Functional segregation and temporal hierarchy of the visual perceptive systems

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SUMMARY

In extending our previous work, we addressed the question of whether different visual attributes are perceived separately when they belong to different objects, rather than the same one. Using our earlier psychophysical method, but separating the attributes to be paired in two different halves of the screen, we found that human subjects misbind the colour and the direction of motion, or the colour and the orientation of lines, because colour, form, and motion are perceived separately and at different times. The results therefore show that there is a perceptual temporal hierarchy in vision.

1. INTRODUCTION

The visual brain is a remarkably efficient organ, capable of providing, within a fraction of a second, a visual image in which all the different attributes of the visual scene—form, colour, motion—are apparently seen in precise spatiotemporal registration. It is, perhaps, the visual physiologist who has been the most obvious victim of this efficiency; it led him to assume for a long time that vision is an essentially passive process, consisting of two stages—the 'impression' of an 'image' of the visual world on the retina and its 'transmission' to the primary visual cortex (Zeki, 1993). Implicit in this terminology, commonly used by neurologists until recently, was the supposition that the 'reception' of the visual image by the primary visual cortex led to 'seeing', a passive activity vaguely resembling a photographic process, an analogy that is commonly drawn. The more active process, the interpretation of what is 'seen', was considered to be the function of the surrounding, and at that time, ill-defined, 'association' cortex. Such a view therefore separated seeing from understanding, and assigned a separate cortical seat to each. But it had another consequence too: it inhibited a consideration of the magnitude of the task that the brain has to perform to construct the visual image, and thus the study of the equally complex strategy and neural apparatus that it has developed to undertake this task.

A hallmark of that strategy is the parallel processing of different attributes of the visual scene in many different, geographically separate, locations (Zeki 1978; Livingstone & Hubel 1988). The discovery of that strategy, through anatomical and physiological work during the past 25 years, has led to a different concept of how the visual image in the brain is produced. This relatively new concept is entirely counter-intuitive, given the brain's integrative efficiency in providing a unitary image. It supposes that vision is an active process, with the parallel and apparently simultaneous processing of the separate attributes being due to the fact that the kind of operation that the brain has to undertake to construct one attribute, say form, is substantially different from the kind of operation it has to perform to construct another attribute, say colour, a difference that requires a different neural apparatus (Zeki 1981; Livingstone & Hubel 1988). But the parallel processing of the separate attributes naturally raises the problem of integration, of how these separate attributes are brought together in another active process to give us our unitary image of the visual world. There is an irony here, again at the expense of the visual physiologist: for it is the demonstration of functional specialization and parallel processing that has led us all now to seek to understand that integrative mechanism in the brain which, because of its high efficiency, initially inhibited us from realizing the extent of the division of labour that is required to construct a visual image.

In a previous paper (Moutoussis & Zeki 1997), we began by addressing the question of whether the attributes of the visual scene that are processed separately are brought into precise temporal registration. We showed that colour and motion, two attributes about whose separate processing there is no doubt (Zeki 1973, 1974; Ramachandran & Gregory 1978; Cavanagh *et al.* 1984, 1985; Carney *et al.* 1987), are also perceived separately, with colour having a lead time of about 50–100 ms over motion. This led us to propose (i) that just as the processing systems are separate and operate in parallel, so do the perceptual systems; and further (ii) that the normal brain binds the outcome of the activity in its different processing systems, and that it therefore misbinds in terms of what occurs in real

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time. This misbinding is very different from the one that is dependent upon spatial location, and is compromised following lesions in brain areas critical for space perception (Friedman-Hill *et al.* 1995). It seemed worthwhile to extend our earlier study for two reasons. First, we wanted to test the generality of our proposition that the brain perceives the two attributes, colour and motion, separately. If this statement is generally true, then it should apply regardless of whether these two attributes belong to the same object, as in our previous study, or not. We therefore developed a new method for this study, in which the two attributes belong to different objects, an approach that had the advantage of validating our previous method and conclusions.

We were concerned, next, to learn whether our conclusion that the perceptual systems are separate generalizes to attributes other than motion and colour and whether there is, therefore, a temporal hierarchy in vision. To do so, we added simple form to our repertoire and studied the relative perceptual times involved in perceiving colour when paired with form, and motion when paired with form. This gave us three pairings: form–colour; form–motion, and colour–motion. The choice of these pairings, as an addition to the colour–motion pairing, is deliberate; both the form–motion and the form–colour pairs have perceptual and physiological ambiguities in them that are far less prominent in the colour–motion pair. While the perceptual distinction between motion and colour has solid anatomical and physiological foundations, reflected in the distinct physiologies of areas V4 and V5 and the distinct M- and P-derived pathways leading to them (Livingstone & Hubel 1988), there is no such unanimity about the physiological and anatomical separation of form and motion or form and colour. With regard to the latter, most would agree that every colour, being confined in space, has a form and that every form has a colour. Similarly, the brain constructs colour by comparing the wavelength composition of the light reflected from one surface and that reflected from surrounding surfaces (Land 1974). This comparison requires the presence of a border, and the border has a form. Hence the impossibility of separating colour completely from form, either perceptually or computationally. Physiologically, too, the separation between form and colour and form and motion is not as neat as that between motion and colour. While the wavelength and directionally selective cells in V1 and V2 are largely restricted to their own compartments and have separate destinations within prestriate cortex (Livingstone & Hubel 1984; DeYoe & Van Essen 1985; Hubel & Livingstone 1985; Shipp & Zeki 1985), the physiological differentiation between form and colour in the prestriate cortex is less well defined than that between motion and colour. Moreover, while the indifference of V5 cells to colour is acknowledged (Zeki 1974; Gegenfurtner *et al.* 1994), their indifference to form has been debated, some maintaining that the cells of V5 are not exigent with respect to form (Zeki 1974; Albright 1984), others finding the contrary (Maunsell & Van Essen 1983). Whatever their exact preferences, the physiological homogeneity of V5 in terms of directional motion selectivity sits in contrast to the apparently more heterogeneous physiology of V4. In the latter, large concentrations of colour- and wavelength-selective cells are separated from each other by orientation-selective cells (Zeki 1975, 1983; Desimone & Ungerleider 1986; DeYoe *et al.* 1994), leading one to suppose that monkey V4 is also concerned with form (Desimone & Schein 1987) and with form in association with colour (Zeki 1990). Thus, the neat separation found between colour and motion is not so obvious in the colour and form systems. Moreover, there have been persistent reports of the presence, in V1 (Ts'o & Gilbert 1988) and V2 (Gegenfurtner *et al.* 1996), of cells that have dual selectivity for orientation and for colour, but the proportion of such cells has not been very impressive (Livingstone & Hubel 1984; Hubel & Livingstone 1987). This dual selectivity is therefore not as significant as the physiologically more impressive segregation of different attributes at the processing level which this and other laboratories have reported (DeYoe & Van Essen 1985; Hubel & Livingstone 1985; Shipp & Zeki 1985). Nevertheless, it seemed interesting to learn whether, at the perceptual level, there is a sufficiently precise temporal integration to give such dual selective cells a more precise integrative role in perception. If so, one might expect form and colour to be perceived in precise temporal registration, quite unlike colour and motion.

2. MATERIALS AND METHODS

Essentially, the psychophysical method that we have used here is similar to the one used previously (Moutoussis & Zeki 1997), with important modifications. Subjects were asked to view a pattern generated by a Macintosh computer on a Mitsubishi Diamond Pro 17TX monitor operating with a resolution of 640 × 480 pixels at 67 Hz vertical refresh rate. In any one sitting, only two attributes (e.g. colour and motion) were present on the screen but, unlike our previous experiment, each attribute was presented in one half of the TV monitor only (figure 1). The variation of each attribute can be described by a square-wave oscillation of period $T = 0.537$ s presented at various phase differences with respect to the square wave oscillation describing the change in the other attribute; the phase differences covered the whole range of 0–360°. The phase difference between the two attributes was varied in steps of 10°, each phase difference being presented four times in random order. Each presentation lasted at most 14 s; the subjects made their choice by selecting from two options using the computer's mouse during this period, or after the termination of each trial. Subjects had to decide which values of the two attributes were present on the screen simultaneously. The data derived from all four subjects were averaged to obtain a value with standard errors.

This new method was used to calculate the perception time differences between four pairs of attributes. These were as follows.

(*a*) *Control experiment: motion and motion (figure 1* a*)*

Two identical, moving, grey and black checkerboard patterns appeared on the two halves of the screen. The pattern to the left changed direction along the vertical axes and the

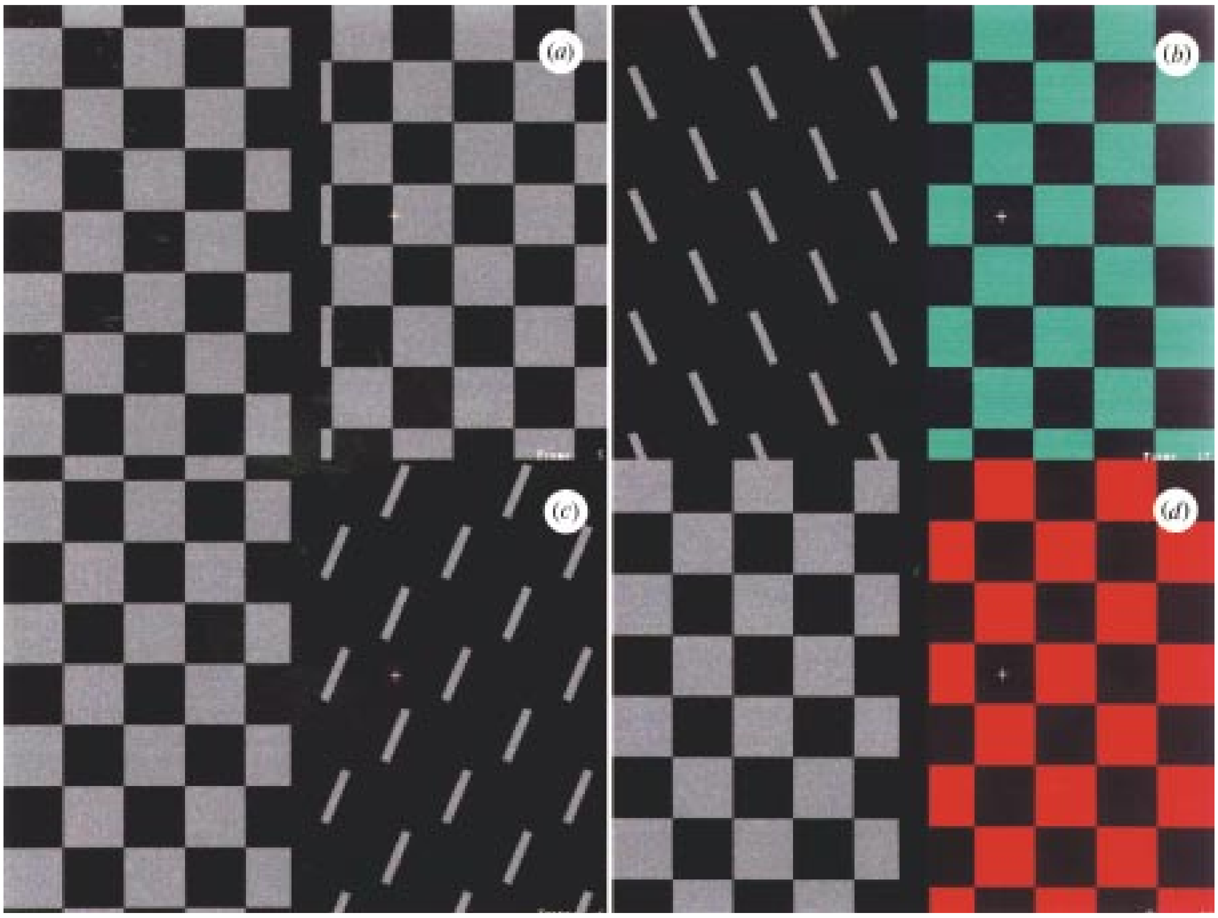

Figure 1. The four experiments done in this study as they appeared on the 30° × 22° computer screen. The screen was always split into two halves, with a different attribute change taking place in each half. The grey, red, and green colours in the motion–colour and form–colour experiments, shown in (*b*) and (*d*) were isoluminant. The 3° × 3° coloured checkerboards were stationary on the screen, the coloured squares switching from red to green and back (X, Y, Z coordinates for red = 3.39, 7.09, 1.39; for green = 12.3, 6.73, 0.732). The oriented lines (3° × 0.5° in size) were also stationary, and switched from left tilt to right tilt and back. The checkerboards made of grey and black squares moved either vertically (when paired with colour or orientation) or horizontally (when paired with a vertically moving checkerboard) with a speed of $19^{\circ}\,\mathrm{s}^{-1}$. Subjects were allowed to fixate the cross on the right or to move their gaze freely around the screen (normally they did both), and had to pair, in terms of simultaneity, the stimuli appearing on the left half with those appearing on the right half of the screen. In (*a*) the vertical motion of the squares presented on the left half of the screen is compared to the horizontal motion presented on the right half. In (*b*) the orientation of lines presented on the left is compared to colour of checks on the right. In (*c*) the vertical motion of the squares on the left is compared to the orientation of the lines on the right. In (*d*) the vertical motion on the left is compared to the colour of the checks on the right.

one to the right along the horizontal axes, following the oscillations described above.

(*b*) *Colour and form (figure 1*b*)*

The right half of the TV monitor contained a coloured checkerboard pattern, while the left part contained grey bars (equiluminant to both the green and the red) on a black background. All the bars were tilted by 23° from the vertical to the right or to the left, following the typical oscillation described above. The task of the subjects was to decide what the colour of the checks was when the bars were tilted to the right, and what colour the checks were when the bars were tilted to the left.

(*c*) *Motion and form (figure 1*c*)*

The left half of the screen contained a moving (up–down) grey–black checkerboard pattern, while the right half contained the oriented bars pattern of the colour–form experiment. The subjects' task in this case was to decide which direction of vertical motion occurred when the bars were tilted to the right or left.

(*d*) *Colour and motion (figure 1*d*)*

The upward and downward motion of a grey–black checkerboard pattern on the left of the screen had to be paired with the colour of an identical stationary checkerboard which changed from red–black to green–black, both colours being equiluminant to the grey. The subjects' task was to decide

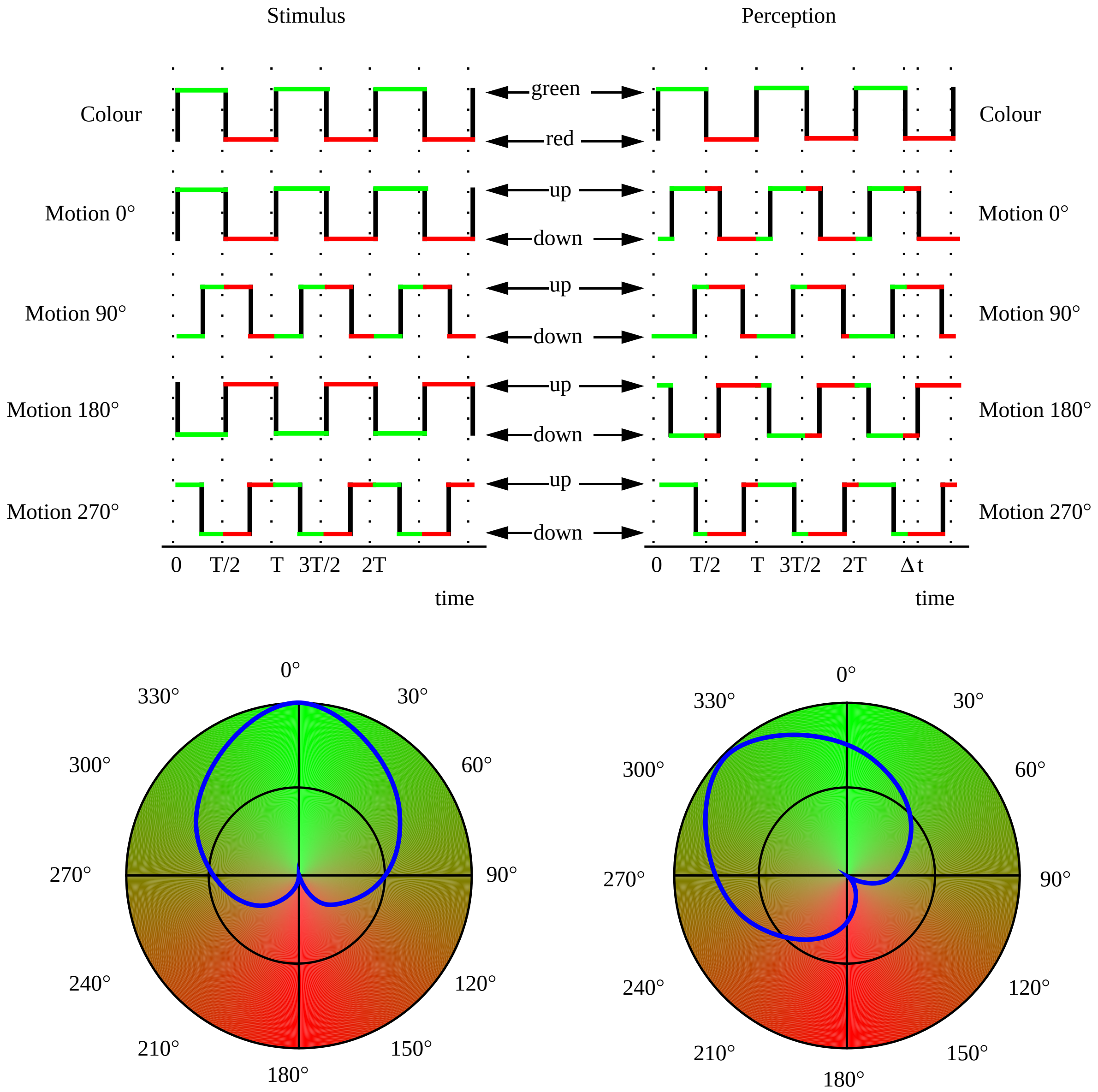

Figure 2. A diagrammatic representation of the relationship between the change in the colour on the right half of the monitor and the motion on the left. The square-wave oscillations describing the attribute changes over time are shown top left (veridical stimulus) and top right (the perceived stimulus). Both oscillations have the same period T, and are presented at various phase differences with respect to each other; 0°, 90°, 180°, and 270° are shown as examples. The bottom part of the figure shows, on the left, a polar plot of the percentage of time green was present on the right half of the screen when there was upward motion present on the left half. The polar plot on the right depicts the consequences of a hypothetical lead of colour over motion. Here the motion oscillations have been shifted to the right by $T/4$, resulting in a 45° anticlockwise rotation of the curve.

what colour the checkerboard was when the motion on the left was upwards, and likewise, when it was moving downwards.

The results described below were obtained from four subjects who viewed the displays in the configuration described above. As a control for positional effects, we repeated all the experiments with three of the four subjects; in these repeats, we changed the position of the attributes on the screen compared to the position that they occupied in the first experiment (for example, colour present on the left and motion on the right). The results we obtained were identical, and thus the position on the screen (right or left) does not seem to bias relative perceptual times in any way.

In the example of colour and motion, figure 2 (upper left) shows four conditions in which the phase differences are arranged in such a way that the upward motion can be entirely correlated with green or red (0° and 180°), or the colour can change midway during the motion (at 90° and 270°). If the time difference between colour and motion perception is equal to Δt and colour is perceived first, then the colour present on the screen at any time t is not perceived together with the motion present on the screen at that time, but with the motion at time $t - \Delta t$. This results in shifting the motion waveform to the right with respect to the colour waveform by an amount equal to Δt (see figure 2 upper right). This shift results in an additional phase difference between the two oscillations equal to $(\Delta t/T) \times 360\,°$, where T is the period of the oscillation.

For each experiment, the set of responses from the four subjects were summed, and plotted as polar curves; these constitute the response curves. For these curves, the percentage of times that the answer was 'X is the property of the right half of the screen when Y is the property of the left half' is plotted for each phase difference. In the example of figure 2 (lower part) the per cent of the time that the green colour was present in one half of the screen while the upward motion was present in the other half (which is the same as the per cent of the time that the red colour in one half and the downward motion in the other were present together) is plotted. 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 (figure 2 lower left). If, on the other hand, there is a difference in the two perception times tested, then the resulting response curve should deviate from the veridical one, clockwise if motion is perceived first and anticlockwise if colour is perceived first (figure 2 lower right); the greater the rotation from the veridical, the greater the separation in perceptual time between the two attributes. 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. From this vector, the difference in relative perceptual times could be calculated, since $360^\circ = 537$ ms, and thus each degree is 1.5 ms (perceptual time is defined as the time interval between the appearance of the stimulus on the screen and its perception by the brain). The polar data were ' unwound' and plotted as a population on a Cartesian graph centred on the rotation angle. A second population was calculated by shifting the original one so that it was centred on zero. Finally, a Z score was calculated by carrying out a Wilcoxon rank sum test (Howell 1992) on the two populations. This was converted to a p value by reference to the two-tailed normal distribution.

3. RESULTS

The expected theoretical result if all attributes of the visual image are seen in precise temporal registration, or are synchronized to 'time 0', is shown in figure 2 (lower left). Figure 2 (lower right) shows the result that might be expected if one of the attributes (in this case colour) is seen first. This would result in a counter-clockwise rotation, the extent of which depends upon the difference in time between the perception of colour and of motion; if motion is perceived first, the rotation will be clockwise and, once again, dependent upon differences in perceptual times. The difference in relative times between the perception of colour and of motion is given by the degree of rotation: the entire 360° circle is equivalent to 537 ms, so that an anticlockwise rotation of, say, 45 ° would amount to a time difference in favour of colour of about 67 ms.

The average response curves of the split-screen experiment are shown in figure 3: (*a*) shows the results of the motion versus motion experiment, which is a statistically insignificant deviation ($Z = 0.94$, $p = 0.35$) of 0.4 ms in the average score. There is therefore no difference in the perception time between the up–down versus left–right motion, presumably because they are both perceived by the same specialized perceptual system. A very similar result was obtained when we compared motion and motion with our older method, where subjects had to decide the direction of motion embedded within the squares when the latter were moving up or down, that is, when the two motions belonged to the same object. These results would seem to constitute a good perceptual demonstration of the simultaneous perception of the two components of motion.

The colour versus orientation curve is shown in (*b*). Significant at the $p < 0.0001$ level ($Z = 7.94$), it shows a 41.9° anticlockwise rotation, i.e. colour is perceived before orientation by 63 ms. The orientation versus motion curve, shown in (*c*), is rotated by 34.8° anticlockwise ($Z = 5.53$, $p < 0.0001$), showing that orientation is perceived 52 ms before motion. Finally, the colour versus motion curve, shown in (*d*), is rotated by 79.0° anticlockwise ($Z = 11.76$, $p < 0.0001$), showing that colour is perceived before motion by 118 ms. This result is similar to the one in our previous paper (Moutoussis & Zeki 1997), if one takes into account the standard errors of the two response curves. The overall similarity between this result and our previous one, where both the colour and the motion of the same object changed, shows that 'binding' of the two attributes to the same object does not in any way influence the perception time differences between different systems.

In summary, the results from this study extend our previous conclusions, and show that the perceptual systems for the different attributes are separate, just as are the processing systems, at least insofar as form, colour, and motion are concerned. This conclusion gains further validity from the numerical additivity of the results in figure 3: colour precedes orientation by 63 ms, which in turn precedes motion by 52 ms. The result that colour precedes motion by 118 ms is not far from the expected $63\,\text{ms} + 52\,\text{ms} = 115\,\text{ms}$. In fact, when one looks at individual results, such a close additivity is seen in only two of the four subjects, although all saw colour before form before motion. Equally, and in spite of this uniformity in the hierarchy of perceptual times, there was a bigger difference between colour and orientation than between orientation and motion for two subjects only: in one subject the difference in the orientation–motion pairing is bigger than the difference in the orientation–colour pairing, while in the last the differences were almost equal. These individual variations should be expected.

4. DISCUSSION

The work described here is an extension of our previous work which showed that, when colour and motion belong to the same object (i) colour is perceived before motion, and (ii) that this results in a 'misbinding' of these two attributes, leading to perception of conjunctions that depart from the reality on the screen. With our new method, each attribute is presented in one-half of the screen only, and is continuously varied in that half so that the two attributes no longer belong to the same object; instead, the changes in one attribute occur in a different part of the screen than those in another, leading to a condition in which the perception of each attribute is spatially independent from the other. The new departure is simpler, and we should really have done it first; it allows us to test perception time differences between different attributes more conclusively because the perceptual 'binding' that

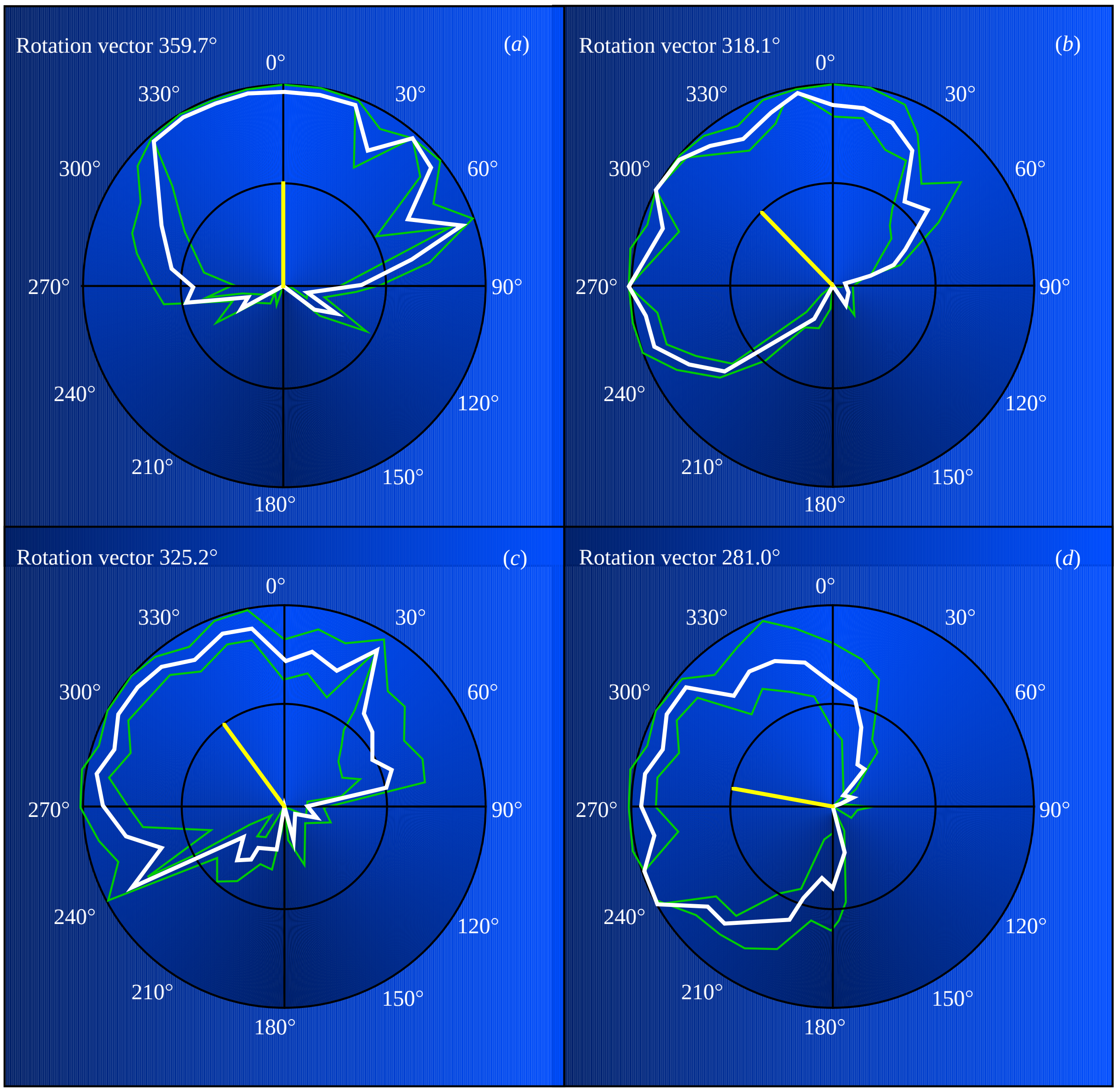

Figure 3. The averaged responses (shown in white) and standard deviations (shown in green) of four subjects to (*a*) motion and motion, (*b*) colour and orientation, (*c*) orientation and motion, (*d*) colour and motion. It is clear that colour is perceived before form, which is perceived before motion. Furthermore, these differences are numerically consistent between them. No difference was found between the times necessary for the perception of vertical versus horizontal motion.

subjects are asked to do here is more clearly time-based and less object-bound. Nevertheless, if our hypothesis of independent perceptual systems, each with its own perceptual time, is correct then this new method should give results identical to the original one; this is exactly what we have observed.

The results that we obtained, both here and in our previous work, are counter-intuitive although they reinforce each other. They suggest that the normal brain does not perceive the different attributes of the visual scene at the same time, nor is it able to synchronize its different perceptual systems to ‘time 0’. Instead, the brain mis-binds in terms of real time, which is the same thing as saying that it only synchronizes the results of its own operations. We are not unaware of the more general significance of these findings, in terms of theories of perception, since it leads us to the general theory of a temporal hierarchy of the visual perceptive systems.

Ever since the demonstration of functional specialization within the primate (Zeki 1978), including human (Zeki *et al.* 1991) visual brain, the question of integration has imposed itself. Whatever solution the brain has adopted to deal with this, it has turned out not to be the kind of solution thought of by neurobiologists. To all of us, intuitively much the most appealing solution was an anatomical convergence, a strategy by which the results of operations performed in all the specialized visual areas would be relayed to one area or a set of areas—which would then act as the master integrator and, perhaps, even perceptive areas. Apart from the logical difficulty of who would then perceive the image provided by the master area(s) (Zeki 1993), there is a more practical difficulty—the failure to observe an area or a set of areas that receive outputs from all the antecedent visual areas. Thus the convergent anatomical strategy is not the brain's chosen method of bringing this integration about. In fact, even when two areas such as V4 and V5 project to a common third area—as they do, in both parietal and temporal cortex—the zone of distribution from the two areas overlaps only very minimally in the territory of the third, an anatomical fact for which we have coined the term 'juxtaconvergence' (Shipp & Zeki 1995). Once again, this suggests that even if two areas with different specializations were to project to a third area, the integration will be brought about not by direct convergence, but by the action of interneurones linking the two territories.

There are of course other anatomical opportunities for the compartments of the brain representing different visual attributes to interact with each other in an integrative manner; such an interaction could, for example, occur in area V2 where the stripes containing cells with different selectivities are concentrated. These stripes are connected to one another by a rich system of horizontal connections (Rockland 1985; Levitt *et al.* 1994) that could conceivably provide the anatomical opportunity for some level of integration. But timing studies of V2 (and also V1) neurones have shown that the motion-related cells are the earliest, and that colour-related cells are the last cells to be activated (Munk *et al.* 1995; Nowak *et al.* 1995). This is quite the opposite hierarchy to that of the perceptual hierarchy revealed in our studies; it is therefore unlikely that V2 can be regarded as a perceptual integrator area where all the different visual attributes come together (Shipp & Zeki 1989; Roe & Ts'o 1995). Our perceptual studies lead us to believe that no such area is indeed necessary; even if it exists, however, it is not equipped with a time-compensator mechanism that could bring the different attributes back into their correct temporal relation. Our hypothesis, derived from our previous and present work, is that the perceptual systems are separate, just like the processing systems, and that, as far as the brain is concerned, it will process two separate attributes such as colour and motion, or motion and form, separately and perceive them separately. Because the perceptual systems for different attributes are separate, it does not matter whether the attributes belong to the same or to different objects.

Our results thus lead us to conclude that integration is brought about by the visual brain using a strategy that is different from what seems the most obvious one—that of integrating the results of its many operations in such a way that what happens in real time is brought into precise temporal registration perceptually. Instead, the brain appears to ignore real time and synchronize with respect to its own time. No doubt, it does that in an ingenious and counter-intuitive way which we have yet to uncover.

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