

# Temporal hierarchy of the visual perceptive systems in the Mondrian world

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## SUMMARY

Our earlier psychophysical work has shown that colour and motion are not perceived at the same time, with colour leading motion by about 50–100 ms. In pursuing this work, we thought it would be interesting to use a more complex colour stimulus, one in which the wavelength composition of the light reflected or emitted from surfaces changes continually, without entailing a change in the perceived colour (colour constancy). We therefore used a Mondrian figure—an abstract multi-coloured scene with no recognizable objects—against which squares (either red or green) moved up and down, changing colour from red to green in various phase differences with the change in direction of motion. The red and green squares changed continually in their spectral characteristics, as did every other patch on the Mondrian. The results showed that colour is still perceived before motion, by about 80 ms.

## 1. INTRODUCTION

Our earlier psychophysical work has shown that different attributes of the visual scene, and in particular form, colour and motion, are not perceived at the same precise time (Moutoussis & Zeki 1997*a,b*) and that there are therefore different perceptual systems specialized for different attributes of the visual scene. We presume this to be the perceptual reflection of the activity in the parallel, spatially distributed and functionally specialized processing systems of the visual brain (Zeki 1975, 1978; Livingstone & Hubel 1984). In showing that the different processing systems need different times to generate their perceptual end-products, our psychophysical experiments have also shown that the brain does not have a mechanism to compensate for the perceptual time differences between its specialized processing systems. The results of our psychophysical experiments have therefore extended the concept of functional specialization into the temporal domain and, taken in conjunction with our previous work on the anatomy and physiology of the primate visual brain (Zeki 1978), have shown that a hallmark of the visual brain is a temporal hierarchy superimposed upon a spatial parallelism.

In developing this work, we thought it important to try and trace the origins of this temporal hierarchy, the work reported here constituting an initial attempt in this direction. One possibility is that the origins lie in temporal integration times—the minimum necessary presentation time at the lowest threshold for a stimulus to be perceived. This gives an idea of the amount of information that needs to be integrated by the brain

before a stimulus can be perceived. By this argument, the perception of motion should require more time than that of colour, because it is the result of the integration of information from at least two points, whereas the colour of a point could be determined by the wavelength composition of light at that point alone. Such a difference in temporal integration times could arguably account for our previous results, because the red and green colours on the TV monitor were determined, respectively, by two pure phosphors, and hence each was determined by one waveband alone (Moutoussis & Zeki 1997*a,b*). If so, then it is obvious that this longer temporal integration time for motion cannot be compensated for by the demonstrated faster conduction velocities of the fibres that carry motion signals and that belong to the magnocellular or M pathway; this courses from the retina to the cortex through two branches, the retino-geniculo-cortical branch and the retino-tecto-cortical branch, the latter by-passing V1 and reaching V5 at latencies of about 35 ms, to which it delivers signals from fast moving objects ( $>10^\circ \text{ s}^{-1}$ ) (Beckers & Zeki 1995; ffytche *et al.* 1995, 1996).

The above argument has a little, though not much, merit. The colour of a point or a given part of the field of view is not determined by the wavelength composition of the light coming from it alone, but by the wavelength composition of the light coming from surrounding regions as well (Land 1974, 1983), even if the surround is black, as it was in our earlier experiments. In other words, to construct the colour of a surface, the brain has to integrate information coming from more than one point in the field of view, just as it does for motion, the difference between the two being that to compute colour, the brain has to integrate

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signals coming simultaneously from many different parts, whereas with motion, it has to integrate signals coming successively from different points. Moreover, temporal integration times are an imprecise guide to perceptual times, because they largely reflect what happens at the very initial stages of the visual system, not the whole visual brain (Krauskopf & Mollon 1971). There is, nevertheless, sufficient merit in the argument derived from temporal integration times to make it worthwhile to complement our previous study by one in which the wavelength (phosphor) composition of the light reflected from the moving green and red squares changes continuously, without changing the perceived colour. We wanted, in other words, to approximate our colour perceptive system to conditions which resemble a little more closely the natural one, in which the brain has to 'discount the illuminant' (Helmholtz 1911). We reasoned, though without much conviction, that this might load the colour system and therefore slow it down relative to the motion system. The experiment was at any rate worth trying, if only to establish more compellingly the temporal hierarchy of the visual perceptual systems.

## 2. MATERIAL AND METHODS

Three subjects, two males and one female (whose average age was 30) were used. All were dextral and had normal colour perception. All three had taken part in a repeat of our previous experiment (Moutoussis & Zeki 1997*a*). In approach, the present experiment was very similar to our earlier one, with two differences: (i) in the present experiment, the red and green (experimental) squares moved up and down against a stationary multi-coloured background, somewhat like the Land colour Mondrian, an abstract scene with no recognizable objects (see figure 1); and (ii) the experimental red and green squares were no longer generated by one phosphor each. In the earlier experiment, the square(s) moved up and down against a black background and changed colour while doing so, from equiluminant red to equiluminant green. The more naturalistic condition would be one in which the wavelength composition of the light coming from the two sets of experimental squares changes. But when that happens in natural conditions, the wavelength composition of the light coming from every other part of the Mondrian scene also changes. In the present experiment, therefore, the phosphor mixture from the experimental (red and green) squares as well as that from all the other squares constituting the Mondrian were continuously changed, to simulate a change in wavelength composition coming from the entire scene. The method we used to vary the illuminants was as follows. Each of the three illuminants was assigned a rate of change (which determined the speed from which it moved from its maximum intensity of one to zero, its minimum intensity). When either the maximum or the minimum intensity was reached, the sign of the rate of change variable was changed. Since each of the illuminants was assigned a different rate of change (0.0031, 0.0017, 0.0013 per frame for the long, middle and shortwave illuminants, respectively), the balance of colour varied constantly. No attempts were made to simulate changing daylight illumination, nor changes orthogonal to this, although such simulations might be interesting. As the ratio of illuminants was constantly changing, the overall luminance of the stimulus also changed. As in the previous experiment, the two attributes under consideration, colour and motion,

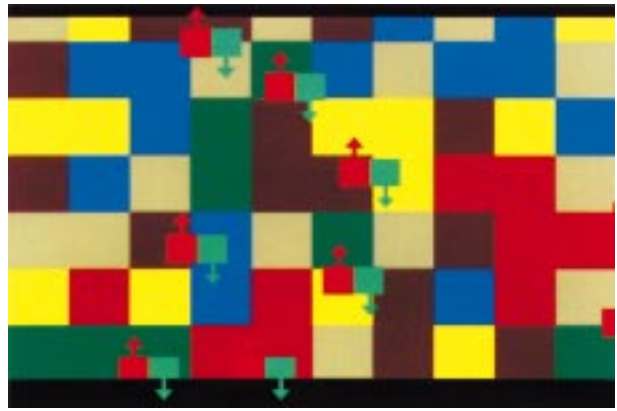


Figure 1. The stimulus used in the experiment. This shows one particular phase offset ( $180^\circ$ ). Note that moving red and green squares are never simultaneously present on the screen. The moving squares subtended an angle of  $1.5^\circ \times 1.5^\circ$ , and moved at a speed of  $3.14^\circ \text{ s}^{-1}$ .

were continuously varied, from red to green (and vice versa) for colour and from up to down (and vice versa) for motion. The variation can be described by two square-wave oscillations of the same period,  $T$ , presented at various phase differences with respect to each other and covering the whole range of  $0$ – $360^\circ$ . The period of the oscillation was  $0.537 \text{ s}$ , and the phase difference between the two attributes was varied in steps of  $10^\circ$ , each phase difference being presented four times in random order. Each trial lasted a maximum of  $14 \text{ s}$  during which subjects had to make their choice—decide what the colour of the square was when it was moving up (and what it was in the contrary direction). The choice was made by pressing a key on the keyboard during this period, or after the termination of the trials. The data derived from all three subjects were averaged, to obtain a value with standard errors.

The appearance of the Mondrian under varying lighting conditions was calculated in the following way; a PhotoResearch PR650 SpectraColorimeter was used to obtain the reflectance spectrum of each patch of an actual coloured Mondrian, in turn. Radiant spectra of three illuminants were also obtained using the same equipment. These were in fact the radiant spectra of the red, green and blue phosphors of an AppleVision 1710AV computer monitor. This information was used to calculate the 1931 CIE XYZ values for each of the moving red and green experimental squares, as well as for every other stationary coloured patch constituting the Mondrian, for each required combination of the three illuminants which were made to vary continuously. The condition therefore approximated closely the natural viewing condition in which, when the wavelength composition of the light reflected from a patch that is part of a complex scene changes, the wavelength composition of every other patch also changes. The PR650 was also used to calibrate the display monitor so that the required  $XYZ$  values could be recreated as closely as possible on the monitor.

Figure 2 is the standard 1931 CIE  $xy$  chromaticity chart on which is plotted the bounds of the  $xy$  values produced by the calculations that generate the red and the green squares. As the display was generated on a monitor screen, the gamut of the three phosphors imposed a limit on the displayable colours, which is indicated by the black triangle. As the illuminants (the phosphors) vary, the red and the green squares move within the area defined by their triangles. Where the two overlap, the wavelength composition of the two is much the same, and the two are seen as differing in colour only because of the context, as happens when viewing

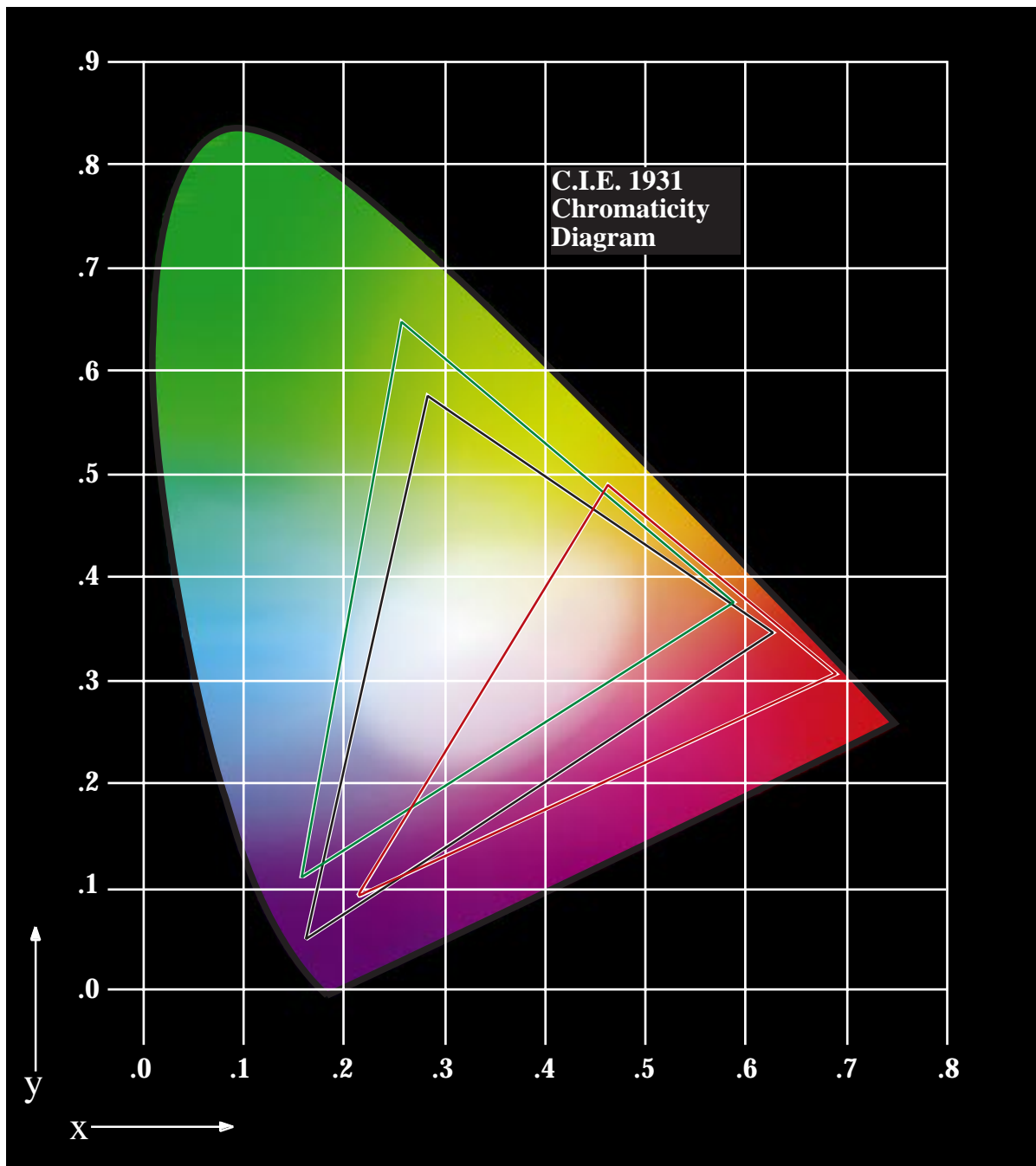


Figure 2. A representation of the 1931 CIE chromaticity diagram on which are superimposed the triangles bounding the colour space that the 'red' and 'green' squares theoretically occupy as the illumination is changed. The black triangle denotes the monitor gamut, and hence the bounds of the actual colour space that the 'red' and the 'green' squares occupied.

successively two different coloured patches of a Mondrian when each is made to reflect the same triplet of energies (Land 1974). In fact, as one colour moves within its space, the other colour moves in parallel within its own space, with the consequence that it would be impossible for the two squares to have the identical wavelength composition at the same time, although of course only one set of squares, all of the same colour, is on the screen at any one time.

As before, one can calculate a theoretical curve for a perceptual system that is totally veridical. This is shown in figure 3a; the squares, in spite of the changes in wavelength composition, are entirely green or red in the  $0^\circ$  and  $180^\circ$  directions, and various mixtures of the two in between; at  $90^\circ$

and  $270^\circ$ , they are green for one half of the upward (or downward) trajectory and red for the other. A veridical perceptual curve should be similar to this one. If colour is perceived before motion, the curve should be rotated anticlockwise, the degree of rotation giving the difference in perceptual time between colour and motion.

For each condition, the set of responses made by the three subjects was summed, then plotted on a polar graph. A rotation angle was calculated by treating each point on the graph as a vector from the centre, calculating a mean vector, and finally measuring its angle to the vertical. The polar data were 'unwound' and plotted as a population on a Cartesian graph centred on the rotation angle. The Wilcoxon signed

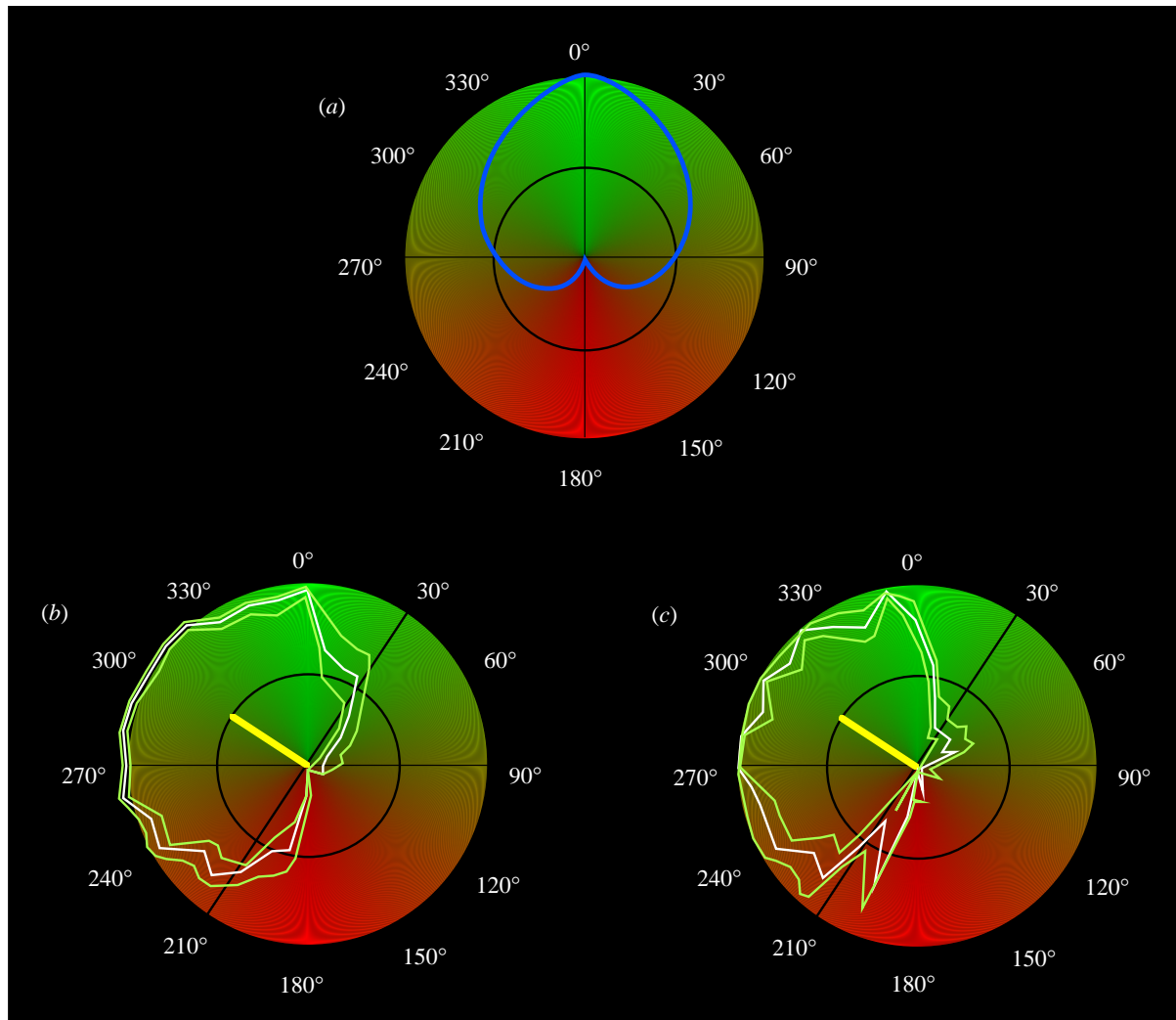


Figure 3. (a) A polar plot showing the relationship of the colour of the moving squares to their direction of motion as produced by the computer. The percentage of time the green squares are moving upwards is plotted against the phase difference between the colour and motion oscillations. The outer circle represents 100%, the inner circle 50%. So, at  $0^\circ$ , upwards motion is always of 'green' squares, while at  $180^\circ$  upwards motion is always of 'red' squares. (b) The average perceptual result under the original paradigm with static illumination and a dark background (Moutoussis & Zeki 1997a). The curve is rotated by  $56.5^\circ$  anticlockwise. (c) The average perceptual result from three subjects under changing illumination (Mondrian condition). The curve is rotated by  $67.2^\circ$  anticlockwise. The dotted lines in (b) and (c) give the standard error of the means. There is no significant difference between the rotations of curves (b) and (c).

rank test was carried out on the population to test for a significant departure from a mean of  $56.5^\circ$  (the earlier result from Moutoussis & Zeki 1997a). The  $z$ -statistic obtained from this test was converted to a  $p$  value with reference to the normal distribution (two-tailed).

### 3. RESULTS

The results were almost identical to the ones obtained in our previous experiment, when the colour was determined by one phosphor alone (Moutoussis & Zeki 1997a,b). Figure 3c shows the actual perceptual curves obtained from the three subjects; it is markedly similar to the curve obtained using our earlier method of stimulation, shown in figure 3b. The rotation was  $67.2^\circ$  for the Mondrian experiment and  $56.5^\circ$  for the 'single phosphor' experiment, a difference that is insignificant ( $z = -1.82$ ,  $p < 0.05$ ).

### 4. DISCUSSION

The response curves derived from the two experiments, the one reported above and the one described earlier (Moutoussis & Zeki 1997a) are almost identical, implying that colour processing is not delayed in the Mondrian condition. This is not surprising, since in both conditions the brain must compare the wavelength composition of the light coming from the moving squares, which are the focus of attention, with the wavelength composition of the light coming from the surrounds, even if these surrounds are black. Hence, there is no extra time needed for integration or for the colour operations in the Mondrian world, compared to the simpler stimulus configuration used in our earlier psychophysical experiment.

It is, nevertheless, interesting to enquire into the steps required for processing the information in this and in our previous experiment. It is obvious that two

surfaces can be discriminated by wavelength alone—if one emits one waveband and the other another. Such a discrimination could conceivably be the result of the physiology of cells in V1 or V2, which respond best when light of their preferred wavelength dominates in the light reaching the eye (Zeki 1983). By contrast, at least some of the cells in V4 have responses that correlate with perceived colour, in that they are indifferent to the exact wavelength composition of the light reflected from the surface in their receptive fields. Our electroencephalographic recordings show that it takes about 30 ms for signals to travel from V1 to V4 (Buchner *et al.* 1994), which should translate into a difference of 20° in the rotation of the perceptual curve between the two conditions. In fact, the difference is 10.7°—in favour of the Mondrian condition, and thus opposite to what one might have expected, although the difference is not statistically significant. We conclude that a simplified stimulus, as used in our previous study, does not lead to a quicker perceptual time.

Our interpretation of this result is as follows: (a) that, in normal subjects, colour is constructed in V4 (Zeki 1983, 1984), regardless of whether the wavelength composition is constant and dominated by one wavelength or whether it is in continuous flux in terms of wavelength composition; (b) that in both this experiment and in the 'single phosphor' one (Moutoussis & Zeki 1997*a,b*), the brain is continuing with its colour-generating calculations within V4; and (c) that therefore colour is perceived before motion, even when the brain has to re-calculate continuously the wavelength composition of the light reflected from a patch and from its surrounds. We also conclude that the situation should be different in achromatopsic or dyschromatopsic subjects. There is a failure in colour constancy mechanisms in such subjects (Kennard *et al.* 1995), but they can apparently continue to discriminate lights of different wavelength surprisingly well, although not as well as normals (Vaina 1994; Fries and Zeki, unpublished results). We would therefore expect that, in such subjects, the 'single phosphor' experiment should give at least qualitatively the same result as we have obtained in normals; by contrast, they should find it impossible to perform the same experiment in the Mondrian world and, if they did, they should be markedly retarded in time, with the consequence that the entire curve should now be displaced clockwise, indicating a precedence for motion. This hypothesis is worth testing.

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