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INTERACTIONS BETWEEN SIMULTANEOUS CONTRAST AND COLOURED AFTERIMAGES

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Abstract—Coloured afterimages were obtained after fixation of a neutral grey spot on a coloured surround. The colour of the spot afterimage was similar to that of the previous surrounding area, and was found to have two components which could be elicited independently. Firstly, complementary afterimages were generated by the subjective contrast colour which was induced into the grey spot during the adaptation period. Secondly, the complementary afterimage of the surround at the end of the adaptation period was capable of inducing contrast colour into the neutral spot of the test field. Thus simultaneous contrast colours can produce afterimages (successive contrast), and conversely, coloured afterimages can induce simultaneous contrast colour.

INTRODUCTION

It is well known that adapting the eye to a coloured stimulus produces a negative afterimage of the complementary hue. For example, after adaptation to a green spot on a grey surround, a pinkish afterimage can usually be seen against any white or grey test field. More surprisingly, if the previous figure–ground relationship of the adapting field is reversed, so that the subject fixates a small grey spot on a green surround, the subsequent afterimage consists of a green spot with a pinkish surround. Thus, a spot which is grey throughout the adaptation period can produce a coloured afterimage. In general, the colour of the spot afterimage is of a similar hue to the surround in the adapting field and is invariably more vivid than the afterimage of the surround, which is often pale or even invisible.

There are at least two possible explanations for this phenomenon, and these two options are represented in the diagram of Fig. 1. First, it is possible that during the adaptation period, colour is induced into the achromatic spot region by simultaneous contrast processes, and that the subjective colour of the spot during the test period is the afterimage of this induced colour. This would mean that subjective contrast colours can produce their own afterimages. Alternatively, it is possible that the coloured surround builds up its own afterimage during the adaptation period, which subsequently induces the complementary hue into the neutral spot region during the test period. This would mean that a surround afterimage can induce simultaneous contrast. Of course, it is possible that both processes may be contributing to the apparent colour of the test spot. This paper demonstrates that in fact both processes do occur, and our experiments investigated each process independently by blocking off one or other of the two processes. We have previously used similar methods to investigate achromatic afterimages from contrast brightness (Rogers and Anstis, in preparation), and also the interactions of induced movement with motion aftereffects (Anstis and Reinhardt-Rutland, 1976).

Shively (1973) obtained contrast afterimages after adaptation to a stimulus made from coloured papers. He used a centre white disc of paper subtending 5° visual angle, with a coloured surround (say yellow) extending to 45°. The subsequent afterimage consisted of a centre spot of a similar colour to the adapting surround (yellow) together with a pale surround afterimage of the complementary colour (blue). Shively described the effect as a "new afterimage", although the phenomenon was first reported by Purkinje (1825), and was later studied by Brücke (1851), Aubert (1862), Ebbinghaus (1902), Ferree and Rand (1912, 1932, 1933, 1934), and King and Wertheimer (1963). Ferree and Rand's paper in 1912 reviewed the earlier literature and contained a number of excerpts in German from the 19th century literature. We have translated

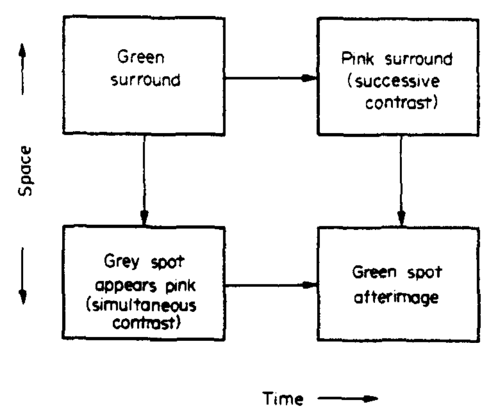

Fig. 1. After adapting to a grey spot on a green surround, the afterimage consists of a green spot (bottom right). This could be an afterimage of the previous contrast (bottom left), or else it could be induced colour from the afterimage of the surround (top right). See text.

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them into English here, retaining Ferree and Rand's explanatory and linking comments.

"This phenomenon was first described by Purkinje in 1825. He says (p. 107):

> If one lays a white square, two lines wide, on a black background, gazes at it for 20–30 seconds, and then looks at a black field, then one will see an even darker square whose edges are surrounded by a greyish halo which gradually fades away. If one places a red square instead of a white one on the black background, its green afterimage (*Spektrum*) shows a reddish halo; in the same way a blue afterimage has an orange halo, and so on. It is clear from this that the objective colour does not affect the retina in depth only, but also in breadth: but not equally over its whole extent, but most intensively at the border of differently coloured illumination."

The same phenomenon was next described with some modification by Brücke (1851, p. 447), who wrote:

> Finally, we can draw a third conclusion from the observation of the negative afterimages which appeared in this experiment, and which show that induced colours as such are capable of generating afterimages in complementary colours."

"His demonstration consists in getting the aftereffect of looking towards the light through squares of red, green and violet glass with small discs of black paper placed at their centers. He describes the aftereffect as follows:

> The negative afterimage from the red glass consisted of a pale red disc on a dark green background. There is nothing remarkable in this, and this result could be explained by analogy with Fechner's experiment, without needing to postulate an aftereffect from the induced colour. But when I use the green glass likewise, I also get a pale red afterimage of the dark disc, and the background is black, or at least so dark that I could not distinguish its colour with certainty. So here the induced green has generated red, whereas the inducing colour at the same time did not produce any clearly coloured afterimage. In the same way, the negative afterimage I got from the violet glass presented itself as a yellow-green disc on a black background."

"In two cases here, Brücke apparently has the positive excitation induced across the black disc, and in two cases the negative excitation. But since he does not make induction apply to the negative excitation, as has been done later, he does not explain this case as afterimage of contrast, but makes it instead analogous to the phenomenon described by Fechner.

"Aubert (1862, p. 259) says:

> Moreover it is remarkable that simultaneous contrast itself gives rise to a successive contrast, inasmuch as white squares which acquire a complementary colour through simultaneous contrast produce afterimages which are once more complementary, so that the afterimages of those squares have the same colour, although very much attenuated, as the background."

"Aubert observed white squares on a coloured ground. In the positive sensation the squares took on a tinge of colour complementary to the background, and in the afterimage of the same colour as the background. That is, a white square on a red background appeared greenish in the stimulus and red in the afterimage. He says: "Afterimages of white squares on a blue ground are especially beautiful, with a characteristic brilliance."

"Ebbinghaus (1902, p. 239) says:

> Place two fair-sized sheets of e.g. a saturated green colour on a grey ground, so that only a narrow horizontal strip, say 5 mm wide, remains visible between them, and let an impartial observer fixate on this for a while. Then let him project the afterimage on a somewhat irregularly patterned background, such as the crossbars of the window frame, and ask him what he sees. Almost without exception, the answer will be "a green strip." Because of the two fold operation of contrast, in the adapting stimulus and in the afterimage (*im Vor- und Nachbilde*), which is concentrated from an extensive surround into its narrow width, the strip which is completely neutral objectively has acquired such an intense colouring that it immediately attracts attention, whereas the reddish colouring of the afterimage in its neighbourhood is usually not noticed at all owing to the irregularities on the irregular surface of the test field."

In their own experiments on contrast afterimages, Ferree and Rand (1912) used 20 × 20 cm squares of red, green, blue and yellow Hering papers as their adapting stimulus fields, each of which was bisected by a narrow strip of grey paper (2 × 20 cm) passing vertically through the centre. They found that the afterimage produced by fixating one of these squares for several seconds consisted of a square of the complementary hue, bisected by a strip of the same colour as the adapting surround. For example, the afterimage of a grey strip on a magenta square was of a greenish square bisected by a strongly saturated pink strip. Ferree and Rand believed that the subjective colour seen in the strip after adaptation was an afterimage of the colour previously induced into the strip by the surrounding field (the lower left path of Fig. 1), rather than the induced contrast colour from afterimage of the surround (the upper right path of Fig. 1). However, their evidence for this conclusion is not convincing. Firstly, Ferree and Rand argued that the strengths and durations of the strip and surround afterimages were somewhat different and therefore it would be unlikely that one was derived directly from the other. Thus, they found that the strip afterimage was usually stronger than the surround afterimage (as noted earlier); the phases of the two afterimages rarely coincided, so that the strip was frequently visible when the surround was not and vice versa; and the strip afterimage frequently developed first and invariably lasted longer than the surround afterimage, returning several times after the surround afterimage had finally disappeared. Secondly, Ferree and Rand reported that when the adapting stimulus field was viewed through tissue paper or under decreased illumination, the durations of both strip and surround afterimages were reduced, but in such a way that the relative duration of the strip to surround afterimage was actually increased. Ferree and Rand argue that this would not happen if the colour in the strip was being induced by the (now weaker) surround afterimage. However, they also found that the tissue paper greatly increased the induced contrast colour in the adapting field. Therefore, if the colour in the test strip is the afterimage of this contrast colour, as Ferree and Rand claim, then the afterimage of the strip should be stronger and more long lasting with the tissue paper, rather than weaker and of shorter duration as they found. Ferree and Rand acknowledge this inconsistency in their interpretation of the results, but suggest in reply that "the contrast sensation is only an equivocal index of the amount of excitation set up on the retina by the neighbouring surface" (lateral inhibition in modern terminology). "This excitation may under one set of conditions arouse an intense sensation, and under other conditions be equally strong, at least as far as the aftereffect goes, and excite no sensation."

Twenty years later, Ferree and Rand (1932) reported that contrast could be increased to an "almost unbelievable" extent if the illumination was made to decrease. They presented a grey ring on a red surround under daylight illumination from a window, which was reduced from 10–15 ft-c to darkness in 1 sec, by swinging closed a heavy lightproof door or shutter. The grey ring looked an apparent blue-green, during the change in illumination, and the "richness and brilliancy of the contrast colour could not be represented in any pigment colour". In further observations, they stared at a grey ring on a red surface for 40–60 sec until adaptation was strongly set up, and then quickly decreased the illumination to one-half or less. The grey ring now changed its apparent colour from blue-green to red, an instant before the surround changed from red to blue-green. Thus, at one instant the ring became apparently red while the surround was still at the neutral stage in its change from red to blue-green, so a contrast colour was present in the ring when no colour was sensed in the surround. Ferree and Rand argued, as before, that the red subjective colour in the ring was an afterimage of previous contrast colour, not contrast induced by the surround afterimage. If a blue or green surround was used, the time relations were different, and when the illumination was reduced the grey ring changed its apparent colour just after, not before, the apparent colour change in the surround.

King and Wertheimer (1963) also studied the afterimages produced by contrast colours. They noted that a grey disc on a green surround appeared slightly pink (by simultaneous contrast), and that the afterimage of this adapting field consisted of a green disc with a desaturated pink surround. In order to determine the cause of the colour in the disc afterimage they added green light to the achromatic disc in the adapting field until the pink colour induced by the surround was completely nulled out, and appeared to be achromatic. Thus they argued, if colour was still seen in the disc during the test period, it must be induced by the surround afterimage, and not the afterimage of the non-existent contrast colour. The afterimage produced by adaptation to this "neutralized" grey disc with a green surround was again of a subjectively green disc with a pink surround, although the green was less saturated compared with the normal contrast afterimage. This result led Wertheimer and King to conclude that contrast afterimages are caused by simultaneous contrast induced by the afterimages of the surrounding field. However, the lack of correspondence between the strength of the induced colour in the adapting field and the strength of the subsequent afterimage, noted earlier by Ferree and Rand, militates against such a conclusion. King and Wertheimer's experiment does serve, however, to demonstrate the strength of these contrast afterimages, since under these conditions a green spot afterimage was produced on a region of retina which had only been stimulated with the green light used to neutralize the induced colour of the adapting spot. In addition, the fact that this neutralization is possible is interesting in itself, since it shows that physical and induced colours can mix phenomenally. This observation led King and Wertheimer to hypothesize that both kinds of colour are produced by the same physiological mechanisms.

The experiments described so far have all demonstrated that colour is perceived in the afterimage of an achromatic spot with a coloured surround. However, none of these experiments has shown conclusively whether the perceived colour is an afterimage from the previously induced contrast colour, or the induced contrast colour from the afterimage of the coloured surround. On the other hand, we have found that both effects can occur, and that each can be elicited independently, under the appropriate experimental conditions. In Experiment 1, a simple green (or magenta) spot produced a strong pink (or green) afterimage. Afterimages of contrast colours were produced in Experiment 2, where the subject adapted to a grey spot on a green (or magenta) surround. In this case, the afterimage of the spot was green (or pink), as described by many previous workers. In Experiments 3 and 4 we obtained the unexpected result that the afterimage of a black spot on a green (or magenta) surround appeared to be pink (or green) on a grey test field. Thus by changing the luminance of the achromatic spot from grey to black (both on the same green surround) we were able to change the apparent colour of the spot afterimage from green to pink.

Experiment 5 was set up to show that subjective contrast colours in an adapting spot are capable of generating their own afterimages, in a setup which ensured that there were no surround afterimages to confound the results. Thus a grey spot on a green (or magenta) surround appeared pink (or green) during the adaptation period as a result of simultaneous contrast, which in turn generated its own green (or pink) afterimage seen against the neutral test field. Conversely, in Experiment 6 the stimulus conditions were set up to show that the afterimage of the green (or magenta) surrounding field could induce apparent colour into the neutral test spot, which had been protected from possible induced colour during the adaptation period. In this case the pink (or green) afterimage of the green (or magenta) adapting field caused the achromatic test spot to appear green (or pink), by simultaneous contrast.

EXPERIMENT 1—AFTERIMAGES OF COLOURED SPOTS

The adapting field consisted of two coloured spots, one green and the other magenta, on a grey surround (Fig. 2). The coloured spots and the surround field were back-projected on to a tracing paper screen using two separate projectors. An opaque slide with two holes cut in it was positioned in the slide plane of the first projector to produce the two spots. Small pieces of coloured filter were taped over the holes to make one spot green and the other magenta. The filters were Edmund 871, light green, $\lambda_{max} = 540$ nm.

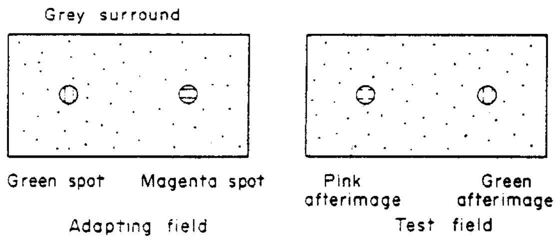


Fig. 2. Adaptation to a green (●) spot and a magenta (●) spot on a grey (⁘) surround produced negative afterimages, i.e. an apparently pink (⊖) and apparently green (⊙) spot. (Continuous hatching denotes physical colours, broken hatching subjective colours.)

transmission = 31%; and Edmund 828, magenta, λ_{max} = 415 and 680 nm, transmission = 31%. The second projector had a slide which was transparent except for two small black spots, so that it illuminated the entire surround field with white light apart from the two spots on the screen which were lit with coloured light by the first projector. The second projector was stopped down to produce a grey surround field of 1800 cd m^{-2}, which was matched in brightness to the coloured spots. A fixation point was provided mid-way between the spots in the adapting field, which were 10° visual angle apart.

The test field consisted essentially of two spots of variable saturation and hue which were under the subject's control. The test and adapting fields were optically superimposed by means of a half-silvered mirror at 45° to the line of sight, so that the coloured spots on the adapting field appeared to lie in exactly the same position as the variably coloured spots in the white test field. Shutters were positioned in front of the two fields, however, permitting the subject to see only the adapting field or the test field at any instant. The test field was made from a piece of front illuminated white card of luminance 79.2 cd m^{-2}, with two holes punched in it on either side of a central fixation point. Immediately behind each hole was the translucent front surface of an optical integrating box, so that the holes in the screen were filled with achromatic light of 18.3 cd m^{-2}. The design of the integrating box also allowed the hue of the test spots to be continuously varied from green via grey to magenta (Fig. 3). This integrating box consisted of a long tube of square cross-section, lined on all four interior surfaces with mirror, and covered at its two ends with translucent milk glass. A vertical septum, lined with mirror on both sides, ran transversely along its interior length to produce two separate integrating boxes side by side. The translucent end of the integrating box furthest from the screen was illuminated by a third projector shining through a filter disc 5 cm in diameter mounted in a rotatable ballrace. The upper half of this filter disc was green, and the lower half magenta, using the same filters as in the adapting field spots (Edmund 871 and 828). When the common border of the magenta and green filters was horizontal, each half of the integrating box, and hence each test spot seen by the subject, was illuminated with an identical mixture of green + magenta (= white) light. When the subject turned the ballrace in a clockwise direction the right test spot became progressively more green as the left spot became more magenta. Turning the ballrace in the opposite direction produced the opposite effect. In this way the subject could adjust the physical hue of the test spots to cancel or null out the subjective colour of his spot afterimages. (We thank Keith White for suggesting constructional details.)

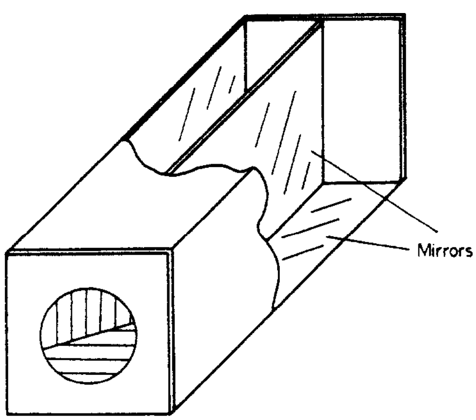


Fig. 3. Optical integrating box produced variable hues and saturations for nulling out afterimages. Two rectangular-section tubes side by side were lined inside with mirrors and covered at each end with flashed-opal diffusing glass. A filter whose upper half was green, lower half magenta, could be rotated in a ballrace under the subject's control: when it was rotated to the right, the diffused light reaching the subject down the right tube became progressively greener and the light in the left tube became more magenta. Filters were either fairly saturated Edmund 871 (green) and 828 (magenta) or pale Kodak CC20G (green) and CC30M (magenta).

Procedure

After dark adapting for several minutes, the subject fixated the adapting field monocularly for 18 sec. The test field was then exposed for 2 sec and the subject was required to adjust the physical hue of the test spots, by rotating the ballrace filter, until they looked the same subjective hue as each other and as the white test surround. The test field was then replaced by the adapting field for a further 8 sec to "top-up" the subject's adaptation before the next test exposure. This cycle was repeated until the subject was satisfied that the test spots appeared achromatic during the brief test periods. Thus if the subject adapted to a green spot to the left of the fixation point and a magenta spot to the right (as in Fig. 2), the afterimages of the spots were pink and green, respectively. By rotating the ballrace and filters anti-clockwise, the subject could simultaneously add in green light to the left spot and magenta light to the right spot until both spots appeared achromatic. The stronger the afterimages, the more physical colour had to be added in to cancel the subjective effect.

Results

The afterimages produced by this continuous "topping-up" procedure were very strong and saturated in colour. Indeed, both subjects judged the test spots to be achromatic when the spots were physically as saturated in colour as the apparatus permitted. In other words, at the subjective null point of achromaticity, the left test spot was illuminated with 100% green filtered light and the right spot with 100%

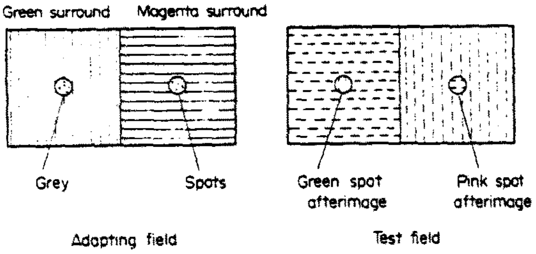


Fig. 4. In Experiment 2, two grey spots were fixated. The spot on the green surround looked pinkish by contrast, and gave a green afterimage, whilst the spot on the magenta surround looked green by contrast, and gave a pink afterimage.

magenta filtered light. Since the coloured filters used in the adapting spots and on the integrating box were the same, this implies that the afterimages were fully as saturated in colour as the original adapting spots.

EXPERIMENT 2—AFTERIMAGES FROM GREY SPOTS ON COLOURED SURROUNDS

The apparatus and procedure were the same as before, except that the adapting field now consisted of two grey spots, one surrounded by a magenta field, the other by a green field. The luminance of the magenta field was 2125 cd m^{-2} and of the green field was 890 cd m^{-2}. (Although both fields came from the same projector, and the green and magenta filters had the same nominal transmission of 31%, the magenta field was inadvertently made about 0.3 log units brighter than the green field.) The grey spots were matched by eye to have about the same brightness as the average of the two coloured fields. After 18 sec adaptation to this display, the subject was required to null out any apparent colour in the neutral test spots during a 2 sec exposure of the test field. Adaptation was then continued for a further 8 sec, and the cycle repeated until the subject was satisfied that the test spots appeared achromatic during the test field exposures. On half the trials the green surround was on the left, as in Fig. 4, and on half the trials it was on the right.

Results

The grey spot which was on a green surround produced a greenish afterimage, and the grey spot on a magenta surround produced a pink afterimage. Thus the spot afterimages were of the same colour as the adapting surrounds. This confirms the findings of Ferree and Rand (1912) and Shively (1973). The strength of the afterimages was such that the test spots appeared achromatic when they were actually illuminated with 34% green and 66% magenta light, for the spot which had been on a green adapting surround, and 66% green and 34% magenta light for the other spot (mean of 2 Ss × 4 trials).

EXPERIMENT 3—AFTERIMAGES OF BLACK, GREY OR WHITE SPOTS ON COLOURED SURROUNDS

Conditions were the same as in Experiment 2, except that the luminance of the achromatic adapting spots was varied on different trials. As well as being made the same brightness as the coloured surround ("grey spot", 0 log units), the spot was also made brighter by $+\frac{1}{2}$ log unit ("white"), or dimmer by $-\frac{1}{2}$ or -1 log unit ("dark grey") or by -2 log units ("black spot"). During the adapting period it was noticed that the simultaneous contrast colour induced into the spot was maximum when the grey spot had the same brightness as the surround (Kirschmann, 1890). Thus, a grey spot on a green surround looked strongly pink, but much less pink if its luminance was increased by half a log unit to give a white spot, or decreased by half a log unit to give a dark grey spot. If the spot luminance was decreased by 2 log units, so that it looked black, it then appeared tinged with green—the colour of the surround. This reversal in the sign of the induced colour may be related to the phenomenon of colour assimilation: scattered light from the surround may play a role, but it cannot be the only explanation, as Experiment 4 below will make clear.

Results for the afterimages of the black, grey and white spots are plotted in Fig. 5. It will be seen that there was a linear relationship between the luminance of the adapting spots, and the hue and saturation of the apparent colours in the resulting spot afterimage. A bright spot produced an afterimage of the same colour as the adapting surround, whilst a dark spot produced an afterimage of the colour complementary to the adapting surround. A dark grey spot which was about half a log unit dimmer than the surround produced an achromatic afterimage.

There is one discrepancy between the apparent colour of the adapting spot and of its corresponding afterimage. A white adapting spot showed less simultaneous contrast than a grey spot, yet it produced a more strongly coloured afterimage. This recalls Ferree and Rand's remark, quoted above, that the contrast sensation is only an equivocal index of the amount of lateral inhibition: a given amount of inhibition may lead to a strong aftereffect, yet excite little sensation during the adapting period.

We cannot fully explain our results, but we tentatively attribute the change in sign of the afterimage, from negative to positive as the spot luminance was varied, to two hypothetical antagonistic processes during the adapting period. One process would be simultaneous contrast, mediated by lateral inhibition, accounting for the results from a grey or white adapting spot. The other process would be a lateral summation or a spread of adaptation (Rushton, 1965). This would account for the results from an adapting black spot. Notice that the black spot behaves rather as though it were a spot of the same colour as the adapting surround: we postulate that the excitation from the coloured surround can spread neurally into the black spot region. Experiment 4 which follows will show that the afterimages produced by a black spot are too strong to be dismissed as merely the result of coloured light from the surround being optically scattered into the black spot region. Some kind of "neural blurring" or spread of adaptation must also be involved.

Although the afterimage from a grey spot can readily be observed using stimuli of coloured paper, we could obtain the afterimage (of opposite sign) from a black spot only if the surround was intensely bright,

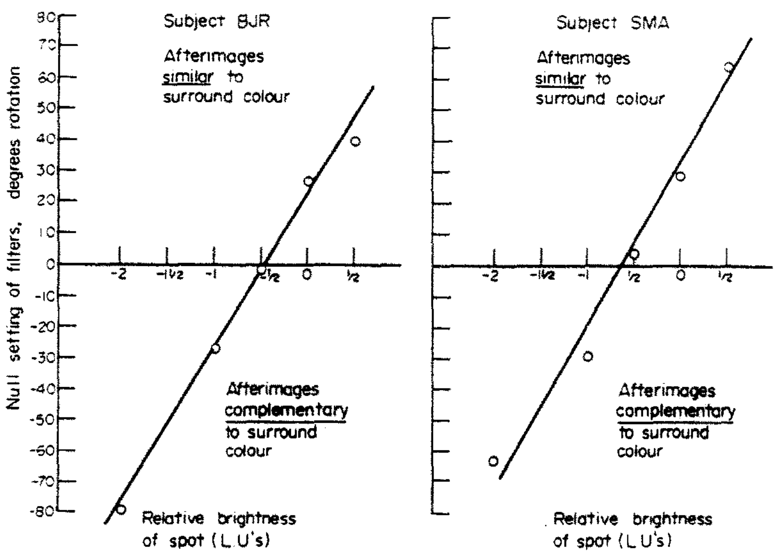


Fig. 5. In Experiment 3, subjects adapted to the stimulus shown in Fig. 4, except that both adapting spots were set to luminances ranging from −2 to +0.5 log units, relative to the brightness of their coloured surrounds. Results: dark spots gave afterimages complementary to the colour of the adapting surround, bright spots gave afterimages of the same colour as the adapting surround.

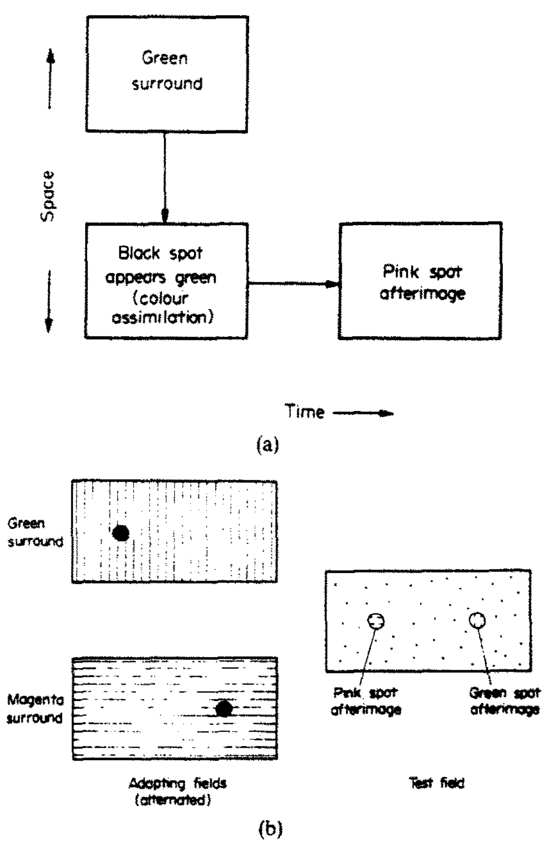


Fig. 6. (a) In Experiment 4, black spot on a green surround looks greenish and produces a pink afterimage. Design of experiment excludes coloured surround afterimages. (b) Adapting and test fields used to produce afterimages from black spots on coloured surrounds.

as it was in our back-projected field. This may explain why no previous experimenters have reported the afterimage from a black spot: they nearly all used stimuli made from coloured papers. The only exception was Brücke (1851). He used pieces of coloured glass held up to the light, and he did report both positive and negative afterimages from a black adapting spot, although he was not able to explain his results.

EXPERIMENT 4—AFTERIMAGE OF A BLACK SPOT ON A COLOURED SURROUND

Experiment 4 was designed to demonstrate that the afterimage of a black spot on a coloured surround was caused by neural processes taking place during the adapting period. This was achieved by arranging to exclude (i) any explanation in terms of optically scattered light during the adapting period (ii) any interactions which might have arisen if a coloured afterimage of the surround were present during the test period.

Experiment 3 showed that the afterimage of a black spot on (say) a green surround appeared to be pink on a neutral test field. However, it did not prove that this effect was the direct result of an afterimage produced by apparent subjective colours of the adapting spot. It is certainly possible that lateral processes resembling colour assimilation made the black adapting spot look greenish, leading to a pink afterimage. However, another possibility is that the green adapting surround produced a pink surround afterimage, which then induced a pinkish colour into the spot afterimage, again by processes resembling colour assimilation. Experiment 4 was specifically designed to exclude any coloured surround afterimages, so that any coloured spot afterimages must be caused by the previously induced assimilation colour (Fig. 6a). Experiment 4 studies afterimages from black spots, whilst Experiment 5 will apply the same logic to the study of afterimages from grey spots. Two adapting fields were presented alternately to the same retinal area. The first field was a uniform green, except for a single jet-black spot to the left of the fixation point. The second field was a uniform magenta, except for a single jet-black spot to the right of the fixation point (Fig. 6b). This arrangement was designed to prevent the formation of coloured surround afterimages which might affect the apparent colours of the spots in the test field. Although the magenta field was somewhat more intense than the green field—2125 vs 890 cd m^{-2}—it will be seen that this did not materially affect the value of the results.

Procedure

After dark adapting for several minutes, the subject monocularly viewed the two adapting fields which were presented alternately every 2 sec for an initial adaptation period of 18 sec. The neutral test field was then exposed for 2 sec and the subject was required to null out any apparent colour in the spot afterimages as before. The adaptation was continued for a further 8 sec and the cycle repeated until the subject was satisfied that the test spots looked achromatic during the 2 sec test field exposures.

Results

On exposure of the neutral test field, subjects reported that the left spot appeared pink and the right spot green. The afterimages were of briefer duration than those in Experiment 3, and decayed perceptibly even during the 2 sec test periods. However, subjects reported no difficulty in nulling them out consistently. The test spot afterimages could be nulled by illuminating the left spot with a mixture of 58% green and 42% magenta light, and the right spot with 42% green and 58% magenta (mean of 2 Ss × 4 trials). These results are particularly surprising when one considers the stimulus conditions. The left spot area was stimulated alternately during the adaptation period with black and magenta light and yet produced a pink afterimage. Likewise the right spot area was stimulated alternately with green and black and yet produced a green afterimage. Thus, the right-hand black spot on the magenta surround was more effective in producing a green afterimage than an actual magenta spot would have been. It was capable of producing a green afterimage, despite the competition from the uniform green field with which it alternated. A black spot which merely received optically scattered magenta light might conceivably produce a weak green afterimage, if viewed on its own, but surely not in competition with a green uniform alternating field: scattered light would be less effective, not more effective, than an actual magenta spot. We conclude that neural processes, not scattered light, underlie the effectiveness of the black spots in producing coloured afterimages.

There was, by design, no perceptible colour in the surround afterimage during the test periods, which is to be expected since the colour of the surround alternated during the adaptation period between the complementary colours green and magenta. Even if there were any unintended residual colour in the surround afterimage, it could not possibly induce green into one test spot and pink into the other. Therefore the colours perceived in the test spots could not be the result of induction by the surround afterimage, but must instead be the afterimages of apparent colours induced into the spots during the adaptation periods (Fig. 6a).

EXPERIMENT 5—AFTERIMAGES GENERATED FROM PREVIOUSLY INDUCED CONTRAST COLOURS

Experiments 2 and 3 showed that the afterimage of a grey spot on a green surround looked green on a neutral test field. However, these experiments did not show whether the effect was an afterimage from previous contrast, or was produced by contrast in the afterimage. Experiment 5 uses the same logic as Experiment 4, but presents both grey and black adapting spots. The experiment was specifically designed to exclude any coloured afterimages of the surround, so that any coloured spot afterimages must be caused by apparent colours previously induced into the adapting spot (Fig. 7a).

To achieve this end, two adapting fields were presented to the same retinal area in alternation. The first field was a uniform green all over except for two spots positioned on either side of a central fixation point (Fig. 7b). The left-hand spot was illuminated with achromatic (grey) light, matched in brightness to the surrounding coloured field, whilst the right-hand spot was jet black. Hence the left spot appeared to be slightly pink in colour, owing to simultaneous contrast from the green surround, whilst the right spot remained unaffected by contrast. (In fact, if anything, it had a faint subjective tinge of green—the same colour as the surround. See Experiment 4.) The second adapting field, which was presented in alternation, was a uniform magenta colour except for the two spots. In this case, the right spot was grey, and appeared greenish by contrast, whilst the left spot was jet black and suffered no induced contrast (or even looked slightly pink). These two adapting fields were generated using the same back-projection methods as the first four experiments. The jet black spot was a small disc of opaque black flock paper (Edmund 70621) stuck on the translucent projection screen. This black disc was positioned to cover exactly one or other of the grey back-projected spots in alternation. When these two fields were presented in alternation to the subject, each for 2 sec, the left spot appeared alternately pink (by simultaneous contrast) and black, whilst the right spot appeared alternately black and green (by contrast) (Fig. 7b).

Procedure

After dark adapting for several minutes, the subject monocularly viewed the alternating adapting fields for an initial period of 18 sec. The test field was then exposed for periods of 2 sec, interspersed with 8 sec re-adaptation periods. The alternating cycle of the two adapting fields was reversed for each 8 sec re-adaptation period so that the adapting field seen immediately before each test period was green on half the trials and magenta on the other half, thereby avoiding any systematic bias.

Results

On exposure of the neutral test field, the left spot appeared green and the right spot pink. The strength of the afterimages was such that the test spots appeared achromatic when the left spot was illuminated with about 31% green and 69% magenta filtered light, and the right spot with 69% green and 31% magenta light (mean of 2 Ss × 4 trials).

If the relationship between the positions of the grey and black spots and the surround colour was reversed during the adaptation period, so that the grey spot was to the right of the fixation point when the surround was green and to the left when the surround was magenta, then the colours of the two afterimages were reversed. In this case the afterimage of the left spot appeared pink and the right spot green.

Experiment 5 was designed, like Experiment 4, to exclude any perceptible colour from the surround afterimage. Hence the apparent colours perceived in the test spots could not be the result of contrast from the surround afterimage, but must instead be the afterimage of the contrast colours already induced into the spots during the adaptation period (Fig. 7a).

MEASURING THE TIME DECAY OF AFTERIMAGES

The results described so far give an idea of the strength of contrast afterimages following a prolonged period of adaptation. However, we found that it was still possible to produce contrast afterimages following a single adaptation period of only 18 sec. In addition, we were able to measure the time course of the decay of the afterimages by asking the subject to adjust continuously the amount of physical colour in the test spots so that they always appeared achromatic as the afterimages died away. The ballrace in the test apparatus was modified by replacing the rather saturated Edmund nulling filters with a double thickness of paler, desaturated pink and green filters (Kodak CC20M magenta and CC30G green). This required a larger angular rotation of the ballrace to produce a given amount of saturation, and gave more sensitive measurements of weak afterimages. These pale filters were also used in Experiment 6. It should be noted that the quantitative results of Experiments 5 and 6 (Figs. 7 and 8) are not strictly commensurable with those obtained with Edmund filters in Experiments 1–4 (e.g. Fig. 5), since the Wratten filters unavoidably had somewhat different spectral transmissions from the Edmund filters. Also, being paler they made the test spots somewhat brighter than before (37 instead of 18 cd m^{-2}).

The test field was exposed at the end of the 18 sec adaptation period and the subject was required to null out the apparent afterimage colours as quickly as possible. When the null point was found, the subject closed his eyes while the experimenter recorded the null setting together with the elapsed time, and reset the filters on the integrating box to the physically achromatic position. The subject then opened his eyes and made another null setting in the same way.

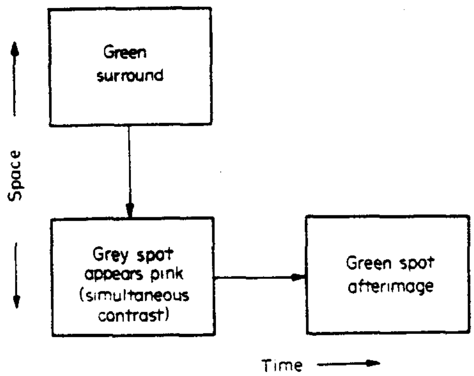
Results

The time decay of the contrast afterimages was recorded for two subjects using the two possible combinations of spot brightness and surround colour (Fig. 7c). The fitted curves are exponential decay functions, with the time constants for different curves lying between 24 and 54 sec.

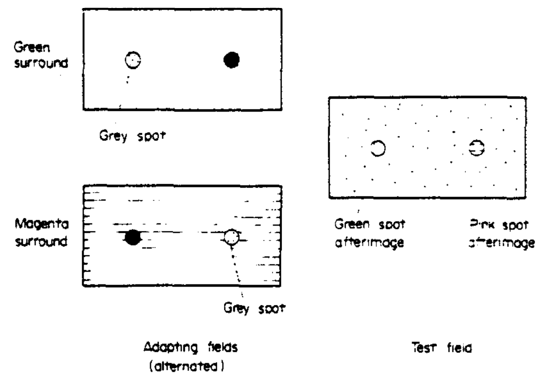
A possible objection to this method of plotting the afterimage decay, is that the nulling procedure involved the use of physical colours in the test spots, which could influence the state of chromatic adaptation of the subject's retina. For example, if the afterimage of the left spot was green and required additional magenta light in the test spot to produce an apparently achromatic spot, the magenta light could by itself generate a green afterimage which would add to the original effect. Such an artifact would artificially extend the time course of the decay. Therefore control trials were run with the same procedure as before, except that the subject did not null out the apparent colour of the afterimage, but merely mimed the nulling procedure by alternately observing the test field for 2.5 sec and then closing his eyes for 2.5 sec. After viewing the test field for 20 sec in this way, the subject made a single null setting to cancel out the colour of the remaining afterimage. If the original nulling procedure had been artifactually prolonging the contrast afterimages, then he would need less physical light to null the afterimage during these control trials than he had before. However, his settings were substantially unchanged, so we conclude that the nulling procedure did not significantly prolong the contrast afterimages.

The afterimages from contrast produced by 18 sec adaptation, shown as decay curves in Fig. 7c, were much weaker than they were after the much longer

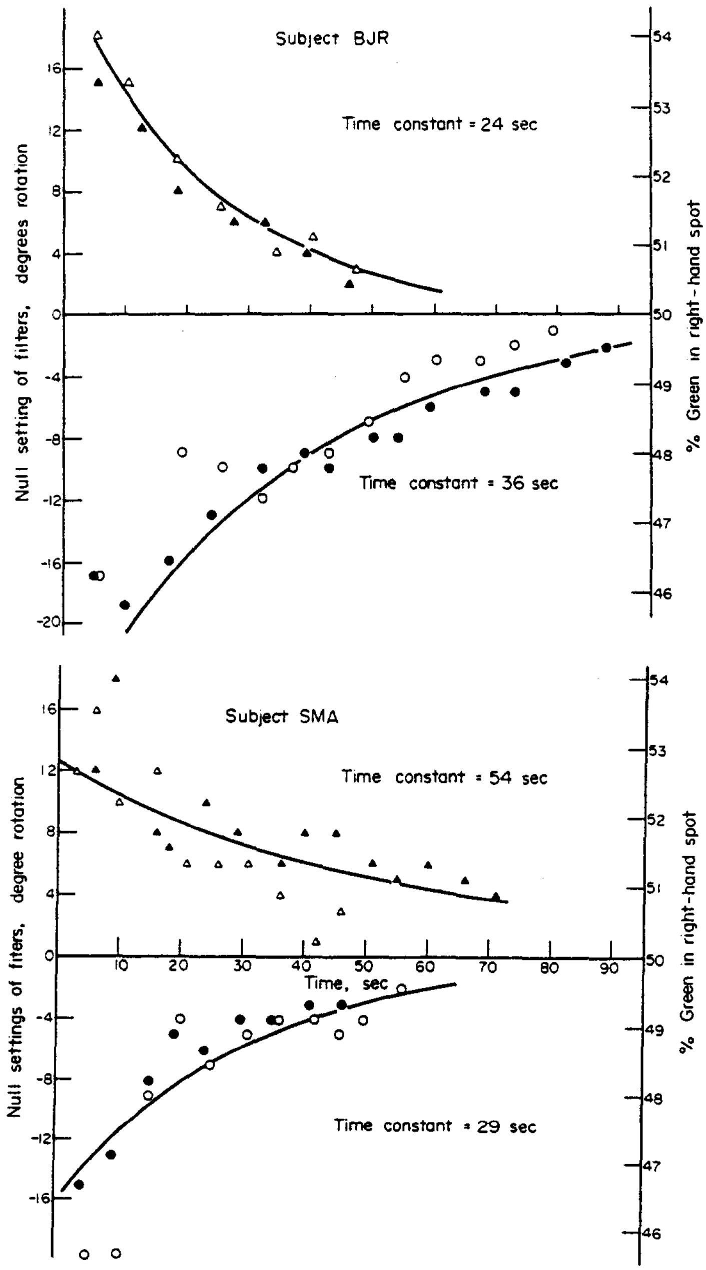
Fig. 7. (a) In Experiment 5, afterimages from previous contrast were produced by eliminating any coloured afterimages from the surround (see text). (b) Two adapting fields were presented in alternation, so that the left spot was alternately grey on a green surround (looking pink by contrast) and black on a magenta surround. The right spot was alternately black on a green surround and grey on a magenta surround (looking green by contrast). On a grey test field, the left spot afterimage looked green and the right spot afterimage looked pink. There was intentionally no perceptible colour in the surround afterimage. (c) After adapting to stimuli shown in (b), the colour in the spot afterimages was measured by a null method. The ordinate on the left shows the null setting of the filters plotted in degrees of rotation of the ballrace. The ordinate on the right shows the equivalent percentage of coloured light illuminating the spots, with respect to the adapting Edmund filters, not to pure monochromatic light. The data points show the decay of the afterimage after an 18 sec adaptation period. The upper curve represents the adaptation conditions shown in (b) with the grey spot on the left in the green surround: the lower curve for the opposite contingency with the grey spot on the right in the green surround. The filled symbols represent trials using the right eye and the open symbols separate trials using the left eye. Fitted curves are exponential functions, with time constants as shown.


Green
surround
Space
Grey spot
appears pink
(simultaneous
contrast)
Green spot
afterimage
Time

(a)


Green
surround
Grey spot
Magenta
surround
Grey spot
Adapting fields
(alternated)
Green spot
afterimage
Test field

(b)


Subject BJR
Time constant = 24 sec
Time constant = 36 sec
Null setting of filters, degrees rotation
% Green in right-hand spot
Subject SMA
Time constant = 54 sec
Time constant = 29 sec
Time, sec
Null settings of filters, degree rotation
% Green in right-hand spot

(c)

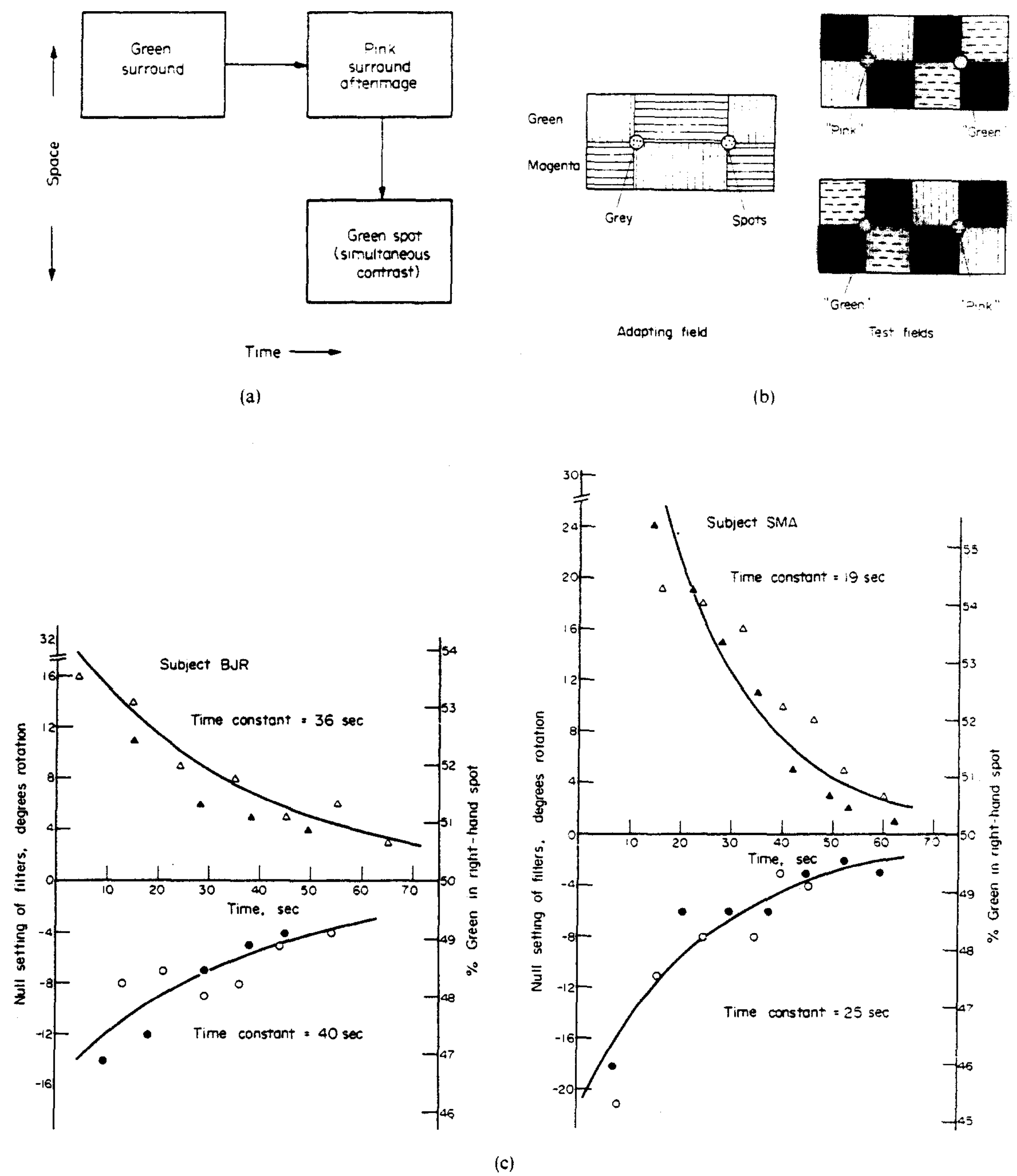


Fig. 8. (a) In Experiment 6, surround afterimages induced contrast colours into spot afterimages. Previous contrast colours were eliminated from adapting spot (see text). (b) Adapting field consisted of two grey spots, each set in a surround consisting of two green quadrants and two magenta quadrants. This induced no net contrast into spots, which looked achromatic grey. Two test fields were used in different trials. On upper test field, left half, previously magenta quadrants fell on white test quadrants, showed strong green afterimage which induced pink into left spot. Right half, previously green quadrants fell on white test quadrants, showed strong pink afterimages which induced green into right spot. Lower test field produced opposite results. (c) Results are adapting to stimuli shown in (b). Upper curves show results from upper test field, lower curves result from lower test field. Filled symbols represent trials using right eye; open symbols using left eye.

"topping-up" adaptation periods (c.f. Experiment 5—Results). Thus it took much more than 18 sec for the contrast afterimages to build up to full strength. Compare this with the much more rapid buildup of adaptation in Experiment 6 (Fig. 8c).

It should be pointed out that this experiment has the disadvantage of adding together, and hence confounding, the afterimages produced by a black spot and a grey spot, which were measured independently in Experiment 3 (Fig. 5). However, the present experiment does have the advantage of cancelling out any coloured afterimage of the surround, which could not be done in Experiment 3. Taken together, Experiments 3, 4 and 5 suggest that a grey spot on a green surround produces a green afterimage, a black spot a pink afterimage: and that each of these afterimages can occur when there is no coloured afterimage of the surround.

EXPERIMENT 6—CONTRAST COLOURS INDUCED BY THE AFTERIMAGE OF A COLOURED SURROUND

The previous two experiments have shown that afterimages can be generated from colour induced by the surround during the adaptation period. In this experiment, on the other hand, simultaneous contrast was purposely excluded from the adapting field so that any colour that was perceived in the neutral spots of the test field must have been induced by the afterimages of the previously coloured surround (Fig. 8a).

The adapting field consisted of two grey spots, positioned on either side of a central fixation point, with each spot surrounded by four coloured quadrants or sectors (Fig. 8b). Two of the quadrants surrounding each spot were green and the other two were magenta. This arrangement ensured that no net colour was induced into the achromatic spots during the adaptation period, since each spot was bordered by equal amounts of the complementary colours green and magenta. The two spots were also sufficiently small (1.75° dia) that each spot looked homogeneous in colour.

The test field, which was again optically superimposed to lie at the same position as the adapting field, consisted of two grey spots surrounded by four quadrants. In the test field, however, two of the quadrants were white and the other two jet-black (test field 1 in Fig. 8b). If we consider the left-hand spot, the upper left and lower right quadrants of the adapting field were green, and were replaced in the test field by black quadrants, whilst the upper right and lower left adapting quadrants were magenta to be replaced in the test field by white quadrants. Thus the green afterimages of the upper right and lower left quadrants appeared strongly on the subsequent white test field, whilst the pink afterimages of the other two quadrants could barely be seen against their subsequent black test fields. The converse situation existed for the quadrants surrounding the right-hand spot. Here the pink afterimages of the upper right and lower left quadrants were extremely visible compared with the green afterimages of the other two quadrants. After dark adapting for several minutes, the subject viewed the adapting field for an initial period of 18 sec. The test field was then exposed and the subject was required to null out any apparent colour in the test spots until they looked achromatic. Adaptation was then continued for a further 8 sec and the cycle repeated until the subject was satisfied that the test spots looked achromatic during the brief test field presentations.

Results

When the neutral test field was exposed, subjects reported that the left-hand spot appeared pink and the right-hand spot green. The spot afterimages could be nulled with a mixture of about 56% green and 44% magenta light on the left-hand spot and a mixture of 44% green and 56% magenta light on the right-hand spot. (Averaged over two subjects and separate trials for the left and right eyes.) If the positions of the black and white quadrants were reversed in the test field (shown as test field 2 in the lower part of Fig. 8b), then the left spot appeared green and the right spot pink. In this case the null settings were opposite in direction (Fig. 8c).

The strengths of the colours induced by the surround afterimages were also measured after a single 18 sec adaptation period, together with the time course of the decay of the effect. In this situation, the black and white test field was exposed immediately after the adaptation period and the subject was required to adjust the colours of the test spots as quickly as possible until the apparent colour had been completely nulled out and the spots appeared achromatic. The subject then closed his eyes whilst the experimenter recorded the null setting together with the elapsed time and reset the nulling filter to the physically achromatic position. The subject then opened his eyes and made a further null setting, repeating this procedure until all the apparent colour in the test spots had decayed away. The recorded time courses for two subjects with the two different test field arrangements of Fig. 8b are shown in Fig. 8c together with the best-fitting exponential functions. The time constants of these functions were between 19 and 39 sec. Control runs were also carried out using the same adaptation and test procedures except that the subject was not required to null out the apparent colour of the test spots until 20 sec after the end of the adaptation period. The null settings under these conditions were sufficiently close to the previously recorded time courses that we can conclude that the nulling procedure was not significantly affecting the nature of the time course of the decay.

The colours induced into the spot afterimages were very nearly as strong after 18 sec adaptation (shown as decay curves in Fig. 8c) as they were after the much longer "topping-up" adaptation periods (shown as stars in Fig. 8c). Thus 18 sec was long enough for the afterimage effects to build up to almost full strength. Compare this with the much slower buildup of adaptation in Experiment 5 (Fig. 7c).

DISCUSSION AND INFERENCES

It was suggested earlier that there could be two ways of generating the colours perceived in the afterimage of a grey spot on a coloured surround (see Fig. 1). Our findings indicate that both pathways can be elicited independently—afterimages can be produced from contrast colours, and contrast colours can be induced from surrounding afterimages. In Experiment 5, the adapting surround was made to alternate between the complementary colours in successive time intervals in order to abolish any temporal buildup of coloured afterimages of the surround. Therefore the colours that were perceived in the test spots under these conditions must be the afterimages of the previously induced colours. In Experiment 6, on the other hand, adjacent spatial areas were composed of complementary colours in order to abolish any spatial induction of contrast colour during the adapting period. The colours that were perceived in the test spots under these conditions must therefore be spatially induced by the surround afterimages during the test field presentation. Simultaneous and successive contrast processes are therefore implicated in both effects—the different experimental manipulations used in Experiments 5 and 6 simply determined which of the two processes was elicited.

Simultaneous contrast effects have often been attributed to lateral inhibitory processes in the visual system. For example, Shively (1973) and King and Wertheimer (1963) have suggested that when a grey spot is viewed against a green surround, lateral inhibition from the active green receptors in the surround area acts to block the neural responses from the green receptors in the spot region. This makes the assumption that lateral inhibitory processes only operate within a given colour system and not between different colour systems (Alpern and Rushton, 1965). Therefore, when achromatic light falls on the spot region of the retina, the red and the blue systems will respond more vigorously than the inhibited green system and the spot will appear subjectively magenta.

Successive contrast effects, on the other hand, have been explained in terms of recurrent self-inhibition rather than lateral inhibition. This implies that prolonged stimulation of a particular area of the retina produces adaptation of the underlying mechanisms so that the sensitivity of the system is subsequently reduced. Barlow (1964, 1972) has likened this adaptation process to "automatic gain control". If we make the similar assumption that adaptation processes are independent for the different colour systems (Rushton, 1965; Du Croz and Rushton, 1966), then it will be predicted that if a particular area of the retina is stimulated with green light, the subsequent sensitivity of the green system will be reduced, and the red and blue systems will fire more strongly when achromatic light is shone on to that retinal area. The afterimage produced by this stimulation will therefore be magenta or pink in colour.

In Experiment 2, where a grey spot was fixated against a green surround, the spot appeared pink as a result of lateral inhibition from the active green receptors in the surrounding area. At the end of the adaptation period, it is assumed that the green receptors will be in a relatively adapted state in the surround region, but in the spot area, the red and blue systems will be more adapted since they were generating the largest signals. Therefore, on presentation of the achromatic test field, the largest activity in the spot region will be produced in the green system, giving rise to an apparently green spot afterimage.

In Experiment 6, the quadrant arrangement of green and magenta sectors in the adapting field ensured that there would be equal amounts of inhibition of the spot region in the different colour systems. Therefore the spot should appear to be achromatic, as was found. However, the coloured quadrants of the adapting field did produce selective adaptation of the colour systems in those surround areas. When the test field was exposed, the selective adaptation should show up as complementary afterimages in those quadrants that were illuminated with white light. The differential responses generated in the white quadrants would in turn produce differential amounts of lateral inhibition of receptors in the spot region, causing the spot to appear to be the complementary colour of the quadrant afterimage.

The results of Experiment 4 are harder to interpret. Here a black spot on a green (or magenta) surround produced a pink (or green) afterimage. Note that the same result would be obtained if the figure ground relationship was reversed and the subject adapted to a green (or magenta) spot on a black surround. It was noted earlier that the black spot sometimes appeared to be tinged with the colour of the surround. A possible explanation of the apparent colour is that it was produced by scattered light from the apparatus or in the optic media, but the results of Experiment 4 rule out scattered light as an explanation of the subsequent afterimages. Here, the black spot on a green surround was alternated with a magenta field, so it is difficult to see how a small amount of scattered light from the green surround could have more effect in adapting the green system than the magenta light on the red and blue systems.

We can draw an analogy here between colour and movement. We found that on a green background, a grey spot acts rather like a pink spot and gives a green afterimage, whereas a black spot acts rather like a green spot and gives a pink afterimages. It has been reported that on a moving background, such as a textured surface which moves slowly to the left, a stationary textured area appears to move to the right, by induced movement, and gives an aftereffect of apparent movement to the left (Anstis and Reinhardt-Rutland, 1976). This aftereffect of contrast motion is analogous to the contrast afterimage we found with a grey spot. However, a large empty black region surrounded by moving stripes or random dots shows a "phantom" pattern apparently moving in step with the surround (Tynan and Sekuler, 1975). The empty area can be as much as 8° in diameter. After observing such phantoms, a stationary pattern in the previously empty region appears to move in the opposite direction—a motion aftereffect occurs (Weisstein, Maguire and Berbaum, 1977). This aftereffect is analogous to the coloured afterimage we found with a black spot. The visual system appears to extrapolate apparent motion into the empty area, rather in the way that it "fills in" the retinal blind spot. In other words, a textured field appears to move against the direction of a moving surround, whereas an empty (non-textured) field appears to move in the same direction as a moving surround. In each case the motion aftereffect is opposite to the direction of the perceived (apparent) movement.

Thus, a grey spot on a coloured surround, or a textured spot on a moving surround, appears to assume the opposite colour or motion to the surround. Perhaps there is some lateral spread of inhibition of colour or motion from the background area into the spot area. On the other hand, a black spot on a coloured surround, or a non-textured spot on a moving surround, both act as if they were an extra piece of the background. They appear to take on the colour or motion of the background which spreads, as it were, into the spot area.

Some unsolved problems remain. We showed that contrast colours can produce coloured afterimages: but we do not know why the afterimage colours were subjectively stronger than the contrast colours which produced them. We also showed that surround afterimages can spatially induce contrast colours into a spot afterimage: but we do not know why the colours of the spot afterimage were subjectively stronger than the surround afterimages which induced them. The fact that contrast can cause (hence precede) afterimages, and vice versa, suggests the existence of recurrent or feedback loops in the visual system, or else that adaptation processes occur at different sites both before and after lateral inhibitory processes.

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