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Opponent Processes In Colour Vision: What Can Afterimages Teach Us?

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ABSTRACT

To investigate afterimage colours, participants (n=14) formed afterimages by fixating on coloured stimuli in bright light for approximately eight seconds. They then chose one colour from a selection that most closely matched the afterimage they were seeing. Afterimages were found to be complementary to the stimulus colour, rather than corresponding to the opponent pairs. Consequently, the hypothesised opponent mechanisms should be revised to reflect the complementary nature of afterimages.

N.B. For the purpose of assessment at the University of Birmingham, this research project was originally submitted as two separate assignments**:** a literature review (submitted September 2009) and a practical report (submitted March 2010). Both sections have been included here in their original form. Consequently, some of the material covered in the literature review is repeated in the introduction to the practical report.

KEY WORDS:	OPPONENCY THEORY	AFTERIMAGES	COMPLEMENTARY COLOURS	OPPONENT COLOURS	GOETHE

Literature Review

The study of colour vision is as old as science itself. Already in ancient Greece, prominent philosophers had begun to investigate the phenomenon of colour. Plato believed that vision occurs because the eye sends 'visual rays' out into the world (Plato, cited at www.colorsystem.com). He identified four basic colours: white, black, red and 'radiant'. White light (considered synonymous with daylight) allows the eye to extend its visual rays, while black (darkness) has the opposite effect. The third colour, red, is the colour of fire. Fire makes the eye produce tears, which cause objects to acquire 'radiance' and glow with different colours. This fourth colour, radiance, is hard to understand, and does not seem to correspond to any basic colour in the modern sense. The ideas of Aristotle are somewhat easier to follow. He believed that colours arise from the interaction between white (daylight) and black (darkness). There are thus seven basic colours: white (as seen at noon), yellow, orange and then red (as sunset approaches), green (also sometimes seen around sunset), followed by violet (after sunset) and finally the dark blue/black of the night sky (Aristotle, cited at www.colorsystem.com).

Although these teachings are now considered archaic, the idea that colour can be reduced to a set of primary or basic hues has lasted to the present day. Most researchers agree that a few 'pure' colours should provide the basis for colour vision, but the definition of a pure colour has often been a point of conflict. Leaving aside the historical confusion between additive (light-based) and subtractive (pigment-based) primaries, the principal disagreement is between those who believe that certain colours are pure because they are perceived as such by the human observer (e.g. Hering, 1878, cited in Shevell, 2003) and those who believe that primary colours are pure because they cannot be formed from mixtures of other colours (e.g. Newton, 2007). Recently, these two approaches were reconciled by the zone theories of colour vision (e.g. Massof & Bird, 1978). The purpose of this literature review is, first, to examine how the historical search for pure colours has contributed to the current theory of colour vision; second, to describe the role of complementary afterimages in the current theory, and third, to question whether (as is generally believed) the afterimage colours can be adequately described by this theory, thus providing the research question for this dissertation.

The physicist Sir Isaac Newton (1704; English translation, 2007) was probably the first to investigate primary colours in the scientific sense (i.e. colours that cannot be formed from mixing). Newton passed a narrow beam of white light through a prism and observed that the white light appeared to be broken up into a spectrum of constituent colours. He identified seven distinct spectral colours: red, orange, yellow, green, blue, indigo and violet, with red being the least refracted and violet the most. Newton then placed a second prism in the path of the coloured light, and found that although the light was refracted once more, the spectral colours remained the same. He thus concluded that these seven colours were pure because they could not be broken down into further colours, nor produced themselves from the mixing of other colours. Together, the seven primary colours produce white light.

Newton also arranged the spectrum into a colour circle, with each colour having an opposite or complementary pairing that, when mixed with the first colour, produces white or near-white (it is now recognised that three primary colours are necessary to produce white; see Maxwell, 1855; 1860, cited in Shevell, 2003).

Newton’s work attracted criticism from the German poet Goethe in his *Theory of Colours* (1840; English translation, 2006). Goethe protested that colour was at least partly the product of human experience and could not be reduced to a set of light rays. He distinguished between physiological or subjective colours (e.g. afterimages, coloured shadows) and physical or objective colours (e.g. coloured objects, coloured lights). Furthermore, he believed that Newton’s spectrum was something of a ‘special case’ in that it only appears when the slit through which the light passes is very small. When the slit is wider, the middle (green) part of the spectrum disappears. Instead there are two coloured fringes: red through to yellow on one edge of the slit (or on the edge of the beam of refracted light, depending on whether one looks through the prism at the light source or at the refracted beam; it makes no difference) and violet to cyan blue on the other. It is only when the edges are moved closer together, so that the yellow and cyan of the fringes overlap, that the whole spectrum appears. Goethe then altered Newton’s experiment by passing a broad beam of white light, interrupted by a small central strip of dark material, through the prism. The fringes now appeared on each edge of the black strip. Goethe then reduced the size of the black strip until the red and violet fringes overlapped, producing magenta in the middle. Goethe referred to the coloured fringes as the ‘primary phenomenon’ and attached little importance to the Newton spectrum, which he considered to be rather contrived. Finally, Goethe also correctly identified the three subtractive primaries, although at that time, the difference between additive and subtractive mixing was not yet understood. Goethe’s work did little to harm Newton’s theory, but his assertion that colour perception is the result of physiological processes rather than light rays alone, is absolutely in keeping with the modern colour vision theory, and thus deserves to be included here.

Following Newton’s work, attention turned to the colour-coding mechanisms used by the eye. The trichromatic theory of colour vision was initially developed by Young (1802, cited in Shevell, 2003). Young believed that the retina could not possibly contain different receptor types for every single colour, and therefore must be responding to just the primary colours instead. At the time scientists still believed that there were seven primaries, but Young initially claimed that only red, yellow and blue were necessary, probably because these colours were widely cited as primaries by artists. However, after further investigation, Young amended his theory to state that red, green and violet were the primary colours used by the eye (it should be noted that Young himself used the term violet; it was his successors who referred to it as blue). Young’s theory was given further credence by Maxwell (1855; 1860, cited in Shevell, 2003) who, influenced by Young, proved that all colours could be mixed from the three additive primaries (although he described them as red, green and blue). Following the progress made by Young and Maxwell, Helmholtz (1896, cited in Shevell, 2003) further developed the concept of trichromacy, citing red, green and violet as the primary colours. In addition, Helmholtz was the first to demonstrate the difference between additive and subtractive mixing, and to distinguish between hue, saturation and brightness.

Despite the widespread acceptance of the trichromatic theory, Hering (1878, cited in Shevell, 2003) believed it contained two major flaws. Firstly, according to the theory, yellow must be coded as a mixture of red and green. Hering, however, took the view that yellow must be a pure colour because people do not experience it as a mixture of red and green (in contrast to purple, for example, which can be perceived as a blue-red mixture). The same could be said for green, red and blue, which, according to opponency theory, are never perceived as mixtures of other colours (Hering was not the first to take this view; Leonardo da Vinci expressed the same idea in his *Treatise on Painting* (2002)). Secondly, Hering noted that certain colours seem to be in opposition to each other. Yellow, for example, can have a red or green tinge but not a blue one, and vice versa. Likewise, green can have a blue or yellow tinge, but not a red one, and vice versa again. Thus, yellow appears to be perceptually opposite to blue, with green being perceptually opposite to red. Hering went on to say that the opponent colours induce each other as afterimages. The same is true for white and black, although ordinarily black and white mix to produce grey, and thus do not oppose each other in the same way. Consequently, Hering proposed that the eye must have a mechanism by which these colours (red, green, blue and yellow) are placed in opposition to one another. The colour red, for example, would stimulate the 'red' mechanism and inhibit the green one, whilst the blue-yellow system would remain in equilibrium. The complementary afterimage would be formed when the mechanism for one colour is stimulated excessively and becomes 'tired', thus reducing it's inhibition of the opponent mechanism to the extent that the opposite colour is perceived. In all, Hering proposed two opponent pairs; red versus green and blue versus yellow, plus a non-opponent black-white system (since black and white can mix to produce an intermediate shade). For a long time, Hering's ideas were dismissed in favour of the trichromatic theory, which was effectively proven by the discovery of short, medium and long (i.e. violet, green and red) wavelength-responsive cone cells in the retina (e.g. Dartnall, 1957, cited in Shevell, 2003). However, the trichromatic theory still could not explain the elementary nature of yellow, nor the phenomenon of complementary afterimages, and thus opponency theory retained some support.

Hering's ideas were later revived in a famous study by Hurvich and Jameson (1957, cited in Shevell, 2003). Using a technique known as hue cancellation, participants were asked to adjust the intensity of two monochromatic lights so that the illuminated area appeared 'neither red nor green' or 'neither blue nor yellow'. Firstly, participants were given a green light paired with a series of red-containing lights (i.e. red, orange, purple etc). For each light, participants had to adjust the intensity of the red and green lights until the resulting colour appeared neither red nor green (in which case it appeared yellow, blue or achromatic). The experiment was then repeated with a red light and green-containing lights, a blue light and yellow-containing lights, and a yellow light and blue-containing lights. In each case, one colour was judged to be a unique hue (i.e. perceptually pure) and the other was any colour containing at least some element of the opposite unique hue (it should be noted that simply by selecting these colours, the researchers had already decided which colours were opposites before the experiment took place; this was criticised by Pridmore (2008); see below). Hurvich and Jameson then recorded the intensity of each colour needed to ‘cancel out’ its opposite, so that the resulting mixture appeared to contain neither of the constituent colours. In this way, they were able to choose a yellow and a blue that appeared neither red nor green and a red and green that appeared neither blue nor yellow. This, according to Hurvich and Jameson, was evidence for the existence of four opponent colours, and the experiment lead to the incorporation of opponency theory into modern vision colour theory. However, it did not replace the trichromatic theory; rather, it became accepted that the opponent mechanisms were located at a post-receptoral level of the visual pathway (more precisely, bipolar retinal ganglion cells connecting to the lateral geniculate nucleus; see de Monasterio & Gouras, 1975, cited in Bruce, Green & Georgeson, 2003), whilst the trichromatic theory held true for the receptoral level. In other words, the three cone types feed into the two opponent-pair mechanisms (in addition to the non-opponent black-white mechanism). Various researchers claim to have found colour-opponent channels in primates and other animals. In some cases, these opponent channels correspond to Hering’s unique hues (e.g. De Valois, Abramov & Jacobs, 1967; cited in Shevell, 2003). In other cases, many more opponent channels were found (e.g. Rocha, Saito, Silveira, De Souza & Ventura, 2007). As Shevell (2003) concludes, there is as yet no real consensus about the physiological evidence for colour-opponent cells.

The amalgamation of opponency and trichromacy is widely accepted (though not universally; see Land, 1977), and the unified theory can be found in most textbooks (e.g. Shevell, 2003; Bruce et al. 2003). Supporters claim that the theory explains how the retina codes colour, without ignoring the elementary nature of yellow or the phenomenon of complementary afterimages. An article by Pridmore (2008), however, raises a potentially serious problem. Drawing partly on earlier research into complementary afterimages by Wilson and Brocklebank (1955), Pridmore argues that Hering’s opponent hues are not opposites at all. Instead, he describes red and cyan (i.e. blue-green), green and magenta (red-violet) and blue and yellow as opposite colours, before claiming that any reddish colour (roughly one third of the colour circle) has a cyan afterimage, greenish colours all have magenta afterimages, and blue colours all have yellow afterimages (and vice versa). Consequently, Pridmore concludes that complementary (i.e. opponent) colours follow a ‘trimodal function’, with yellow, cyan and magenta forming the afterimages for all other colours. Although he provides a colour circle from which the reader can form afterimages, he offers no experimental evidence for his assertion (nor is it clear, from the colour circle, that the afterimages are really limited to only three colours). However, anecdotally at least, his criticism of the traditional opponent hues seems to be valid; the green, red, blue and yellow of his colour wheel do not seem to induce their opponent colours (as described by Hering) as afterimages. Pridmore goes on to say that Hurvich and Jameson’s (1957) study was too narrow in scope to describe the true complementary colours, because the researchers limited the study to red, green, blue and yellow lights only (as opposed to mixing every spectrum colour with all other colours). Furthermore, they did not study afterimage colours. Consequently, Pridmore concludes, there is no evidence that Hering's colours really oppose each other.

In summary, the literature on colour vision demonstrates two historical schools of thought; first, the idea that red, green, blue and yellow are 'psychologically pure' colours (da Vinci, 2002; Hering, 1878; Hurvich and Jameson, 1957, both cited in Shevell, 2003) and second, the view that pure colours are the primary colours that cannot be formed by mixing (Newton, 2007; Goethe, 2006; Maxwell, 1855; 1860; Helmholtz, 1896; Young, 1802, cited in Shevell, 2003). Recently, these conflicting approaches were reconciled in the modern zone theories of colour vision (e.g. Massof & Bird, 1978), in which trichromatic theory holds true for the receptoral level and opponency applies to a later stage of processing. However, Pridmore (2008) casts doubt on the assertion that opponent mechanisms can describe the complementary afterimage colours. Given that afterimage colours are central to opponency theory, this presents a serious problem. Currently, the available literature varies in its description of afterimage colours, which have not been properly investigated. Since complementary afterimages are believed to result from the opponent mechanisms, there is an obvious need to establish exactly what the afterimage colours (and by extension the opponent mechanisms) are. This question will form the basis of the current research.

Introduction

The currently accepted theory of colour vision is a combination of two separate theories: trichromatic theory (Young, 1802) and opponency theory (Hering, 1878; both cited in Shevell, 2003). According to trichromatic theory, the retina codes colour as a combination of the three additive (light-based) primaries: red, green and violet (often called blue). Opponency theory is now applied to a later stage of processing that receives input from the cone cells (at the level of retinal ganglion cells). There are three types of opponent cell, each corresponding to one of Hering's opponent pairs: red-green, blue-yellow, and white/light-black/dark. Each of these colours inhibits perception of the opposite colour, so that each colour can never appear to contain any hint of its opposite. The third pair, white/light versus black/dark, is more accurately described as an achromatic lightness mechanism (see, e.g., Healey, Shafer & Wolff, 1992). This mechanism is not considered to be an ordinary opponent mechanism, since unlike the chromatic pairs, white and black can mix to form intermediate shades (grey). Nonetheless, it is included in opponency theory, perhaps because black and white are afterimage pairs, and afterimages are thought to result from the opponent mechanisms (see below). The currently accepted theory of colour vision is shown in **Figure 1**.

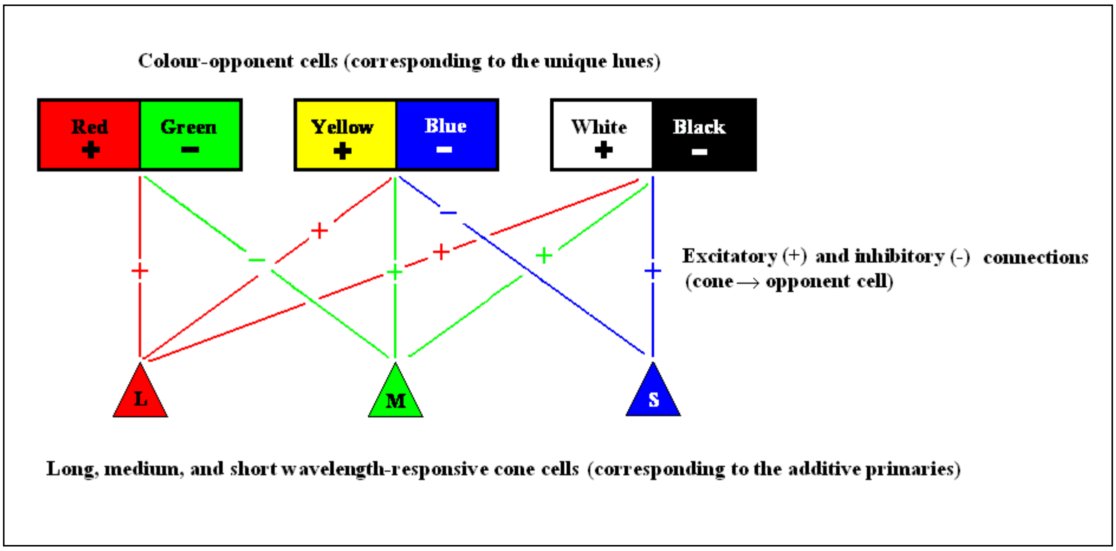

Figure 1. The three cone types and their connections to the opponent cells (note that the short-wavelength cone is shown here in blue, as is conventional, but the correct colour is actually violet). The black/white mechanism is a non-opponent achromatic lightness mechanism.

As shown in **Figure 1**~~.~~, the opponent cells receive either inhibitory or excitatory inputs from two or more of the cone types. Each opponent cell codes for one colour when stimulated (red, yellow, or white/lightness), and the opposite colour when inhibited (green, blue, or black/darkness respectively).

There appear to be two problems with the opponent stage. The first relates to the way in which the cone and opponent cells are 'wired up'. An examination of **Figure 1**. reveals that stimulation of the red-green opponent mechanism (leading to the percept of red) results from activation of the red (long-wavelength) cones. At the same time, however, the red cones must also activate the yellow-blue opponent mechanism (since yellow is coded as an additive combination of red and green). This creates the percept of yellow. Thus, it is apparently impossible to create a percept of pure red, since it would always contain yellow. The same problem occurs with green; the green (medium-wavelength) cones must be firing in order to inhibit the red-green mechanism (leading to the percept of green), but in doing so, they must also activate the yellow-blue mechanism, with the overall effect being a mixture of yellow and green. Similarly, a lack of stimulation from the cone cells should presumably have the same effect as inhibition of the opponent cells, in which case, a lack of colour would be perceived as a dark blue-green. In reality this clearly isn't the case.

The second problem lies in the afterimage colours, which are frequently cited as critical evidence for the opponent mechanisms. According to opponency theory, excessive stimulation of one opponent mechanism (e.g. blue) leads to neural fatigue, thus releasing inhibition of the mechanism for the opposite colour (yellow). Consequently, prolonged exposure to a blue stimulus will result in a yellow afterimage, and vice versa. The same is said to be true for red and green (the achromatic white-black luminance mechanism also produces afterimages, although it is not considered to be an ordinary opponent mechanism, since (unlike the other pairs) black and white can mix to form perceptually intermediate shades). Despite the importance of the afterimage colours to opponency theory, there does not appear to be any experimental evidence to suggest they are correct; even the study credited with re-igniting the argument for opponency theory (Hurvich & Jameson, 1957) did not include afterimage colours, and the physiological evidence for colour-opponent cells is not yet clear (Shevell, 2003). Furthermore, an investigation of afterimage colours by Wilson and Brocklebank (1955) found that, contrary to the predictions of opponency theory, the afterimage pairs for the primary colours were red-cyan, green-magenta, and violet-yellow, and the afterimage for blue was orange.

Wilson and Brocklebank's findings make sense for several reasons. First, each pair consists of a subtractive primary that is formed from a mixture of the remaining two additive primaries, e.g. red is complementary to cyan, which is a mixture of green and violet. Consequently each pair forms white when mixed together additively, and black when mixed subtractively, as shown in **Figure** 2. These colours are therefore 'true' opposites in the scientific sense (although it should be noted that the additive opposites are not exactly the same as the afterimage opposites due to hue shifts, especially for the blues and oranges; Wilson & Brocklebank, 1955).

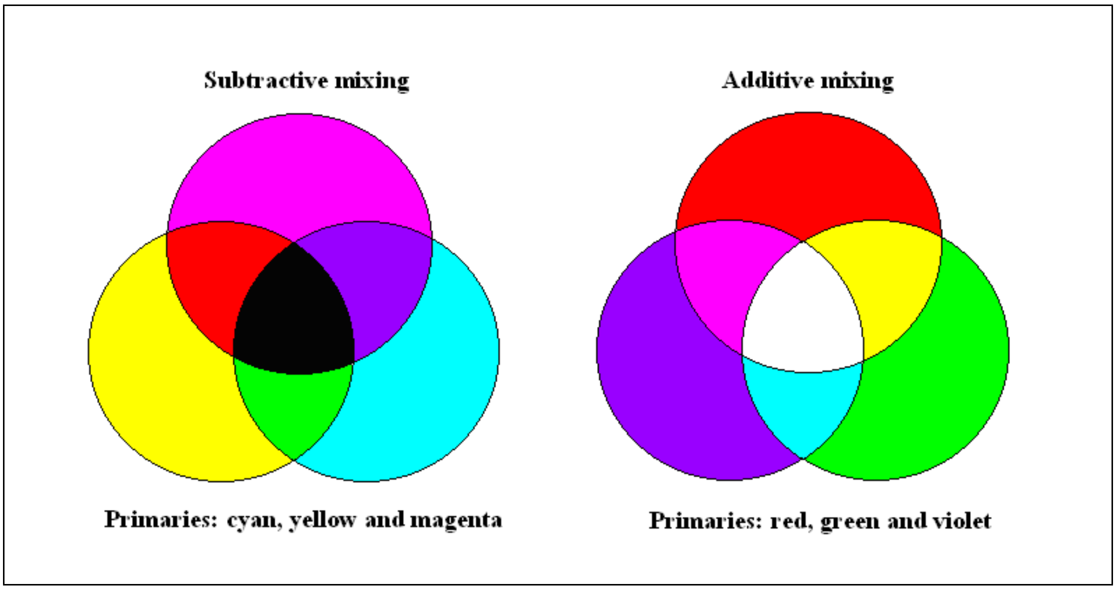

Figure 2. Additive and subtractive mixing of the primary colours (note that these colours are only an approximation, since they depend on the colours available in the printer or computer screen used for viewing).

Second, the usual argument in favour of the traditional opponent pairs is that they are perceived as opposites. For example, a blue colour could have a red or green tinge, but never a yellow one. However, the same argument can be made for Wilson and Brocklebank's complementary colours; it is just as impossible for violet to have a yellow tinge as it is for blue to have one. Indeed, there would presumably be a whole range of colours that would never be described as having a hint of yellow to them, from magenta through purple and violet to blue. Common sense suggests that although they are sufficiently distant from yellow to have no trace of it, they cannot all be the opposite colour of yellow. The 'perceptual opposites' argument cannot pinpoint the opposite colours with any real precision, and it works just as well for the complementary colours as for the unique hues. The complementary colours, on the other hand, have a more accurate and precise definition based on colour physics, as well as some evidence to suggest that they correspond to the afterimage colours. Consequently, the purpose of the present study is to investigate the afterimage colours, with the prediction that they will correspond to the complementary, rather than the traditional opponent, colours. Black and white should also be afterimage pairs, since they are complementary (as well as opponent) pairs. When investigating this mechanism it is important to stress that while black and white are considered opposite colours in terms of afterimages, the white/light-black/dark mechanism is in fact considered to be an achromatic mechanism. Thus, black and white appear as 'colours' only when no colours are present, such that the stimulus can only be distinguished from the background in terms of its relative lightness/darkness. Lightness and darkness, in the absence of colour, appear as white, black, or various intermediate shades of grey. On a neural level, the chromatic mechanisms are in equilibrium due to lack of, or equal, stimulation of all three cone types, and only the light-dark mechanism is stimulated. Since the achromatic mechanism deals with lightness rather than chromaticity, it makes sense that it should also play a role in the formation of coloured afterimages, as long as there is a lightness contrast between the stimulus and the background. Consequently, stimuli on lighter (white) backgrounds (i.e. ‘dark’ stimuli) should create an afterimage that is lighter than the background (i.e. a ‘light’ afterimage) and stimuli on darker (black) backgrounds (i.e. ‘light’ stimuli) should create an afterimage that is darker than the background (i.e. a ‘dark’ afterimage), regardless of stimulus colour. In other words, the lightness mechanism should exert its effects whenever there is a luminance contrast between the stimulus and background (thus making the stimuli appear relatively light or dark), independently of the stimulus colour.

Method

Participants

Participants were either Psychology undergraduates from the University of Birmingham (n=8) or friends of the researcher (n=6). Participants were aged between 18 and 66 (mean=23.5). There were 11 females and three males. All participants reported having normal colour vision.

Materials

Since there were no paints available in the correct colours, the stimuli consisted of coloured modelling clay, pressed into a 3mm-deep, 6cm-diameter circular depression in the centre of a 24*24cm square of white roof-cladding, with a laminated cardboard backing (see **Figure 3**). There were 10 colours: red, orange, yellow, green, cyan, blue, violet, magenta, black and white. Each circle had a small central fixation cross. There was an additional white square containing a ring of eight 3.5cm-diameter circles of modelling clay in red, orange, yellow, green, cyan, blue, violet and magenta, which was used to compare similar colours if participants had difficulty choosing an afterimage colour.

Afterimages were projected onto a 24*24cm white board (as above) with a central fixation cross marked out in pencil, and eight 3.8cm-diameter coloured circles arranged in a circle around the fixation cross (see **Figure 4**~~.~~). The coloured circles were cut from the reverse side of photographic paper (to create the ‘glowing’ effect seen in afterimages) using a large hole-punch, and coloured in pastel shades of each stimulus colour using a mixture of highlighter pens and water, applied with a tissue. All the stimuli used were covered with a sheet of transparent book-covering to prevent damage. For the second half of the experiment (concerning the relative brightness of afterimages), a 24*24cm black card with a 6cm-diameter central hole was used to cover the white background of the stimulus colours. Afterimages were then projected onto a 24*24cm white board with a central 6cm-diameter circle and fixation cross marked in pencil.

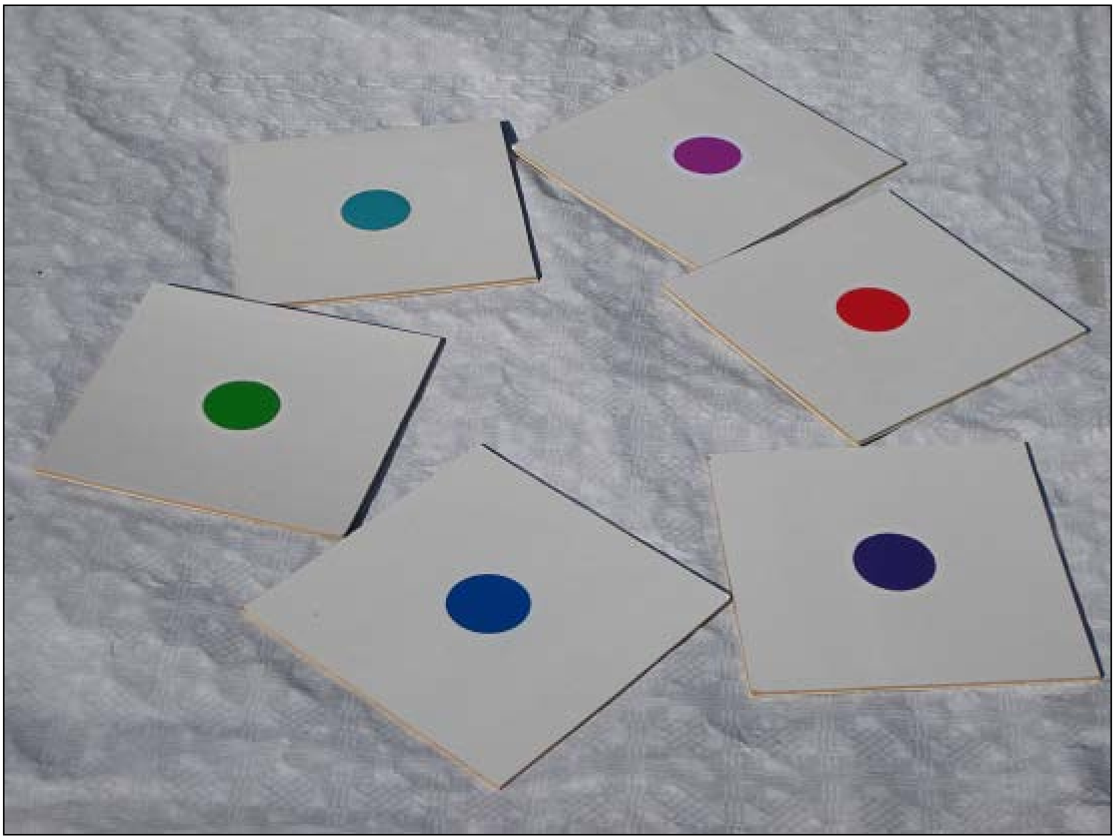

Figure 3. Examples of coloured stimuli used to form afterimages (note that the colours shown in this photograph are not completely accurate due to limitations of the camera and computer screen/printer.

Figure 4. Board of afterimage colours (again, note that the colours cannot be reproduced accurately**;** in particular, the background appears quite grey here, but it is actually white).

Procedure

Participants filled in a consent form and received written instructions (see Appendix, pages I-II). They then completed one practice trial followed by the main experiment. The practice trials were conducted with the green, yellow or red stimuli, since these produced the clearest afterimages. For the rest of the experiment, the colours were presented in no particular order, with the exception of black and white, which came last. For the first task, participants were given each colour in turn and asked to fixate on the central cross for at least eight seconds, or until an afterimage formed. This was done under a daylight lamp. They then projected the afterimage onto the board of afterimage colours and chose one colour that matched their afterimage. Participants could repeat each colour as many times as they liked, until they were confident of their answer. On the few occasions when they struggled, they were encouraged to use the circle of smaller stimulus colours to form two or three similar afterimages simultaneously. This made it easier to judge the difference between visually similar colours. Participants had been instructed to describe the afterimage verbally if it did not appear to match any of the colours, but this situation never arose. The black and white afterimages were projected onto the plain white board and described verbally. Descriptions such as ‘black’, ‘grey’ or ‘dark’ were categorised as black. ‘White’ and ‘light’ were categorised as white. There were two reasons for not including black and white on the circle of afterimage colours. First, being achromatic, they do not fit easily into the circle. Second, placing them between two colours would make it harder for participants to compare the two neighbouring colours with each other when matching them to an afterimage. In addition, the white stimulus was only presented against the black background and the black stimulus only against the white, since the contrast is necessary to form an afterimage. In all other respects, however, black and white were treated in the same way as the coloured stimuli.

For the second task, participants were once again asked to form afterimages, with each stimulus presented first against the white background and then against the black background. In each case, they projected the resulting afterimage onto the plain white board and were then asked whether the afterimage appeared to glow brighter than the background, or whether it appeared duller than the background.

Results

Results for Colour-Matching

Table 1. Number of participants choosing each afterimage colour for each stimulus colour. The complementary colours are highlighted in yellow, and the opponent pairs in red.

Stimulus Colour	**Number of Participants Choosing Each Afterimage Colour**									
	Red	Orange	Yellow	Green	Cyan	Blue	Violet	Magenta	Black*	White*
Red	0	0	0	0	13	1	0	0	0	0
Orange	0	0	0	0	0	13	1	0	0	0
Yellow	0	0	0	0	0	0	14	0	0	0
Green	0	0	0	0	0	0	0	14	0	0
Cyan	13	1	0	0	0	0	0	0	0	0
Blue	1	13	0	0	0	0	0	0	0	0
Violet	0	0	14	0	0	0	0	0	0	0
Magenta	0	0	0	14	0	0	0	0	0	0
Black	0	0	0	0	0	0	0	0	0	14
White	0	0	0	0	0	0	0	0	14	0

*These were the number of participants describing the afterimage as black/grey/dark or white/light.

As can be seen from **Table 1**, the majority of participants chose the predicted afterimage colours for each stimulus colour. The results (though clearly significant) were analysed with binomial tests for each stimulus colour, in which the null hypothesis was that participants would choose an afterimage colour at random (thus giving a 0.1 probability of choosing any individual colour). As expected, the results for all the stimulus colours were highly significant ($p<0.001$, $n=14$). The SPSS output for these tests is shown in Appendix, page III. There were only four non-complementary pairings. These occurred for the red, orange, blue and cyan stimulus colours, each of which had a single pairing with blue, violet, red and orange respectively. **Figure 5** shows the number of complementary pairings for each stimulus colour. As can be seen, the small number of unexpected or 'incorrect' pairings occurred only for the red, orange, blue and cyan stimulus colours, where the difference in hue between neighbouring colours was smallest. Each of these colours had only one non-complementary pairing, and the results were well above chance performance for all colours.

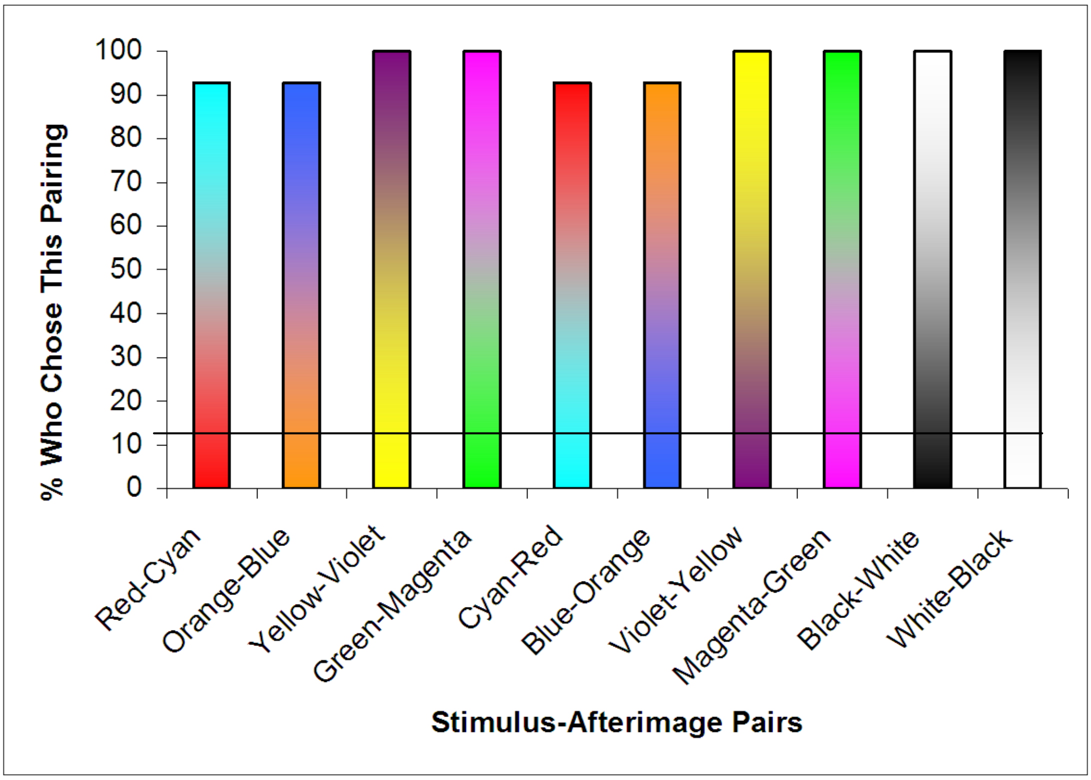

Figure 5. Percentage of 'correct' pairings (as predicted from the hypothesis) for each stimulus colour. Pairs are shown with the stimulus colour followed by the predicted afterimage colour, e.g. cyan (stimulus)-red (afterimage). The black line at 14% denotes chance performance.

Results for Light/Dark Judgements

Table 2. Number of afterimages judged to be lighter or darker than a white background, having originally been formed against a black or white background.

	Number of Afterimages Judged to be Lighter/Darker than Background	
Background Colour	Lighter	Darker
White	122	4
Black	6	120

As can be seen from **Table 2**, participants were significantly more likely to judge the afterimage as being lighter than the background when the stimulus had been presented against a white background, and more likely to judge it as being darker when the stimulus had been presented against a black background (binomial tests, n=126, p<0.001). Overall, dark stimuli (i.e. presented against white backgrounds) formed light afterimages (i.e. lighter than the background), and light stimuli (i.e. presented against black backgrounds) formed dark afterimages (i.e. darker than the background).

Discussion

The results of the colour-matching experiment are unambiguous; participants consistently paired red with cyan, green with magenta, violet with yellow, blue with orange and black with white. The few exceptions to this occurred for the bluish and red/orange colours. It is interesting to note that these colours roughly correspond to those areas of the spectrum where hue shifts occur (see Wilson & Brocklebank, 1955). However, the more obvious explanation in this case is that these colours were closer in hue to their neighbouring colours than the rest of the colour circle, and thus discriminating between them was more difficult. Whilst the differences between colours would ideally have been equal, it was of course necessary to include blue (and its complementary) because of its status as a unique hue in opponency theory. Thus, blue and orange had to be inserted between the otherwise equally spaced primary colours. Nonetheless, the vast majority of participants were able to match the afterimage colours accurately and easily. Furthermore, none of the responses were predicted by opponency theory; not one person paired red with green or blue with yellow. Indeed, the four non-complementary pairings that did occur were all in the opposite direction (on a colour circle) from that predicted by opponency theory (e.g., red paired with blue rather than green, when the complementary is the intermediate cyan). The results thus far can be conceptualised as in **Figure 6.**

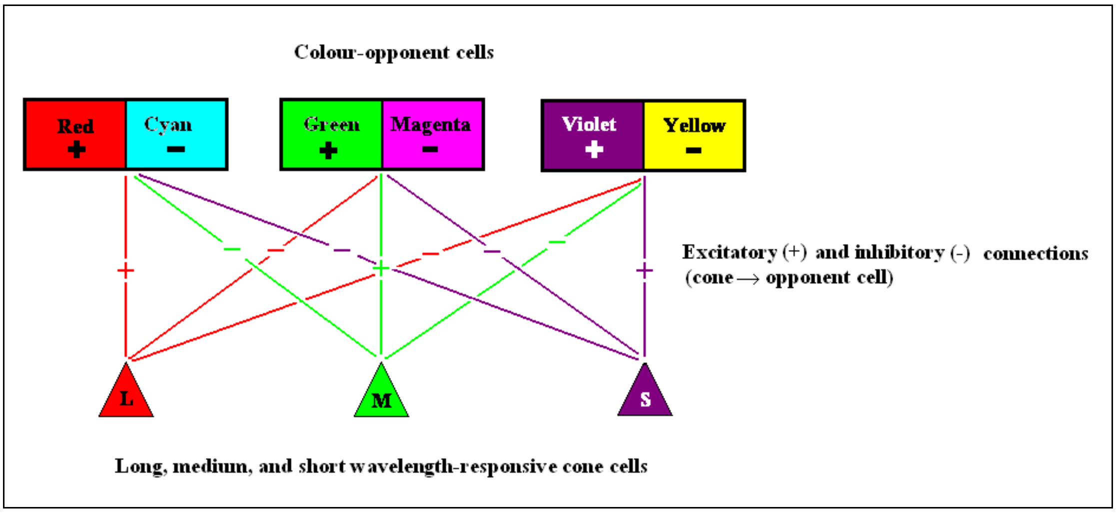

Figure 6. Hypothesised colour-opponent cells and their cone inputs based on the current findings. Note that in this model the excitatory connections (denoted by '+') have been assigned to the additive primaries, in keeping with the original model in which red and blue are excitatory, but this is purely theoretical; the inhibitory and excitatory connections could just as easily be reversed.

As shown in **Figure 6**~~.~~, the colour-opponent cells now correspond to the complementary colours, thus giving the correct afterimages. This arrangement also solves the two earlier mentioned problems with opponency. First, in the original model, a red or yellow stimulus would be perceived as orange, since stimulation of the red cones would activate both the red and yellow opponent mechanisms. Likewise, green stimuli would appear yellowish-green. In the revised model, activation of the red cones excites the red mechanism and inhibits the others, leading to the perception of yellow and magenta; these mix subtractively to form red (assuming, of course, that there are further ‘colour mixing’ mechanisms with input from the opponent cells). Thus, the percept would be pure red. The remaining colours are also perceived correctly. However, when ‘mixing’ colours, the brain must interpret the excitatory inputs as colours to be mixed additively, and inhibitory inputs as colours to be mixed subtractively. This might seem odd when one considers that the brain is dealing with electrical impulses rather than pigments or light, but nonetheless, it is necessary to hypothesise such a mechanism in order to correctly predict the colours perceived. Second, in the previous model, lack of excitation of the cone and opponent cells led to the percept of a dark blue-green. In this model, lack of excitation leads to perception of all three subtractive primaries, which correctly results in a lack of colour.

One remaining question is the way in which afterimages to non-primary colours are formed. Non-primary colours clearly have complementary afterimages, as in the case of blue and orange in this experiment. However, the opponent mechanisms are traditionally limited to the most basic colours (i.e. the unique hues, or in this case, the primary colours). Consequently there is a need to ‘mix’ these colours at a later stage to form the non-primary colours such as orange, purple, etc. However, there is no obvious reason why primary and non-primary colours would be represented at different levels of the visual pathway (with the possible exception of the cone cells). A more plausible suggestion might be that there are opponent cells for the non-primary as well as the primary colours, each receiving differing levels of input from the three cone cell types, although even this does not totally eliminate the need for further colour mixing mechanisms.

The data for light/dark judgments were equally clear. As expected, participants consistently judged the afterimage to be lighter than the background when the original stimulus colour had been darker, and vice versa when the stimulus had been lighter than the background. This was the case regardless of colour, thus demonstrating that afterimages are opposite from their stimuli in terms of lightness as well as hue. However, it is not possible to deduce the nature of the light-dark opponent mechanism from these results. The traditional explanation, that the light-dark mechanism receives input from the cone cells, is problematic for these results. If this were the case, afterimages would always be darker than the stimulus, since the ‘light’ mechanism would always be excited by any stimuli, and the ‘dark’ mechanism would always provide the afterimage. This clearly is not the case, since afterimages can be lighter or darker than their stimuli. Moreover, the ‘lightness’ or ‘darkness’ of a stimulus is judged relative to its surround. A simple light-dark mechanism with cone inputs would not be capable of carrying out such calculations. However, it would theoretically be possible to have a white-black ‘colour’ system receiving cone inputs (as hypothesised in the original opponent model), and a separate, more complex light-dark system. This seems somewhat unlikely, but has been included here because the white/light-black/dark system is traditionally illustrated as having cone inputs. This alternative suggestion is illustrated in **Figure 7**, although this is of course highly speculative and cannot be proved or disproved on the basis of these findings.

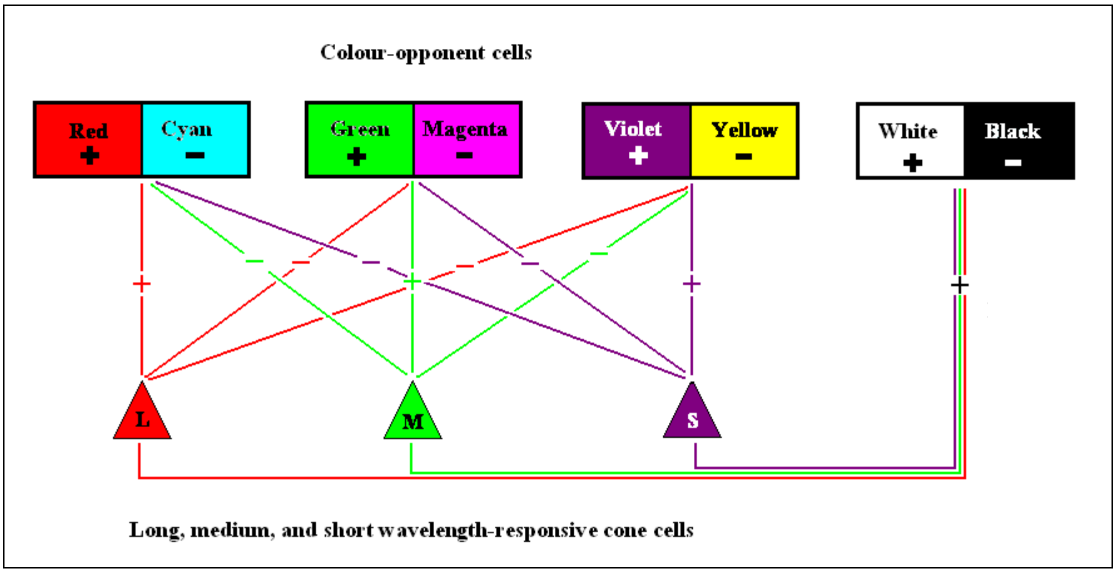

Figure 7. Hypothesised colour-opponent cells and their cone inputs based on the current findings, including white-black.

Finally, it is important to note that there are many phenomena in colour vision that cannot be explained by the opponent mechanisms. Positive afterimages (non-complementary afterimages caused by transient, very bright light), coloured shadows, colour constancy, and hue shifts, are just a few such examples. The opponent mechanisms are a reasonably satisfactory explanation for negative afterimages, but they do not provide a complete explanation for colour vision.

In summary, the most important finding is that the afterimages are indeed complementary to their stimulus colours, and thus the hypothesised opponent mechanisms should be based on the complementary, rather than opponent, colours. Light and dark stimuli (as judged relative to their surround) were also shown to be complementary. However, given that afterimages can be lighter or darker than their stimuli (depending on the lightness of the surround), this system cannot be an ordinary opponent mechanism with cone inputs (unless black and white are considered separately from light and dark, which seems unlikely). In addition to predicting the correct afterimages, this revised model also eliminates several problems with incorrect colour mixing that occurred in the earlier model. However, the opponent mechanisms alone are not sufficient to explain colour vision in its entirety, firstly because there is still a need for additional colour mixing mechanisms further up in the visual system, and secondly, because there are a number of phenomena that cannot be explained by opponency. Nonetheless, the opponent mechanisms, when based on the complementary (rather than opponent) colours, provide a reasonable model of afterimage colours.

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