforth H_m , RD_m , and $(H/RD)_m$]. The space average luminances (in cd/m^2) for the inspection stimuli were $H_m = 73.75$, $V_g = 50.60$, $RD_m = 67.57$, $LD_g = 51.00$, $(H/RD)_m = 35.67$, and $(V/LD)_g = 24.08$, as measured by a Tektronix J16 photometer with a 1° luminance probe.

The angular subtense and spatial frequency of the test patterns were identical to those of the inspection patterns. A schematic of the two test patterns occurs in Figure 1b. Since the construction and presentation of the two test slides (HV_{test} and D_{test}) were identical, we will describe only the H_{test} . The method is quite similar to that of Riggs, White, and Eimas (1974). Portions of the test slide having H and V stripes were covered with polarizing filters, oriented in orthogonal directions such that the direction of polarization was orthogonal for adjacent quadrants. The test slides were projected using a Kodak Ektographic (Model AF-2) 35-mm slide projector. At a position corresponding to the focal plane of the projector light source, a rotatable screen target mount (Ealing 22-8767) was mounted orthogonal to, and centered on, the light beam. The beam passed through multiple strips of green (Kodak Wratten No. 53) and magenta (Kodak Wratten No. 32) filters. Each piece of gelatin color filter was covered with a polarizing light filter, with the polarizing material mounted in orthogonal directions for the two colors. Between the strips of combined color and polarizing filters were clear apertures. The net effect was to project the test pattern with a mixture of green, magenta, and white light. The optimal width of the clear aperture was determined in pilot work, and the resultant range of color saturation optimized the range of colorimeter settings for generation of the ME in the formal experiments. By rotating the colorimeter, one could adjust the relative amounts of green and magenta in the H and V parts of the test pattern. At one extreme, the horizontal stripes received only magenta and white, while the vertical stripes received only green and white light. At the other extreme, the colors were reversed for the striped patterns. Between these extremes, a position could be found in which green and magenta were mixed in any desired proportion. Though the spectral composition of the test quadrants changed with rotation of the polarizer, there were only minor changes in luminance. Within each quadrant of the H-V test pattern, the mean luminance (34.30 cd/m^2) did not change by more than 4.45 cd/m^2 . This was also the upper limit of luminance differences between test quadrants. These differences are most likely due to the transmission characteristics of the Wratten filters used. The same variations were found in the diagonal test pattern, whose mean luminance was measured to be 41.16 cd/m^2 .

In the absence of a color AE, a null position could be found such that quadrants appeared matched and achromatic. In the presence of a color AE, however, this null point would no longer appear achromatic, and the colorimeter setting would be adjusted so that more green was added to one set of stripes and more magenta to the other. The direction and extent of rotation required to make the test patterns appear achromatic was taken as an index of the magnitude of the color AE. (This cancellation procedure assumes that the test color is exactly complementary to the AE colors. In keeping with most previous research on MEs, no special procedures were introduced to ensure strict fulfillment of this requirement in the present experiments.) During testing, the experimenter very gradually rotated the colorimeter from a random position yielding saturated colors, towards decreasing saturation (i.e., towards the null position). The subject's task was to inform the experimenter when all portions of the test pattern seemed to be colorless. The

subject could not see the calibrated dial on the colorimeter. The experimenter read this position off the calibrated dial and rotated the colorimeter to a randomly chosen position yielding saturated colors of the opposite hue (i.e., the subject's null point was approached from both directions). The average of four measures was taken as the subject's setting for each of the two test patterns.

Procedure. Following satisfactory completion of the Dvorine color test, the subjects adapted themselves to the darkened testing room for 5 min. During all inspection and test periods, the subjects viewed the stimuli while using a chin- and headrest to minimize head movements. The task was explained to the subjects, who were subsequently given practice at finding the null point. When the subjects showed good consistency in making these settings, the experiment was begun. Each subject was randomly assigned to one of four groups, each group having 10 subjects. The temporal course of the experiment, which was identical for all groups, is illustrated schematically in Figure 1a. After the practice session, the first test sequence occurred; these measurements served as each subject's baseline. A 3-min dark interval preceded each test sequence. Measures on HV_{test} and D_{test} were taken alternately.

Phase 1 (P1) consisted of an initial 15-min inspection period; a test; a 5-min inspection period; a test; another 5-min inspection period; a final test. (The multiple tests were introduced to assess whether the AE had reached a saturation level.) Phase 2 (P2) consisted of a 15-min inspection period followed by a test. Figure 1c schematically illustrates the stimuli being inspected in P1 and P2 for each of the four groups.

In the element-element (E-E), element-compound (E-C), and element-blank (E-B) conditions, the subjects inspected the patterns for a total of 25 min in P1. Each pattern was presented for 10 sec in the sequence shown (H_m , V_g , RD_m , and LD_g). In the compound-compound (C-C) condition, the $(H/RD)_m$ and $(V/LD)_g$ slides were alternated every 10 sec, also for a total of 25 min in P1. For P2, the E-E group continued to get the same sequence of stimuli as in P1; the E-B group received no stimulation (they remained seated in a darkened room); the E-C group received the compound stimuli, again alternating every 10 sec; and the C-C group continued to get the same alternating compound stimuli as in P1.

Figure 1. (A) Schematic of time course of inspection in P1 and P2 (the dark blocks denote rest intervals prior to testing). (B) The test stimuli. (C) Schematic of the inspection stimuli for a 40-sec sequence in each phase of Experiment 1.

Table 1
Three-Way Analysis of Variance on AE Difference Scores (Experiment 1)

Source	Difference Scores	df	<i>Ms</i>	<i>F</i>	<i>p</i>
Between Groups					
Conditions	692.8174	3	230.9391	5.981	.0024
Error	1390.0957	36	38.6138		
Within Groups					
Test pattern	385.2759	1	385.2759	42.384	.0000
Conditions × Test	14.9243	3	4.9748	0.547	n.s.
Error	327.2433	36	9.0901		
Time	133.4424	3	44.4808	17.739	.0000
Conditions × Time	319.7339	9	35.5260	14.168	.0000
Error	270.8168	108	2.5076		
Test × Time	15.9790	3	5.3263	3.177	.0266
Conditions × Test × Time	15.0684	9	1.6743	0.999	n.s.
Error	181.0622	108	1.6765		
Total	3746.4609	319			

Results

For each subject, the mean of the four baseline measures was subtracted from the mean of the four measures in each of the subsequent test sequence. In the element adaptation conditions, the resulting positive values for the difference scores indicate the presence of a negative chromatic AE with larger numbers, indicating stronger AEs. In cases involving compound adaptation, positive values also indicate negative chromatic AEs relative to the cardinal orientation in the compound pattern. For example, a greenish AE on the horizontal component of the HV_{test} would be indexed positively following adaptation to $(H/RD)_m$. The difference scores were analyzed using a

4 (conditions: E-C, E-E, E-B, and C-C) × 2 (test pattern: HV_{test} and D_{test}) × 4 (inspection time: 15, 20, 25, and 40 min) three-way analysis of variance. Pertinent planned comparisons were also carried out. The results of this analysis are presented in Table 1.

The average difference scores for each group are presented in Figure 2 as a function of inspection time for each test pattern separately. All three main effects were significant. The data for the three element conditions in P1 revealed no differences in AE magnitude for either test pattern following any of the P1 inspection periods. AE magnitude was significantly larger for the three element conditions than for the compound condition.

Figure 2. Aftereffect magnitude measured for the HV_{test} (left) and D_{test} are shown as a function of cumulative inspection time for the four conditions in Experiment 1.

The comparisons of most interest, however, occur in the P2 data. There was a significant conditions $\times$ inspection time interaction. Further analysis of this interaction indicated that the effect of inspecting the P2 stimuli differed among the groups [$F(3,36) = 11.37$, $p < .0001$]. There was no conditions $\times$ inspection time interaction for P1 data alone ($p > .95$). The overprediction hypothesis that condition E-C would show a larger decrease relative to E-B following inspection of compound stimuli was supported [$F(1,36) = 7.325$, $p = .01$]. Examination of the E-C versus E-B comparison for the test patterns individually showed that the prediction was supported for D_{test} [$F(1,36) = 6.20$, $p = .016$], but only marginally supported for HV_{test} [$F(1,36) = 2.97$, $p = .0897$]. The only between-groups comparison which did not show a significant effect of P2 inspection was that between the E-E and C-C conditions. Both these functions continued to rise at the same rate with continued inspection of the same stimuli. As was seen in P1, AEs measured in the C-C condition were significantly smaller than those in the E-E condition.

The inspection time $\times$ test pattern interaction was significant. AE magnitude for the D_{test} pattern was typically weaker, and it increased at a slower rate than for the HV_{test} . However this interaction did not differ across conditions. Neither the conditions $\times$ test pattern nor the three-way interaction was significant.

Discussion

The data from Experiment 1 support the overprediction hypothesis as formulated by the Rescorla-Wagner theory. For overprediction to occur optimally, the associative strength of the individual components should be close to the asymptotic level prior to simultaneous compound conditioning. In Figure 2 we see that the AE magnitude at the end of P1, when compared to the final measure in the E-E condition, was reasonably close to asymptotic levels. This suggests that the values of V_a and V_b were approaching λ ; therefore, in the E-C (overprediction) condition, their sum was well in excess of λ . Thus, a decrease in associative strength (AE magnitude) would be predicted.

How could a neural adaptation model account for the larger decrease in AE magnitude in the E-C condition than in the E-B condition? One would have to posit some mechanism whereby the effects of prior adaptation were negated at a faster rate than the normal decay function. Even if observers in the E-C condition perceived the compound stimulus as novel and if the magnitude of the ME was determined by the perceptual appearance of the induction pattern—which Green, Corwin, and Zemon (1976) and May and Mapperson (1976) argue it is not—then the AE magnitude should have been equivalent to that in the E-B condition. The data do not support this interpretation. The compound adaptation stimuli, as mentioned previously, contain Fourier fundamental components at orientations of 22.5° and 112.5° . For the (H/RD)_m pattern, the fundamental at 22.5° is closer in

frequency to the cardinal component grating, while for the (V/LD)_g pattern, the component at 112.5° is closer in frequency. With alternating adaptation to these compound stimuli, the major and minor Fourier components at both orientations are coupled with both magenta and green, which may or may not lead to a cancellation effect. The Fourier component closer in orientation to the cardinal component of the compound is also the one closer in spatial frequency, but, given the poor spatial frequency selectivity of the ME, this is unlikely to bestow any advantage. To account for the difference between E-B and E-C found in the present experiment, one would have to argue that the Fourier component closer in orientation to the cardinal component, while being paired with both green and magenta, is more effective when paired with the color complementary to that with which the cardinal component was paired. This might then serve to weaken the AE measured after compound adaptation. It must be pointed out that inspection of the compound stimuli in P1 (see C-C) could generate substantial color AEs contingent on the orientation of the compound components (H, RD, V, & LD), although these effects were significantly smaller than when the components were alternated individually (see Figure 2).

The finding of reduced AEs with compound induction stimuli is not novel, nor is it uniquely predicted by the associative learning or visual adaptation models. Brand, Holding, and Jones (1987) found diminished AEs following compound inspection, relative to the AEs measured when the compound components were viewed alone, while Westbrook and Harrison (1984) found no decrements. One argument that has been offered to explain such decrements is that the effective conditioning stimulus in the compound condition is the configuration, or gestalt percept, of the stimuli rather than the sum of two individual components (Mackintosh, 1975; St. Clair-Smith & Mackintosh, 1974). Also, the parameter β in Equation 1 is affected by factors such as US intensity, and since the space average luminance of the compound stimuli was lower than that of the element stimuli, the Rescorla-Wagner theory would predict smaller effects in the C-C condition. Reduced AEs in the C-C condition would also be predicted on the basis of the literature on visual adaptation. Luminance, contrast, and color saturation are known to affect ME magnitude (Ellis, 1976; Shute, 1979; White, 1976). Note, however, that since there were only two compound stimuli alternating in the C-C condition, the total exposure time for each was twice that for the individual stimuli in the element conditions. One could also propose that the pairing of the Fourier components with both colors did not lead to mutual cancellation, but instead yielded more potent effects for the color complementary to that with which the cardinal component was paired. Smaller AEs following adaptation to compound stimuli have been explained in terms of disinhibition, wherein the presence of component A in a compound adaptation may serve to weaken the AEs generated by component B (see Kurtenbach & Magnussen, 1981;

Levinson & Sekuler, 1975a, 1975b; Magnussen & Kortenbach, 1980a, 1980b). It is unclear, however, how the presence of inhibition or disinhibition in the E-C condition in P2 would reduce the AE magnitude relative to that in the E-B condition. Brand et al. (1987) suggested that the superimposition of gratings introduces visual geometric distortions of the Zöllner and/or Poggendorf type. The very broad orientation tuning of the ME (Ellis, 1976) and the finding that the color AEs can also be contingent on the perceived orientation of the test stimuli (Mikaelian, 1976) weaken this argument.

It is not clear why there was an overall effect of test pattern. The difference between the two test patterns was similar in the compound and three element conditions in P1 [$F(3,36) = 0.27, p > 0.84$], which suggests that the stimuli were of equivalent salience. An asymmetry in lateral inhibition could yield consistently smaller AEs for the latter (Carpenter & Blakemore, 1973).

EXPERIMENT 2

In terms of the Rescorla-Wagner theory, prior inspection of one component, such that the associative strength reaches an asymptote, will prevent an increase in associative strength of the other component. Thus, in Equation 1, $V_t = (V_a + V_b)$ would be close, or equal, to λ , since, with prior conditioning of one component, either V_a or V_b would be close to its asymptote. Hence there would be no increase in total associative strength to the second component, resulting in a reduced AE for that component. For example, prior inspection of the HV component before inspection of the compound should serve to reduce the AE measured on D_{test} , relative to the AE measured in a condition where there was no prior exposure to either component before the inspection of the compound stimuli.

Although not following traditional methodology for the generation of the ME, Westbrook and Harrison (1984) found evidence for blocking, as did Siegal and Allan (1985), who used a paradigm more typical for the generation of MEs. In the latter study, the diagonal stimuli were more salient than the horizontal-vertical stimuli, as evidenced by their overshadowing results; thus, blocking in only one direction was obtained. However, bidirectional blocking has been found using components differing in salience (Brand et al., 1987). In the present experiment we used components that were equally salient (according to the results of Experiment 1); therefore bidirectional blocking was expected.

Method

Subjects. Forty undergraduate students (9 male, 31 females) participated in Experiment 2 to satisfy a course research requirement. The male-female ratio was roughly equivalent across experimental groups. No subject had participated in Experiment 1 or had any familiarity with the ME. As before, none of these subjects had any color deficiency as assessed by the Dvorine plates.

Apparatus and Stimuli. The apparatus and the spatial characteristics of the inspection and test stimuli were the same as in Experiment 1, except for one change. In Experiment 1, a few sub-

jects noticed that they could not find a neutral point where the test stimuli were completely colorless. This is most likely due to the difference in percent transmission of Kodak Wratten filters Nos. 53 and 32. The result is a luminance difference when magenta and green are projected on the screen, which could, in turn, lead to color AEs of different strength. Riggs et al. (1974) attempted to compensate for this problem, but most investigators have ignored it. In Experiment 2, we equalized the luminance of the projected magenta and green patterns by using neutral density filters. The space average luminance for the inspection patterns expressed in cd/m^2 were: $H_m = 18.59$, $V_g = 19.69$, $RD_m = 19.62$, $LD_g = 19.31$, $(H/RD)_m = 10.15$, and $(V/LD)_g = 10.19$.

Procedure. There were four conditions, with 10 subjects randomly assigned to each one. The temporal course of inspection and testing was the same for each condition. It was different from the previous experiment, in that one of the 5-min periods of P1 inspection was dropped. All groups therefore had an initial (baseline) test; 15 min of P1 inspection; a test; 5 min of P1 inspection; a test; 15 min of P2 inspection; a final test. Figure 3 schematically illustrates a 20-sec sample of P1 and P2 inspection stimuli for each of the four conditions (HV-C, D-C, MG-C, and W-C). Each test, as before, was preceded by a 3-min dark interval. Since all groups inspected the $(H/RD)_m$ and $(V/LD)_g$ compound stimuli in P2, the stimuli seen during the 20-min P1 inspection period differentiated the groups. The stimuli were alternated every 10 sec as in Experiment 1. In P1, the HV-C group saw H_m and V_g ; the D-C group saw RD_m and LD_g ; the MG-C group saw homogeneous color stimuli of magenta (mean luminance = 34.71 cd/m^2) and green (34.19 cd/m^2). The W-C group saw homogeneous white stimuli (35.74 cd/m^2).

Results

The difference scores, as defined previously, are plotted separately for the D_{test} and HV_{test} patterns for the four conditions, as a function of inspection time, in Figure 4. The difference scores were analyzed by using a 4 (conditions: HV-C, D-C, MG-C, and W-C) $\times$ 2 (test pattern: D_{test} and HV_{test}) $\times$ 3 (inspection time: 15, 20, and 35 min) three-way analysis of variance. Pertinent planned

GROUP	PHASE ONE		PHASE TWO	
HV-C
D-C
MG-C
COLOR	M	G	M	G
W-C
COLOR	W	W	M	G

Figure 3. Schematic of inspection stimuli for a 20-sec sequence of P1 and P2 for each of the four conditions in Experiment 2.

Figure 4. Aftereffect magnitude measured for the HV_{test} (left) and D_{test} (right) as a function of cumulative inspection time in Experiment 2.

comparisons were also carried out. The results are given in Table 2.

With respect to the P1 data in Figure 4, the most obvious and predictable finding is the large AE for the test pattern for which there had been prior inspection. No orientation-contingent AEs were found following inspection of white light or alternating homogeneous colors (W-C and MG-C conditions). Likewise no AEs were found for the test patterns whose orientations had not been previously seen. These conditions did not differ significantly from each other or from baseline measures ($p > .92$). Phase 2 inspection of the compound stimuli differentially affected the conditions when AE was measured for both HV_{test} [$F(3,36) = 45.36, p < .0001$] and D_{test} [$F(3,36) = 12.08, p < .0005$].

The crucial comparisons in the context of the blocking paradigm are those (1) between AE magnitude for HV_{test} in the D-C and in the W-C conditions, and (2) between AE magnitude for D_{test} in the HV-C and in the W-C conditions. The aftereffect on HV_{test} was significantly smaller [$F(1,36) = 14.01, p < .001$] in the D-C condition. In other words, prior inspection of the RD_m and LD_s before inspection of the compound stimuli served to reduce or block the growth of the aftereffect for HV_{test} , relative to the aftereffect for HV_{test} found when there was no prior inspection of compound components (i.e., the W-C condition). Similarly, the AE for the D_{test} pattern in the HV-C condition was smaller than that measured in the W-C condition [$F(1,36) = 7.56, p < .01$]. Bidirectional blocking was therefore obtained.

Table 2
Three-Way Analysis of Variance on AE Difference Scores (Experiment 2)

Source	Difference Scores	df	Ms	F	p
Between Groups					
Conditions	1375.8596	3	458.6199	31.605	.0000
Error	522.3936	36	14.5109		
Within Groups					
Test pattern	4.5337	1	4.5337	0.360	n.s.
Conditions $\times$ Test	3085.5359	3	1028.5120	81.760	.0000
Error	452.8647	36	12.5796		
Time	333.6005	2	166.8002	75.474	.0000
Conditions $\times$ Time	243.7674	6	40.6279	18.383	.0000
Error	159.1224	72	2.2100		
Test $\times$ Time	11.7621	2	5.8810	4.577	.0134
Conditions $\times$ Test $\times$ Time	134.0781	6	22.3463	17.392	.0000
Error	92.5076	72	1.2848		
Total	6416.0293	239			

There was a reduction in AE magnitude for the HV_{test} in the HV-C condition following P2 inspection [$F(1,36) = 22.42, p < .0001$], while the reduction in AE for D_{test} in the D-C condition did not reach statistical significance [$F(1,36) = 2.97, p = .09$]. This supports the results of Experiment 1. AE magnitude had not saturated at the end of P1, as indicated by the data for an additional 8 subjects who continued to view the diagonal patterns through P2 (labelled D-D' in Figure 4). There was no main effect for test pattern, but the significant test pattern $\times$ inspection time interaction suggests that the AEs had different growth and decay rates. In addition, there was a smaller AE for D_{test} than for HV_{test} in the W-C condition following P2 viewing [$F(1,36) = 12.12, p < .005$]. Finally, AEs in the MG-C condition were smaller, relative to those in the W-C condition [$F(1,36) = 7.21, p < .05$].

Discussion

Blocking was bidirectional, but this blocking appears to be incomplete, since there were measurable and statistically significant AEs for the compound component to which there was no prior exposure. Partial blocking suggests that the associative strength for the blocking component had not reached asymptote prior to inspection of the compound ($V_a < \lambda$ in Equation 1). In previous studies using AE magnitude in a blocking paradigm that reported either total (Westbrook & Harrison, 1984) or partial (Siegal & Allan, 1985) blocking, there was little indication as to how close AE magnitude had come to asymptotic levels. Brand et al. (1987) found total blocking in both directions, which would be expected if indeed the AEs had asymptoted prior to compound inspection; this appears to be the case for the grating component but not for the spiral component (see their Figure 1). Of course, the data for their 5- and 10-min adaptation periods were collected on different observers. Given that the present experiment used a very similar method, it is surprising that Brand et al. found no increase in AE magnitude between these two adaptation periods while AEs in the present study continued to increase in magnitude up to 35 min (Experiment 2) and 40 min (Experiment 1). Although AE magnitude for the two components in the Brand et al. study were not equal, blocking was symmetrical; in the study of Siegal and Allan (1985), the components were clearly different with regard to both their amplitude and frequency spectrum, and this difference in salience resulted in unidirectional blocking effects. In the present study, there was no difference in AE magnitude at the end of P1 for HV_{test} in HV-C or for D_{test} in D-C [$t(18) = 0.12, p > .05$].

Let us examine the blocking results in terms of visual adaptation. The AE measured for the blocked component in the HV-C and D-C conditions was smaller than the AE for this component in the W-C condition. Since the time of adaptation to this component was equivalent, the change in AE strength had to be a consequence of the prior adaptation history (either to a homogeneous white pattern or to a grating differing in orientation by 45°). The block-

ing paradigm used here is very similar to a composite adaptation technique employed by Levinson and Sekuler (1975b), who examined threshold elevation AEs for one component (A) following adaptation to either a compound (A,B) or to that compound following prior adaptation to the other component (B). They found that AE magnitude for component A was larger following the B-(A,B) adaptation sequence than following adaptation to the compound (A,B) alone. This pattern of results was attributed to disinhibition, whereby prior adaptation to component B rendered it less effective in the compound (i.e., reduced its inhibition of A). The blocking results of the present experiment require the reverse effect, namely that prior adaptation to B [in a B-(A,B) condition] reduces the AE measured for A relative to that found following (A,B) adaptation.

Let us consider for a moment the fate of the Fourier components in the compound patterns for the W-C and D-C conditions with regard to HV_{test} (a symmetrical argument applies for D_{test} across the W-C and HV-C conditions). In both the W-C and D-C conditions, both fundamental Fourier components are paired with both green and magenta, yet the AE for HV_{test} is significantly decreased in the D-C condition relative to the W-C condition. The difference between the two conditions is, of course, the complementary color AEs built up at the 45° and 135° orientations. However, these negate each other for an HV_{test} pattern, as evidenced by the absence of any AE for HV_{test} at the end of P1 in the D-C condition. Assuming for a moment that the complementary AEs of the 22.5° and 112.5° Fourier components had not cancelled each other, and that there was a more potent AE for the color complementary to that with which the cardinal component was paired, then these residual effects should be severely reduced, or eliminated, by the potent complementary AEs previously generated at 45° and 135° . We feel, therefore, that an explanation for the results of this experiment couched in terms of the fate of the Fourier fundamental components is weak and strained.

A result that could be explained either by an associative learning approach or by a visual adaptation approach is that the aftereffects for D_{test} were smaller than for HV_{test} in the W-C condition. This occurred despite the fact that P1 inspection yielded AEs of equivalent magnitude for HV_{test} and D_{test} in the HV and DC conditions, respectively. In addition, the AE for D_{test} in the HV-C condition was smaller than that for HV_{test} in the D-C condition. Both of these findings suggest that the diagonal component was at a disadvantage, or less salient, in the compound stimuli. Salience in the present studies is difficult to characterize, since the components were equivalent in the Fourier domain, and their high contrast rules out simple explanations in terms of meridional difference in contrast sensitivity. The pattern of results could result if one of the components was closer to asymptotic levels of AE magnitude. In the absence of a second control group (like D-D) that viewed the HV component through P2, we cannot directly address this alternative. As with the previ-

ous experiment, one could also discuss this result in terms of an asymmetry, in suprathreshold inhibition, between orientation-selective mechanisms during compound adaptation.

Another result that does not lend itself to unique interpretation is that the AEs in the MG-C condition were smaller than those in the W-C condition. In an associative learning framework, prior exposure to the US serves to reduce the associative strength resulting from subsequent pairings of CSs with that US. Preexposure to the US is known to have blocking-like effects (see, e.g., Mis & Moore, 1973) and has previously been noted in the ME literature (Bonnet, 1975; Murch, 1976; Westbrook & Harrison, 1984). One could also discuss this result in terms of altering the response characteristics of color-opponent neurons, such that the color dimension of subsequently presented orientation-color contingencies would be less effective.

GENERAL DISCUSSION

As noted in our introduction, explanations of the ME have typically been couched in either conditioning or feature-adaptation terms. This theoretical dichotomy is somewhat arbitrary when one considers the modifiability of operating characteristics required by a visual system that has, as a desired goal, the signalling of covariation among various stimulus dimensions. Adaptation and habituation phenomena reflect an environmentally sensitive coding of signal probability, and they are implemented, in part, by alterations in the operating characteristics of neurons and in the effectiveness of variable synapses. If it is useful for an organism to register what stimulus characteristics change concurrently, it should not be unreasonable to expect to find a neural process that facilitates the registering of stimulus covariations. If stimulus probability is coded by changes in neuronal operating characteristics, one can consider an adaptation AE as the system's inability to immediately reverse or reset the code for stimulus presence. Simple AEs occur often and have been described as a first-order redundancy (Anstis, 1975). Contingent AEs, involving the pairwise covariation between stimulus dimensions, occur less often and therefore are potentially more informative. The build-up and decay times for contingent AEs are slower than for simple AEs, indicating higher order adaptation (Riggs et al., 1974; see also Favreau, 1979). Barlow (1985) has argued that the main function of the cortex is to note "suspicious coincidences" in its afferent input as a means of gaining knowledge about nonrandom, causally related features of the environment. In the typical induction of the ME, we present the rather uncommon pairings of orientations and colors that persist over multiple presentations for a relatively long period of time. The cooccurrence of orientation and colors could be effectively coded by neurons sensitive to both stimulus dimensions, with the subsequent contingent AEs arising from alterations in the operating characteristics of such neurons. Alternatively,

the two stimulus dimensions could be processed in separate topographically organized modules with subsequent convergence of neural information.

There are several indications that the site of the ME is at least one step removed from sensory processing in striate cortex. The ME can be obtained long after any measurable threshold elevation for chromatic gratings is found, which suggests that the mechanisms underlying the ME are not those responsible for threshold elevation (Timney, Gentry, Skowbo, & Morant, 1974). The ME is not localized to retinally adapted areas (Caelli, O'Neill, & Miller, 1977), and it can also be obtained even in the absence of locally defined orientation-color contingencies (Dodwell & O'Shea, 1987; see also Emerson et al., 1985). The spatial frequency and orientation specificity of orientation-contingent color AEs are, to a large extent, a by-product of the type of induction and test stimuli typically used. Using a single test orientation, which precludes the color contrast present in the typical test pattern, one can obtain complementary AEs that are largest for the inducing orientation but are also present at orthogonal orientations (MacKay & MacKay, 1977). All of the above suggests that the site of the ME is removed from the modular preprocessing of stimulus dimensions. This preprocessing is mediated by mechanisms with such a limited range of connectivity as to preclude any assessment of global information. It has been suggested that the results of the local analysis are redistributed to extrastriate areas (perhaps according to nontopographical principles) to facilitate the registering of covariation among stimulus dimensions (Barlow, 1980; Phillips, Zeki, & Barlow, 1984). Contingent AEs, within such a scheme, could be conceived as resulting from changes in operating characteristics of neurons in these regions. As Grossberg (1980) has pointed out, one does not have to revert to a conditioning type of model to explain the dynamic changes in neuronal operating characteristics subsequent to repeated or prolonged stimulation. Uttley (1979) has elaborated on the formal similarity between models of synaptic variability (during a conditioning paradigm) and the Rescorla-Wagner theory. Clearly, in explaining the ME in terms of conditioning, one is dealing with a type of conditioning in which the association between the elements is very much constrained by the neural coding and information classification. As has been pointed out, one does not get color AEs contingent on arbitrary patterns (White & Riggs, 1974), but rather on stimulus dimensions, for which there is a well-defined local and topographic analysis.

In summary, the ability to detect the conjoint presence of different stimulus attributes and their continued copresence is adaptive for the perceiver. The neural mechanisms facilitating this capacity may be removed from the initial, local, topographical analysis of sensory information in striate cortex. The alterations in operating characteristics of mechanisms signalling covariation between stimulus attributes underlie contingent AEs. The dynamics of these alterations may well be formally similar to the characteristics of classical conditioning.

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