

A direct demonstration of perceptual asynchrony in vision

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SUMMARY

We have addressed the question of whether, in addition to being processed separately, colour and motion are also perceived separately. We varied continuously the colour and direction of motion of an abstract pattern of squares on a computer screen, and asked subjects to pair the colour of the pattern to its direction of motion. The results showed that subjects misbind the colour and the direction of motion because colour and motion are perceived separately and at different times, colour being perceived first. Hence the brain binds visual attributes that are perceived together, rather than ones that occur together in real time.

1. INTRODUCTION

A striking characteristic of the primate visual system is that it is functionally specialized, by which we mean that different attributes of the visual scene are processed in geographically distinct parts of the visual brain (Zeki 1978; Livingstone & Hubel 1988). The most convincing evidence for this comes from the study of motion and colour vision, which are processed in different areas of the prestriate cortex (Zeki 1973, 1974) and in distinct subregions of areas V1 and V2 (DeYoe & Van Essen 1985; Shipp & Zeki 1985; Hubel & Livingstone 1987). This specialization is itself based in part at least on differences in the physiological properties of the ganglion cell layers in the retina, with the Pa cells that feed the motion system through the magnocellular or M layers of the lateral geniculate nucleus (LGN) being indifferent to the colour of the stimulus and having faster conduction velocities than the Pb cells, which are commonly wavelength-selective and feed into the cortex via the parvocellular or P layers of the LGN (Leventhal *et al.* 1981; Perry *et al.* 1984). A separate processing of colour and motion has also been suggested by psychophysical experiments. The perceived velocity of equiluminous gratings is slower than that of luminance gratings moving in the same way, suggesting that colour information is not available to the motion system (Cavanagh *et al.* 1984). This is also confirmed by the loss of apparent motion at equiluminance (Ramachandran & Gregory 1978; Cavanagh *et al.* 1985). A further indication for an independent processing between colour and motion is the fact that, in some cases under the same stimulus condition, the motion system can integrate information coming from the two eyes continuously whereas binocular rivalry prevents such integration with respect to the colour system (Carney *et al.* 1987). It seemed reasonable to suppose, therefore, that there might be a time difference in the perception of motion and of

colour; this, in turn, would imply that the brain may misbind different visual attributes, assuming that it perceives separately, and at different times, what it evidently processes separately.

2. MATERIALS AND METHODS

Nine male subjects discriminated the direction of motion of isoluminant red and green squares that moved vertically up and down on a computer monitor (figure 1). By setting them in motion against a black background we were able to define the motion by luminance and thus avoid the 'motion slow-down' effect that is observable at equiluminance (Cavanagh *et al.* 1984). In essence, this was a study in the perceptual binding of two attributes, the subjects being asked to assign the appropriate colour to each direction of motion and the appropriate direction of motion to each colour. If the colour and motion of the squares are varied with the appropriate frequency, though not necessarily in phase, and if the two attributes are perceived with different latencies, then any delay in processing between motion and colour should lead subjects to bind the motion and colour 'incorrectly'.

The changes in colour (green/red) and direction of motion (up/down) of the squares were 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°. At any one time all the squares on the screen were either red or green (although the substitution of other colours yielded the same results) and all were moving either up or down, i.e. all the squares were considered as being a single object having one of two possible colours and one of two possible directions of movement. The use of 30 squares made the precise position of a single square on the screen irrelevant and gave subjects the opportunity of fixating on one of several forms: an individual square, a pattern created by the random distribution of all the squares over the entire screen, or the pattern created by their random distribution in only one small part. Form was thus de-emphasized, and it is noteworthy that we obtained identical results irrespective of the number of the squares used (including a single square), thus showing that the precise configuration on the screen was indeed irrelevant. Figure 2 (left) shows only four conditions, in which the phase

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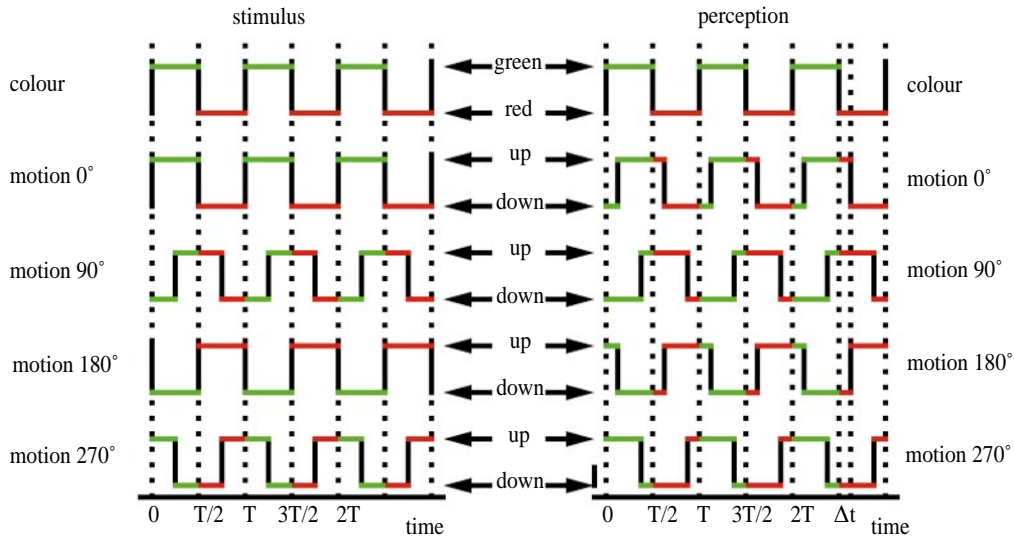


Figure 2. A representation of the colour and motion oscillations at the four basic phase differences is shown to the left. The top row shows the colour of the squares and the four successive rows the direction of their motion. At any given time all the squares were of one colour only. The upward and downward motion can be that of green or red squares exclusively (as in 0° and 180°) or a mixture of the two. To the right is shown the perceptual effect that would result if colour is perceived before motion: all the motion waveforms are shifted to the right by a time equal to Δt (in this example $\Delta t = T/8$) with respect to the colour waveform. This shift would in turn produce a strong perceptual effect at 90° (red seen as moving upwards and green as moving downwards) and 270° (the opposite), but no effect at 0° or 180° .

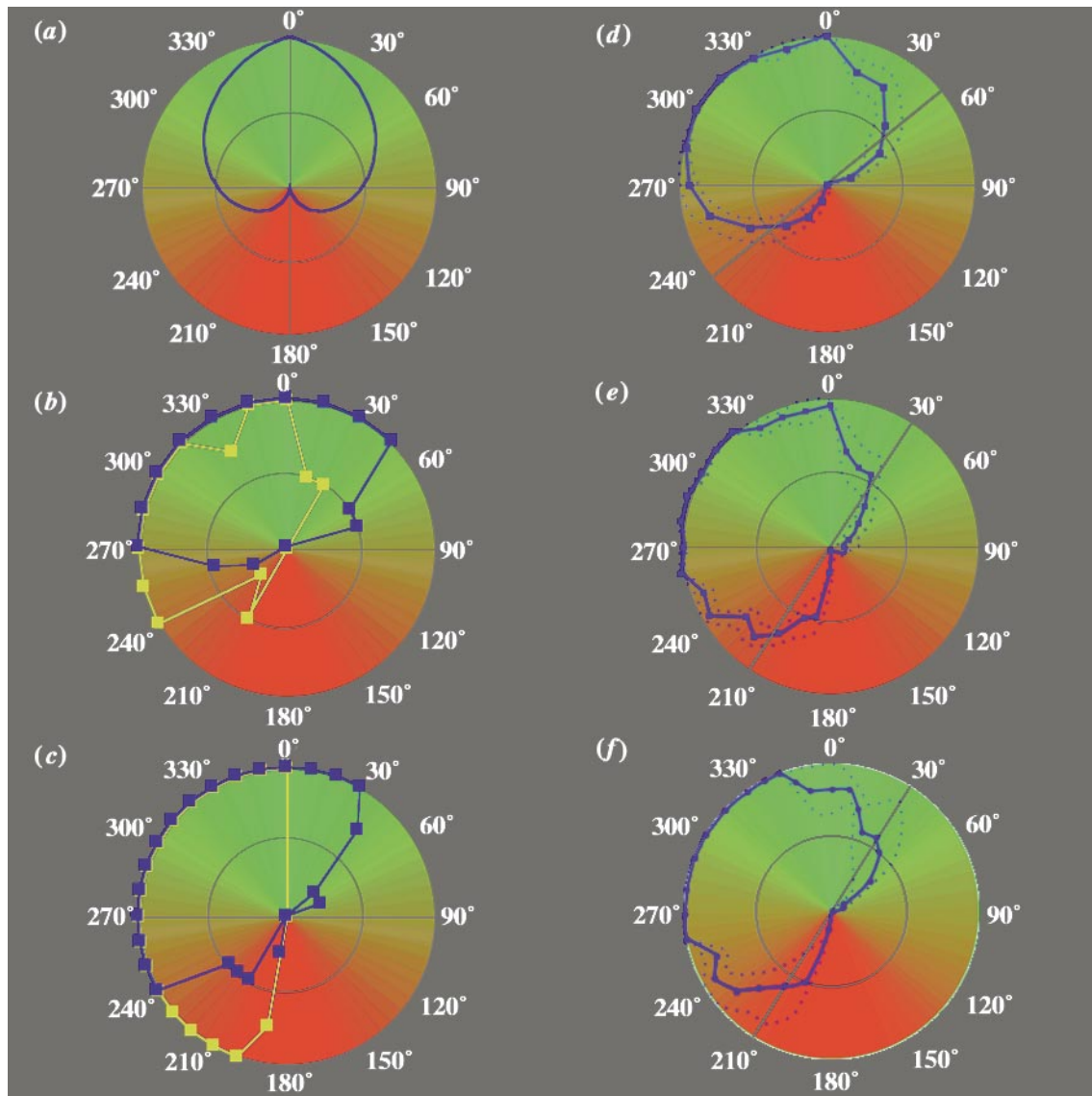


Figure 3. (a) is a polar plot representing the relationship of the colour of the moving squares to their direction of motion, for all different phases, as produced by the computer. The percentage of time the green squares are moving upwards is plotted as a function of the phase difference between the colour and motion oscillations. The outer circle represents 100% and the inner circle 50%. A green–red gradient is also drawn to indicate the change in the upward movement as the phase difference varies. At 0° , the upward motion is of green squares only, and the downward motion is of red squares only, while at 180° the reverse condition prevails; in between these two, the colour of the squares changes during the motion, so that, while moving in either direction, they are green part of the time and red part of the time. The amount of time that they are red or green varies with distance from 0° and becomes equal at 90° and 270° . (b) and (c) represent the results for the perception of the colour of the moving squares in two subjects, at two frequencies, the lower shown in blue and the higher in yellow. In each the curve is rotated counter-clockwise proportionally to the frequency. (d) and (e) represent the average result obtained from all nine subjects, at the lower and higher frequencies, respectively. The best-fit ‘red/green reversal’ line is drawn and the curve describing the standard error of the means for each phase difference is also shown with dotted lines. (f) represents the average result of three subjects, for a slightly different configuration and presentation of the stimulus when the screen was divided into two halves, with each half having the reverse colour–motion relationship (see text); the high frequency was used for these three experiments ($T = 0.537$ s).

differences are arranged in such a way that the upward motion can be entirely that of the green or the red squares (0° and 180°), or the colour can change midway during the motion, with the result that (at 90° and 270°) the red and the green squares move up or down for identical times. At other phase differences one of the colours predominated during upward motion and the other during downward motion. Trials were presented in two blocks: in block A, the period of the colour and motion oscillations was 0.716 s and the phase difference between them was varied in steps of 15° ,

and in block B the period was 0.537 s and the phase difference was varied in steps of 10° . Each phase difference in both blocks was presented four times in mixed order. Subjects were asked to press one key if the colour of the upward motion was green and that of the downward motion red, and another key if the reverse was what they perceived. Because of the symmetrical stimulus configuration (red and green were always moving in exactly the opposite way; see below) there was never a case where one colour was seen as moving in one direction but the other colour not seen as

moving in the opposite direction. All trials were forced-choice, and subjects indicated the confidence level in their choice after each trial by pressing one of four keys, with 1 showing the least and 4 the most confidence. Their response curves are presented as polar plots in which the percentage of times that the answer was 'green up, red down' is plotted for each phase difference (figure 3).

Figure 3*a* shows the percentage of time that the green squares were moving upwards (and the red squares downwards), for each phase difference. If there is no delay between the perception of colour and motion, the response curves should be broadly similar in shape and position to this veridical curve. The latter is symmetrical with respect to the 0–180° axis, with the percentage of time that the squares are red or green during their excursion being the same on either side of the line of symmetry. The 90–270° line is the 'red/green reversal' line, because whatever is happening for green on one side is happening for red on the other side. Any significant deviation from a veridical perception due to a time delay should be reflected in a change in the two axes of the curve, whereas its general shape should remain similar (but not identical, because this is a forced-choice experiment). If the time difference between colour and motion perception is equal to Δt and colour is perceived first, then the colour of the squares at any time t is not perceived with the motion of the squares at that time, but with the motion of the squares at time $t - \Delta t$. This results in shifting the motion waveform of figure 2 to the right with respect to the colour waveform, by an amount equal to Δt (see figure 2, right). If the period of the colour and motion oscillation is equal to T , then this shift results in an additional phase difference equal to $(\Delta t/T) \times 360^\circ$ between the two oscillations. The resulting perceptual effect of this shift depends on how small the period of the oscillations can be made. If, for example, $T = 2\Delta t$, then the motion waveform would be displaced by half a cycle to the right and the red squares would be perceived as moving upwards (and the green downwards) at 0°. In the format of figure 3, if colour is perceived first, then the response curve should rotate anticlockwise with respect to the expected veridical curve, and it should rotate clockwise if motion is perceived first. The extent of the rotation would indicate the extent of the mismatch between colour and motion. Moreover, if the perception is not veridical, the higher the frequency of the colour and motion oscillations, the larger should the resulting 'mismatch', and therefore the rotation, be.

3. RESULTS

For all nine subjects the response curves were rotated anticlockwise, and for eight of them the degree of rotation was proportional to the frequency of the colour and motion oscillations. The amount of rotation was not the same for each subject, suggesting a possible uniqueness to each individual; the two extremes of rotation, and thus the degree of mismatch, are shown (figures 3*b* and 3*c*, blue curves). In both, the curves are rotated anticlockwise, suggesting that colour is perceived before motion. Additionally, the degree of the rotation is greater for the higher frequency (figures 3*b* and 3*c*, yellow curves), suggesting that the mismatch is greater there. Figures 3*d* and 3*e* give the average rotation for the lower and higher frequencies, respectively, in all nine subjects. These curves show that subjects report one colour as moving upwards at phase differences where it is the other colour that predominates during upward motion, and vice versa for

the downward motion. When drawing the best-fit 'red/green reversal' line (figures 3*d* and 3*e*), the anticlockwise rotations of the average curves were found to be 39.1° for the lower frequency and 56.5° for the higher frequency, giving an average value for the time difference Δt between the perception of colour and of motion of 78 ms and 84 ms respectively. In a modification of the stimulus we subdivided the screen into two halves, with each half having the reverse colour–motion relationship to the other (phases differing by 180°). Moreover, in each half, the change in colour and direction of motion started at a different point in the sequence for each square, instead of being the same for all the squares. Subjects were asked to choose whether green was moving upwards and red downwards on the right or the left part of the screen. The result was, however, identical to the one obtained above (figure 3*f*).

The results show that colour is perceived before motion. We considered other explanations but found them implausible. Subjects may, for example, develop the strategy of reporting the colour at the end of each upward excursion, before the motion reverses. We tried to avoid situations like this by instructing subjects to bind each direction of motion to a colour, and each colour to a direction of motion, pay no attention to position, and not follow any particular square but rather look at the screen as a whole. Moreover, if each subject used a particular strategy, it is not clear why response curves were always rotated in the same direction, and why their rotation was always proportional to the frequency. Comparison of the confidence levels with which the choices were made at each phase difference reinforced our view that the response curves reflect a genuine difference in the time required to perceive colour and motion. Figure 4 shows one subject whose response curve was identical to what the strategy described above would have resulted in. However, he was most confident of having made the correct choices when there was an equal time span for red and green squares and least confident when the upward or downward motion was purely green or red. If the subject had developed the strategy described above to obtain a response curve rotated anticlockwise by 90° but his perception had not been tricked, one would have expected him to be more, or at least equally, confident at 0° (and 180°), than he was at 270° (and 90°). But even when the nature of the experiment had been explained to him, the subject still reported that the green was much more obviously moving up (and the red down) at 270° than at 0°. Similar confidence level results were obtained from all the subjects and, although the confidence rating varied from subject to subject, they were consistent within subjects. In other words, the confidence level curve corresponded to, and could be predicted by, the response curve.

Our stimulus could be manipulated by deleting various segments of the colour or motion components, in a sense producing a transient akinetopsia (Zeki 1991) or achromatopsia (Zeki 1990). The result of the manipulation is to produce a new veridical curve, which should then be subject to the same amount of

rotation if motion and colour are perceived at different times. It can be deduced from figure 2 (left) that if one 'deletes' the first half of each motion from the oscillation, the response curve should be rotated by 45° anticlockwise, and if one deletes the second half, the curve should be rotated by 45° clockwise, with respect to the curve obtained by the 'normal' stimulus. The opposite is true for 'deleting' the early and late halves of the colour changes. We thus selectively replaced either the early or the late motion component with stationary squares (having the same colour that they would have if moving), or the early or late colour component with grey squares (moving in the same direction that they would if coloured), and repeated the experiment. Figure 5 compares the results of the 'normal' response curves with the ones obtained by the deletions, from the same subject. It shows that motion and colour deletions produce the opposite rotations, as predicted. The predictable response curves obtained after the deletions greatly strengthened our conviction in our conclusion.

4. DISCUSSION

Given the existence of a different processing system for colour and motion, is there evidence to suggest that one is faster than the other? A direct comparison between the temporal properties of the colour and motion systems, using maximum alteration frequencies, was done by Livingstone & Hubel (1987), who concluded that the motion system is faster. Another way of measuring the temporal properties of different systems is through their temporal integration periods. These can be measured by relating stimulus presentation time to the threshold of detection. The 'integration time' or 'critical duration' value of the minimal necessary presentation at the lowest threshold gives an idea of the amount of information necessary to be integrated by the system before the stimulus can be perceived. But temporal integration periods give a very imperfect guide to perception times because they are principally determined at a very early stage in the visual system, and thus do not reflect the properties of the system as a whole (Krauskopf & Mollon 1971). Perception time is the end result of the processing of the system as a whole; different psychophysical measures of sensory latency (such as temporal integration period) are probably related to different elements of the neural response, not to the whole perceptual process (see Sternberg & Knoll 1972). Furthermore, integration times vary depending on the conditions and the method used: for example, they can vary depending on the wavelength (Pokorny *et al.* 1979) or the adaptation level (Kawabata 1994); with motion, humans are more sensitive in the temporal detection of direction changes than of speed changes (Nakayama 1985; De Bruyn & Orban 1988). Nothing such as a 'standard temporal integration period' for motion or colour exists, and therefore no conclusions on whether colour or motion is seen faster can be drawn from temporal integration times.

Psychophysical evidence is not the only one available: the temporal properties of the colour and motion

systems have also been studied physiologically. Here the unanimous view seems to be that the M system, which largely feeds the motion pathway, is faster than the P system, which feeds the colour pathway (Dreher *et al.* 1976; Schiller & Malpeli 1978); that the colour cells of V2 are activated after the non-colour cells by 10–20 ms (see Munk *et al.* 1995; Nowak *et al.* 1995); that the thick stripes and interstripes of V2, which are relatively poor in colour cells, are activated before the thin stripes, which are rich in wavelength-selective cells; and, finally, that direction-selective cells are activated earlier than cells lacking such a selectivity (Munk *et al.* 1995). Area V5, specialized for motion, and whose cells have the shortest recorded latencies (Raiguel *et al.* 1989), receives signals (from fast moving stimuli) before V1 (see ffytche *et al.* 1995) and V4 (see Buchner *et al.* 1994; ffytche *et al.* 1995).

What does all this tell us? Nothing much, because there is no simple and obvious relationship between cell response latencies, temporal integration periods and perceptual times. On the other hand, the present experiment deals with the final percepts of both colour and motion, the end result of the processing in the two independent processing systems. Our results can be summarized as follows: the colour of an object at time t is perceived together with the motion of the object at time $t - \Delta t$, where $\Delta t = 70\text{--}80$ ms. There are three basic implications of this result, which have a very general and important application to all visual attributes and the way in which the brain integrates them into a single percept. These are:

1. We have developed a method that can demonstrate and also calculate perception time differences between different visual attributes.
2. A particular colour and a direction of motion that occurred simultaneously in real time are perceived separately and at different times, i.e. functional segregation is maintained at the perceptual level.
3. The brain does not compensate for the differences in perception times between its specialized systems, and thus binds together attributes that are perceived simultaneously, rather than attributes that occur simultaneously in real time.

The different attributes characterizing an object at a certain time must be brought together at the correct spatial and temporal registration, so that an object is perceived as having the colour, form, motion and stereoscopic depth it really had at that particular time. With our method we have manipulated the temporal dimension of this binding to show that colour and motion are not only processed but also perceived independently from one another. This implies that the brain does not have a mechanism to compensate for the perceptual time differences between its specialized systems. One hypothetical mechanism could be the existence of a final 'perception area', equipped with a 'synchronizer', which would receive information from all the different systems and bind it in the appropriate spatiotemporal way. Our results speak against such a strategy, and instead imply that the perception of each attribute is solely the result of the activity in the specialized system involved with its processing, irrespective of the other specialized systems.

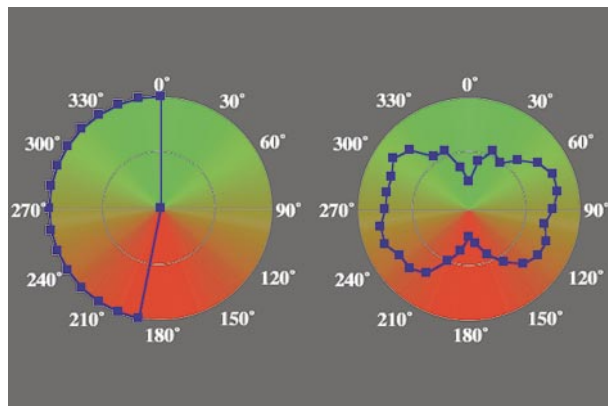


Figure 4. The response curve for one subject, plotted as before, is shown to the left: at the frequency used ($T = 0.478$ s), this curve was rotated anticlockwise by about 90° . The confidence curve, when assigning a colour to the upward motion of the squares for each particular phase difference, is shown to the right. The outer circle represents a confidence level of 4 (rarely chosen by this particular subject), and the inner circle a confidence level of 2. The subject was most confident of having assigned the right colour when the colour was mixed, that is to say when during the excursion of the stimulus the colour changed midway from red to green, and least confident when it was pure, that is to say when it maintained its colour for a full upward excursion.

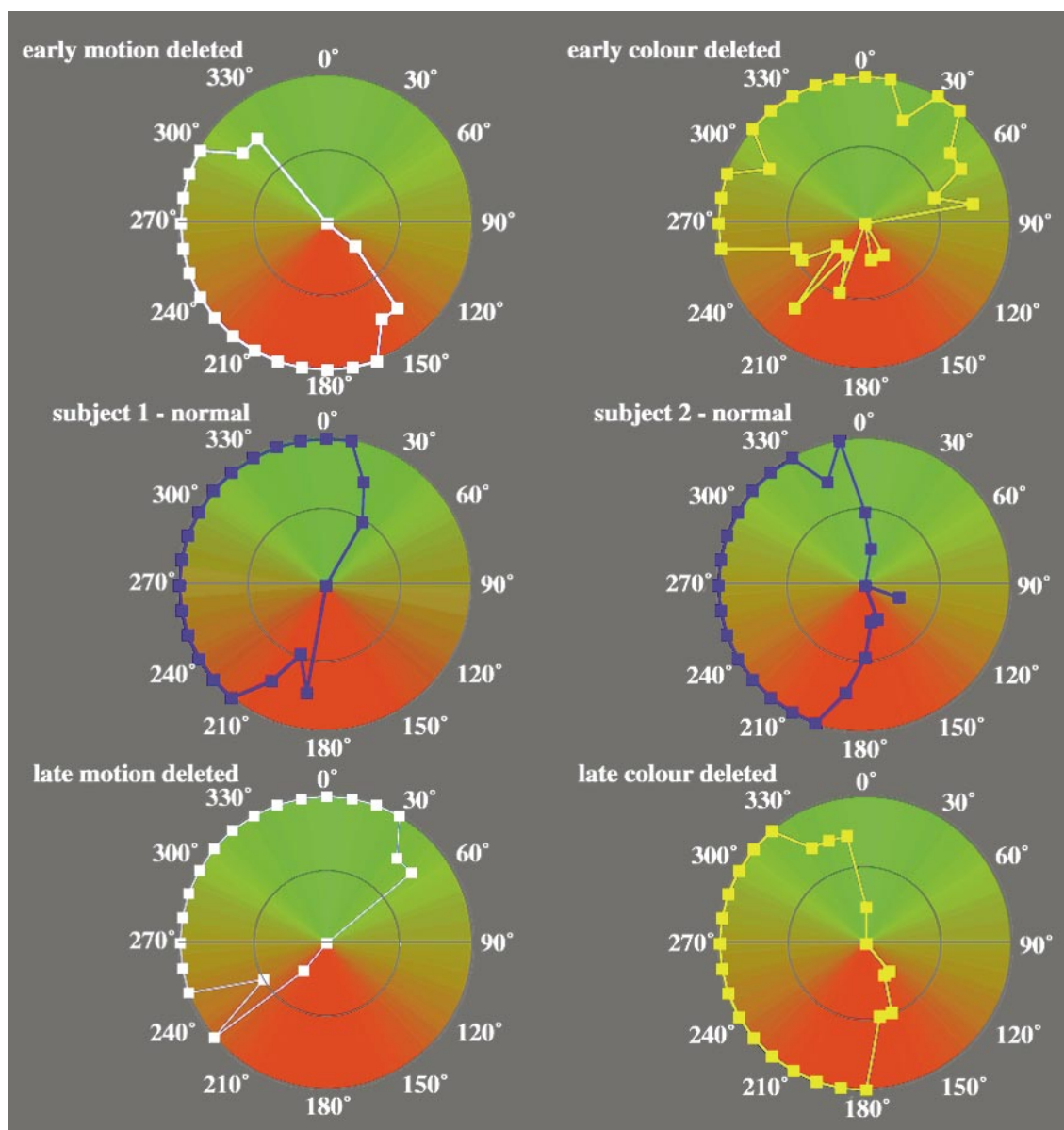


Figure 5. Comparisons between the response curves of two subjects, to the normal stimulus and to stimuli produced after deleting either the early or the late half of the motion or the colour. The deletions always produce a 45° rotation towards the predicted direction (see text).

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REFERENCES

- Anstis, S. & Cavanagh, P. 1983 A minimum motion technique for judging equiluminance. In *Colour vision, physiology and psychophysics* (ed. J. D. Mollon & L. T. Sharpe), pp. 155–166. London: Academic Press.
- Buchner, H., Weyen, U., Frackowiak, R. S. J., Romaya, J. & Zeki, S. 1994 *Proc. R. Soc. Lond. B* **257**, 99–104.
- Carney, T., Shadlen, M. & Switkes, E. 1987 *Nature, Lond.* **328**, 647–649.
- Cavanagh, P., Boeglin, J. & Favreau, O. E. 1985 *Perception* **14**, 151–162.
- Cavanagh, P., Tyler, C. W. & Favreau, O. 1984 *J. Opt. Soc. Am.* **1**, 893–899.
- De Bruyn, B. & Orban, G. A. 1988 *Vision Res.* **28**, 1323–1335.
- DeYoe, E. A. & Van Essen, D. C. 1985 *Nature, Lond.* **317**, 58–61.
- Dreher, B., Fukada, Y. & Rodieck, R. W. 1976 *J. Physiol., Lond.* **258**, 433–452.
- ffytche, D. H., Guy, C. N. & Zeki, S. 1995 *Brain* **118**, 1375–1394.
- Hubel, D. H. & Livingstone, M. S. 1987 *J. Neurosci.* **7**, 3378–3415.
- Kawabata, Y. 1994 *Vision Res.* **34**, 1007–1018.
- Krauskopf, J. & Mollon, J. D. 1971 *J. Physiol., Lond.* **219**, 611–623.
- Leventhal, A. G., Rodieck, R. W. & Dreher, B. 1981 *Science, Wash.* **213**, 1139–1142.
- Livingstone, M. S. & Hubel, D. H. 1987 *J. Neurosci.* **7**, 3416–3468.
- Livingstone, M. S. & Hubel, D. H. 1988 *Science, Wash.* **240**, 740–749.
- Munk, M. H. J., Nowak, L. G., Girard, P., Chounlamountri, N. & Bullier, J. 1995 *Proc. natn. Acad. Sci. USA* **92**, 988–992.
- Nakayama, K. 1985 *Vision Res.* **25**, 625–660.
- Nowak, L. G., Munk, M. H. J., Girard, P. & Bullier, J. 1995 *Vis. Neurosci.* **12**, 371–384.
- Perry, V. H., Oehler, R. & Cowey, A. 1984 *Neurosci.* **12**, 1101–1123.
- Pokorny, J., Bowen, R. W., Williams, D. T. & Smith, V. C. 1979 *J. Opt. Soc. Am.* **69**, 103–106.
- Raiguel, S. E., Lagae, L., Gulyas, B. & Orban, G. A. 1989 *Brain Res.* **493**, 155–159.
- Ramachandran, V. S. & Gregory, R. L. 1978 *Nature, Lond.* **275**, 55–56.
- Schiller, P. H. & Malpeli, J. G. 1978 *J. Neurophysiol.* **41**, 788–797.
- Shipp, S. D. & Zeki, S. M. 1985 *Nature, Lond.* **315**, 322–325.
- Sternberg, S. & Knoll, R. L. 1972 The perception of temporal order: fundamental issues and a general model. In *Attention and performance* (ed. S. Kornblum), pp. 629–685. New York: Academic Press.
- Zeki, S. 1990 *Brain* **113**, 1721–1777.
- Zeki, S. 1991 *Brain* **114**, 811–824.
- Zeki, S. M. 1973 *Brain Res.* **53**, 422–427.
- Zeki, S. M. 1974 *J. Physiol., Lond.* **236**, 549–573.
- Zeki, S. M. 1978 *Nature, Lond.* **274**, 423–428.

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