A paradox of temporal perception revealed by a stimulus oscillating in colour and orientation

Colin W.G. Clifford [a,*], Derek H. Arnold [a,b], Joel Pearson [a]

[a] *Colour, Form and Motion Lab, Visual Perception Unit, School of Psychology, The University of Sydney, Sydney, NSW 2006, Australia*
[b] *Department of Psychology and Institute for Cognitive Neuroscience, University College London, Gower Street, London WC1E 6BT, UK*

Abstract

Psychophysical experiments with stimuli oscillating concurrently in colour and orientation revealed an apparently paradoxical dissociation between the perceived simultaneity of stimulus changes and the perceptual pairing of the events demarked by those changes. When subjects were required to report whether changes in colour and orientation were simultaneous, judgements were generally accurate within ± 10 ms. When subjects were required to report which colour was paired predominantly with which orientation, judgements showed a systematic temporal bias of up to 50 ms in favour of colour. This dissociation between different temporal judgements concerning the same stimulus sequence is not predicted by any of the current models of binding in conscious vision. We propose an account of these data based on the temporal response properties of colour- and orientation-selective model neurons such that the perceived pairing of visual attributes is modelled as the cross-correlation of time-varying neural response profiles and thus reflects both neuronal latencies and the rate of rapid adaptation rather than simply the temporal pattern of responses to stimulus transitions.
© 2003 Elsevier Ltd. All rights reserved.

1. Introduction

The nature of the relationship between the timing of neural activity and the subjective time course of the events represented by that activity has long been a matter of debate amongst philosophers (Dennett & Kinsbourne, 1992; James, 1890). Here, we employ a perceptual pairing task (Arnold & Clifford, 2002; Moutoussis & Zeki, 1997a, 1997b; Nishida & Johnston, 2002; Patel, Chung, Bedell, & Ogmen, 2002; Viviani & Aymoz, 2001) that allows us to explore how the perceptual representation of an event is distributed over time. For example, the predicted pairing judgements of the model we propose rely upon both the latency and the rate of decay of activity distributed across neuronal populations. This proposal assumes a close correspondence between the time of representing and the time represented in perception, consistent with the view that

visual awareness is an on-line monitor of visual processing (Arnold, Clifford, & Wenderoth, 2001; Jeannerod, 1992; Zeki & Bartels, 1998) rather than being necessarily subjected to subsequent interpretive processes (Dennett & Kinsbourne, 1992; Eagleman & Sejnowski, 2000; Nishida & Johnston, 2002).

We investigated the perceptual pairing of two primary visual attributes, colour and orientation. Recent studies concerning the perception of stimuli alternating in colour and orientation have yielded apparently contradictory results, prompting conflicting interpretations. It has been reported that colour is perceived before orientation by around 63 ms. This has been taken as evidence that different processing systems for colour and orientation create their corresponding percepts independently and with different delays (Moutoussis & Zeki, 1997b; Zeki & Bartels, 1998). However, it has since been reported that colour and orientation can be correctly paired at oscillation rates of up to 18.8 Hz (Holcombe & Cavanagh, 2001; see also Holcombe, 2001; Suzuki & Grabowecky, 2002), corresponding to a period of 53 ms. Given that a processing delay of one quarter of a temporal cycle or

*Corresponding author. Tel.: +61-02-9351-6810; fax: +61-02-9351-2603.
E-mail address: colinc@psych.usyd.edu.au (C.W.G. Clifford).

more would lead to systematic errors in pairing, this would seem to place an upper bound of around 13 ms on the amount by which the processing of colour could lead that of orientation. Instead, Holcombe and Cavanagh (2001) proposed that colour and orientation are coded in combination explicitly by early stages of the visual hierarchy. The available empirical evidence therefore seems to provide a paradox between an apparent temporal advantage for colour relative to orientation within the context of perceptual pairing (Moutoussis & Zeki, 1997b) and the ability to pair in-phase oscillations in colour and orientation at high rates of alternation (Holcombe & Cavanagh, 2001).

In an attempt to resolve this paradox, we presented subjects with a single grating stimulus oscillating in colour and orientation at the same temporal frequency. The relative phase of colour and orientation changes was manipulated from trial to trial (Fig. 1A). In Experiment 1, subjects were asked to make one of two perceptual judgements, which we refer to as "pairing" and "simultaneity", in different sessions. The pairing task required subjects to make a forced-choice judgement as to which colour was paired predominantly with

which orientation. The simultaneity task required subjects to report whether or not colour and orientation appeared to change at the same time.

We also sought to investigate the neural mechanisms underlying the perceptual pairing of colour and orientation. For stimuli oscillating at frequencies above 3 Hz, subjects can only make correct pairings of colour and orientation if the stimuli are spatially superimposed (Holcombe & Cavanagh, 2001). This has prompted the suggestion that colour and orientation are coded in combination at the early stages of visual processing. Specifically, it has been suggested that chromatic signals might be segregated as early as the retina, after which they are fed independently into orientation-selective cortical mechanisms (Holcombe & Cavanagh, 2001).

Chromatic and luminance signals are carried from the retina via the lateral geniculate nucleus (LGN) to primary visual cortex (V1) in three channels (Derrington, Krauskopf, & Lennie, 1984; DeValois, Abramov, & Jacobs, 1966; DeValois, Cottaris, Elfar, Mahon, & Wilson, 2000). Each of these channels can be stimulated in isolation by modulating (1) only the response of the S cones, (2) only the difference between L and M cone
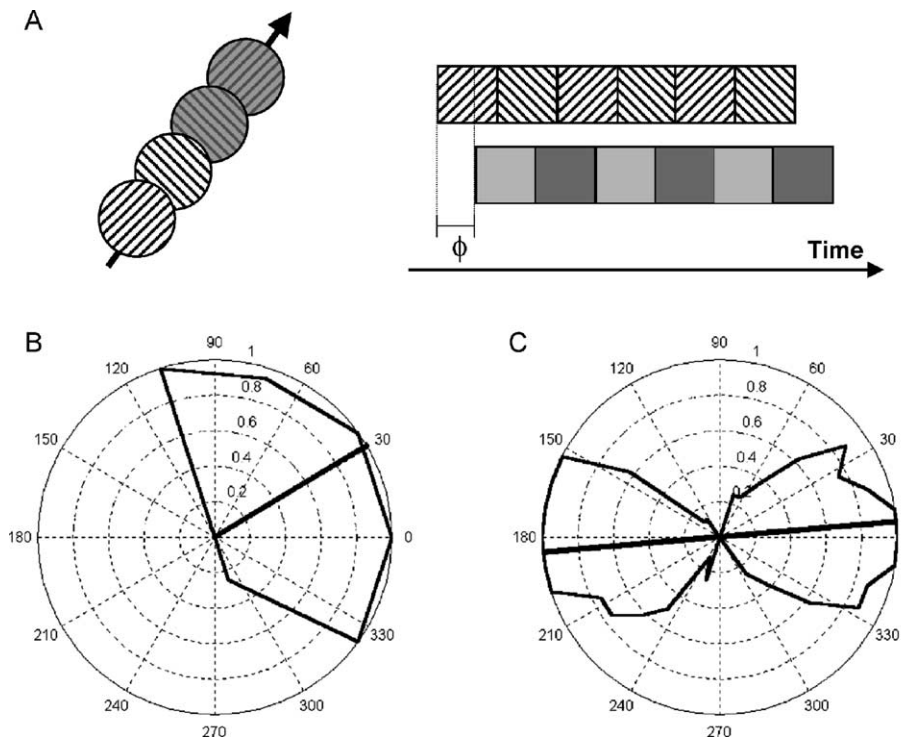

Fig. 1. (A) Schematic of stimulus sequence. A single grating stimulus oscillates in time between two orientations (45° left and right) and two colours (red and green). The square-wave temporal oscillations in colour and orientation have the same period but their relative phase, ϕ, can vary from trial to trial. Subjects perform one of two tasks on any given run of trials. On the pairing task, subjects make a forced-choice judgement as to which colour is paired predominantly with which orientation. On the simultaneity task, subjects report whether or not colour and orientation appear to change at the same time. Results from (B) the pairing task (C) the simultaneity task for subject CC at an oscillation period of 600 ms as a function of the relative phase of oscillation, ϕ. For the pairing task, the radial dimension shows the proportion of times that the colour red is paired with rightwards orientation. This distribution is centred on a phase of 31.0°, corresponding to a stimulus in which changes in colour lag orientation changes by 51.6 ms. For the simultaneity task, the radial dimension shows the proportion of trials in which the changes were judged to be simultaneous. This distribution is centred on a phase of 5.0°, corresponding to a stimulus in which changes in colour lag orientation changes by 8.4 ms.

responses, or (3) the sum of the three cone responses (luminance), respectively. These modulations define the cardinal axes of a three-dimensional colour space (Derrington et al., 1984).

We reasoned that, if chromatic segregation occurs at the level of retinal ganglion cells, it should not be possible to segregate in this way pairs of stimuli that produce the same pattern of excitation across these channels. Therefore, in Experiment 2, we repeated the pairing task using pairs of equiluminant grating stimuli either modulated along respective cardinal chromatic axes (S and L–M) or along a pair of non-cardinal directions of colour space. Adding cardinal chromatic modulations produces modulations along non-cardinal axes which are perceptually quite distinct, appearing to modulate between magenta and lime (S+(L–M)) and orange and cyan (S−(L–M)) depending on the relative spatial phase of the cardinal chromatic components. Each cardinal chromatic stimulus is designed to excite a different population of retinal ganglion cells, while each non-cardinal stimulus should activate the two sub-cortical chromatic channels to the same extent.

2. Methods

Three subjects (one naïve: PH) participated as observers in these experiments. Stimuli were generated using Matlab software to drive a VSG 2/5 Graphics Card (Cambridge Research Systems) and displayed on a gamma-corrected $21''$ Sony Trinitron GM 520 monitor (1024×768 resolution; 100 Hz refresh rate).

Subjects were presented with a single sinusoidal grating stimulus oscillating in colour and orientation at the same temporal frequency. The grating had a spatial frequency of 0.6 cycles/° and subtended an angle of 9° from the viewing distance of 55 cm. The temporal profile of the oscillations was a square-wave, such that each colour and orientation was present for one half of each period. The orientation of the grating could be 45° left or right of vertical. Prior to the stimulus, a mask oscillating between the two component gratings at 50 Hz appeared for 500 ms to obscure stimulus onset. The stimulus remained on the screen until the subject made a response. The relative phase of the colour and orientation changes was manipulated from trial to trial (Fig. 1A).

In Experiment 1, the colour of the grating could either be red (CIE: $x = 0.59$; $y = 0.35$) or green (CIE: $x = 0.41$; $y = 0.34$). The luminance of the red grating modulated between 16.1 and 53.7 cd/m^2 and the luminance of the green grating between 16.7 and 52.7 cd/m^2. These values were chosen to ensure that the orientation of the two components was camouflaged in the sum (Holcombe & Cavanagh, 2001), such that the stimulus

appeared as a yellow horizontal–vertical plaid. This was verified for each observer.

In different sessions subjects were asked to complete either the pairing or the simultaneity task. For the pairing task, each subject made judgements on colour (what is the predominant orientation while the stimulus is red or green?) or orientation (what is the predominant colour while the stimulus is inclined to the left or right?) during four different runs of the experiment. These reports were then recorded so as to represent the proportion of times that red was paired with leftwards orientation as a function of the relative phase of the colour and orientation changes. If the pairing was veridical, this distribution would be centred on physical synchrony (zero degrees of phase). The deviation of the centroid of this distribution from physical synchrony was taken as a measure of the perceptual asynchrony of colour and orientation processing (Moutoussis & Zeki, 1997b), as illustrated in Fig. 1B. The centroid was fitted according to the equation:

$$\phi_{\mathrm{p}} = \tan^{-1}\left(\frac{\sum_{i=1}^{N} P_i \sin \phi_i}{\sum_{i=1}^{N} P_i \cos \phi_i}\right)$$

where φ_{p} is the phase of the (pairing) centroid, φ_i is the relative phase of colour and orientation changes at the ith stimulus level, and P_i is the proportion of trials at the ith stimulus level in which red was paired with leftwards orientation. This is mathematically equivalent (Salinas & Abbott, 1994; Swindale, 1998) to fitting a periodic function of the form:

$$\widehat{P}(\phi) = \cos(\phi_i - \phi_{\mathrm{p}}).$$

For the simultaneity task, veridical judgements would be at 0° and 180° of phase (i.e., when either red–green or green–red changes were simultaneous with a given orientation change). To calculate the perceptual asynchrony in this case (Fig. 1C), a centroid was fitted to a double-angle representation of phase according to the equation:

$$\phi_{\mathrm{s}} = 0.5 \tan^{-1}\left(\frac{\sum_{i=1}^{N} S_i \sin 2\phi_i}{\sum_{i=1}^{N} S_i \cos 2\phi_i}\right)$$

where φ_{s} is the phase of the (simultaneity) centroid, φ_i is again the relative phase of colour and orientation changes at the ith stimulus level, and S_i is the proportion of trials at the ith stimulus level in which the changes in colour and orientation judged to be simultaneous. This is equivalent to fitting a periodic function of the form:

$$\widehat{S}(\phi) = \cos 2(\phi_i - \phi_{\mathrm{s}}).$$

In Experiment 2, one subject completed the 'pairing' task while viewing equiluminant stimuli. Equiluminant L–M and S-cone isolating axes were determined using a minimum motion technique (Anstis & Cavanagh, 1983) and detection thresholds were measured in each of the

three cardinal directions of colour space (Derrington et al., 1984). Stimuli were presented at 40× detection threshold.

All experiments were performed in accordance with protocols approved by the Human Ethics Committee of The University of Sydney.

3. Results

The results of Experiment 1 reveal a dissociation between the perceptual asynchronies measured by the respective tasks (Fig. 2). For the most rapid oscillations (100 ms period), the centroids of the data from both tasks fell between 0 and 10 ms, corresponding to a situation in which colour changes in the stimulus *precede* orientation changes by less than 10 ms. For slower oscillations, there was a marked difference in the measures of perceptual asynchrony derived from the two tasks. Perceptual asynchrony measured using the simultaneity task generally remained within ±10 ms, with little evidence of a systematic dependence on oscillation rate. In contrast, perceptual asynchrony measured via the pairing task tended to increase with oscillation period such that, at the longest period measured (1 s), it was around 50 ms. This corresponds to a situation in which changes in the colour of the stimulus *follow* orientation changes by around 50 ms. The two judgements can thus be seen to yield apparently paradoxical results.

When completing the pairing task, any difference in the measured perceptual asynchrony between judge-

ments made on colour and those made on orientation could be due to a "prior entry" effect of attention speeding up processing of the attended attribute (Reeves & Sperling, 1986; Sternberg & Knoll, 1973). Such effects are evident in the data of two of the three observers at the longer stimulus durations (Fig. 3). However, while attention affects the magnitude of the measured perceptual asynchrony it does not affect its sign. Thus, when the results from the two attentional conditions are averaged, observers still show a systematic temporal bias in favour of colour over orientation (Fig. 2A).

In Experiment 2, when the pairing task was completed with equiluminant stimuli, orientation and colour

Fig. 3. Estimates of perceptual asynchrony from the pairing task in Experiment 1 for judgements on colour (hollow circles) or orientation (filled squares) for subjects (A) CC (B) JP (C) PH as a function of oscillation period.
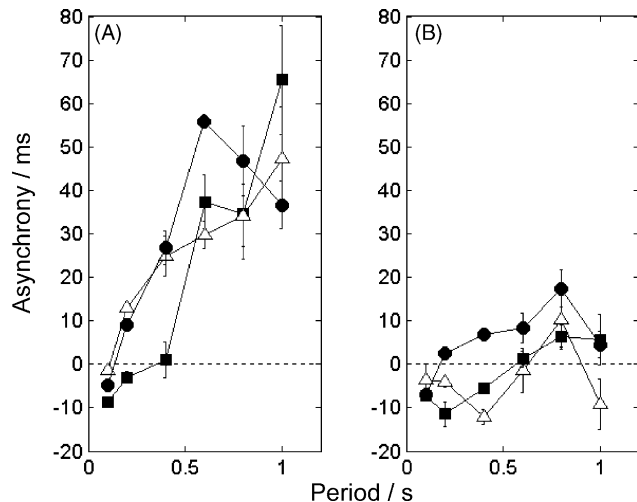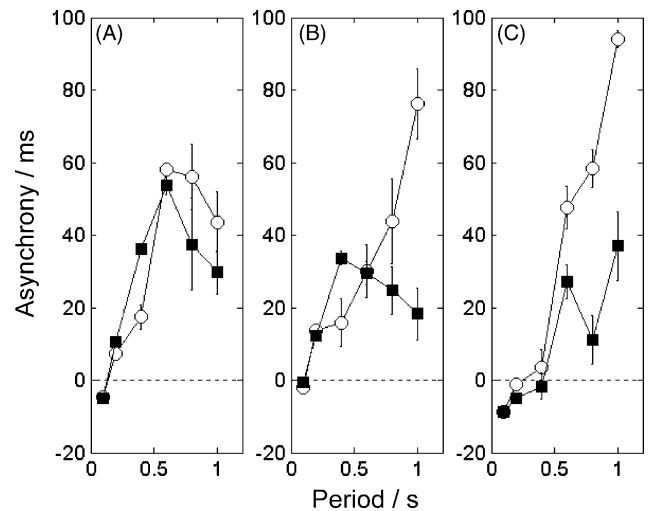

Fig. 2. Estimates of perceptual asynchrony in Experiment 1 from (A) the pairing task (B) the simultaneity task for subjects CC (filled circles), JP (hollow triangles) and PH (filled squares) as a function of oscillation period. Positive values correspond to a stimulus in which colour changes lag orientation changes, indicating a temporal bias in perception in favour of colour. Negative values correspond to a stimulus in which colour changes lead orientation changes, indicating a temporal bias in perception in favour of orientation.
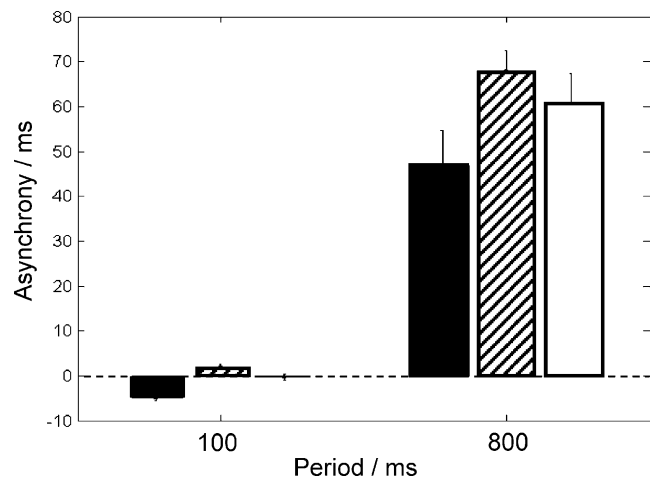

Fig. 4. Perceptual asynchrony for subject CC in Experiment 2 measured using the pairing task at oscillation periods of 100 and 800 ms. Stimuli were modulated either along cardinal (hashed bars) or noncardinal (white bars) equiluminant chromatic axes. Data from the corresponding conditions of Experiment 1 using red and green luminance-modulated stimuli are shown for comparison (black bars).

could be accurately paired at a period of 100 ms. At a longer period of 800 ms, the derived distribution of reported co-existence was consistent with an apparent perceptual asynchrony of 64 ± 5 ms (Fig. 4). This pattern of results is very similar to that of the original experiment, even when the two chromatic stimuli provide no differential excitation of sub-cortical channels.

4. Discussion

Over the range of oscillation rates tested, judgements of the simultaneity of changes in colour and orientation were almost veridical. However, pairing of the attributes within the same stimulus was biased away from veridical by up to 50 ms and showed a marked dependence on oscillation rate. What are we to make of this apparent paradox?

4.1. Possible computational mechanisms

From a functional perspective, the aspect of neuronal response profiles that has received most attention is their onset latency (Bair, Cavanaugh, Smith, & Movshon, 2002; Barbur, Wolf, & Lennie, 1998; Gawne, Kjaer, & Richmond, 1996; Moutoussis & Zeki, 1997a, 1997b; Raiguel, Xiao, Marcar, & Orban, 1999; Schmolesky et al., 1998; Zeki & Bartels, 1998). Using a pairing task, Moutoussis and Zeki (1997b) reported a perceptual asynchrony between colour and orientation of around 63 ms. They proposed that this apparent asynchrony was due to the operation of independent processing systems with different delays. Although little data exists on responses to rapidly oscillating stimuli (Bair et al., 2002; Buracas, Zador, DeWeese, & Albright, 1998), electrophysiological recordings from the macaque monkey suggest that visually evoked response latencies typically vary by no more than 20 ms across the cortical visual areas (Schmolesky et al., 1998). Given such a small variance, it is hard to envisage how differential processing latencies between visual areas specialized for the analysis of different visual attributes (Moutoussis & Zeki, 1997a, 1997b) could account for the apparent temporal advantage of colour over orientation revealed by the pairing task. Moreover, it is not clear how an explanation based purely on latency differences could account for the task-dependence of the asynchronies reported here.

Using a stimulus varying in pseudorandom temporal sequence, it has recently been found that response onset latencies across the macaque visual system are longer and more variable than corresponding offset latencies (Bair et al., 2002). This raises the interesting possibility that neuronal response offsets might provide the more reliable substrate for determining the relative timing of events. In principle, the perceived timing of a change

from stimulus A to stimulus B could be based upon either the offset of the response to stimulus A or the onset of the response to stimulus B. Response offsets might provide a reliable substrate for determining simultaneity. However, while response offsets could in principle be used when making perceptual pairing judgements, it seems unlikely that in normal vision the association of the attributes within a temporally extended stimulus should be delayed until that stimulus itself changes.

Regardless of whether simultaneity judgements are based upon response onsets or offsets, it is possible that different judgements about the temporal properties of a stimulus are based upon different aspects of the temporal response profile generated in the visual brain (McClurkin, Optican, Richmond, & Gawne, 1991; Stelmach & Herdman, 1991). The simultaneity task used here involves judgements about instants of stimulus transition. The pairing task requires observers to assess the perceptual co-existence of stimulus attributes over an extended period of time. Accordingly, we hypothesise that simultaneity judgements are determined by the differential latency of responses to colour and orientation while pairing judgements are determined by the degree to which the response to each colour and orientation correlate (Johnston & Nishida, 2001; Stelmach & Herdman, 1991). This correlation could operate between conventional rate-modulated neural representations (Shadlen & Movshon, 1999) rather than relying upon temporal synchronization of neuronal spiking (Singer & Gray, 1995). According to this view, we base our perceptual judgements not upon a single, internally consistent representation of the world, but rather use different aspects of the neural activity elicited by visual events to perform different tasks.

The correlation of the responses to colour and orientation depends upon the whole temporal profile of the responses to the two attributes. This includes not only the differential response latency but also the degree and rate of response adaptation. Rapid adaptation appears to be a fundamental property of the responses of cortical neurons (Muller, Metha, Krauskopf, & Lennie, 1999). Psychophysically, a fast phase of adaptation has been observed for colour appearance and discrimination judgements with a time constant of the order of 80 ms, although this might be attributable to photoreceptor adaptation which could affect all post-receptoral processing (Rinner & Gegenfurtner, 2000).

If a neural response to a given colour were to adapt over the course of its presentation then the earlier part of the presentation of that colour would be more strongly weighted than the latter part within the context of a pairing judgement. If the response to colour were to adapt more rapidly, or more strongly, than the response to orientation then a systematic bias to respond as though colour were processed more rapidly than orientation would arise. Moreover, if pairing judgements

were weighted by the temporal distribution of the neural activity, the effect of response adaptation upon the perceptual asynchrony measured through the pairing task would be expected to increase with oscillation period. For rapid (10 Hz) oscillations, the degree of adaptation occurring in one presentation of a given colour (50 ms) would be negligible and any differences in response latency to colour and orientation would be expected to dominate. This would bring pairing judgements into line with the corresponding simultaneity judgements. As the oscillation period increases, the degree of perceptual adaptation and hence the bias in pairing judgements would be expected to increase while synchrony judgements remained essentially unaffected (Fig. 5). Mathematical details of the proposed model are given in Appendix A.

4.2. Possible neural substrates

In Experiment 2, the perceptual asynchrony measured using the pairing task was not significantly different for non-cardinal chromatic stimuli than for cardinal chromatic stimuli or the stimuli used in Experiment 1. Orientation and colour were reliably paired for all stimuli at a period of 100 ms (Fig. 4). If chromatic segregation occurs at the level of retinal ganglion cells, it should not be possible to segregate pairs of non-cardinal chromatic stimuli that produce the same pattern of excitation across these channels. Our results are thus inconsistent with chromatic segregation at the retina, instead suggesting chromatic processing at the cortical level where the coding of colour and luminance information is no longer restricted to three independent mechanisms (Clifford, Spehar, Solomon, Martin, &

Zaidi, 2003; DeValois et al., 2000; Johnson, Hawken, & Shapley, 2001; Lennie, Krauskopf, & Sclar, 1990; Thorell, DeValois, & Albrecht, 1984).

Our results are also inconsistent with the suggestion that active participation of broad-band achromatic mechanisms is required for the activity of chromatic cortical mechanisms to reach awareness (Gur & Akri, 1992; Gur & Snodderly, 1997). Gur and Snodderly (1997) found that the activity of colour-opponent cells in macaque V1 followed colour alternations in a heterochromatic stimulus flickering at rates where no colour change is detected by humans or monkeys. They suggested that the activity of colour-opponent mechanisms is only available to awareness when bound to activity of broad-band mechanisms which, above moderate flicker frequencies, requires luminance modulation. However, when equiluminant stimuli contain oriented structure, we have shown that colour can be perceived even at high flicker rates (10 Hz).

The dissociation between synchrony and pairing judgements reported here for oscillations in colour and orientation stands in contrast to recent reports concerning the perceptual asynchrony of colour and motion. For relatively rapid (1–2 Hz) oscillations in colour and motion, both simultaneity and pairing tasks yield apparent asynchronies of the order of 100 ms (Moutoussis & Zeki, 1997a, 1997b; Nishida & Johnston, 2002). Thus, synchronous perceptual pairing occurs when changes in the colour of the stimulus follow the motion changes by around 100 ms. This is far longer than any delay (∼10 ms) inherent in presenting motion stimuli in discrete frames. Instead, failures to make accurate pairing judgements between colour and motion at short oscillation periods (Moutoussis & Zeki, 1997a,
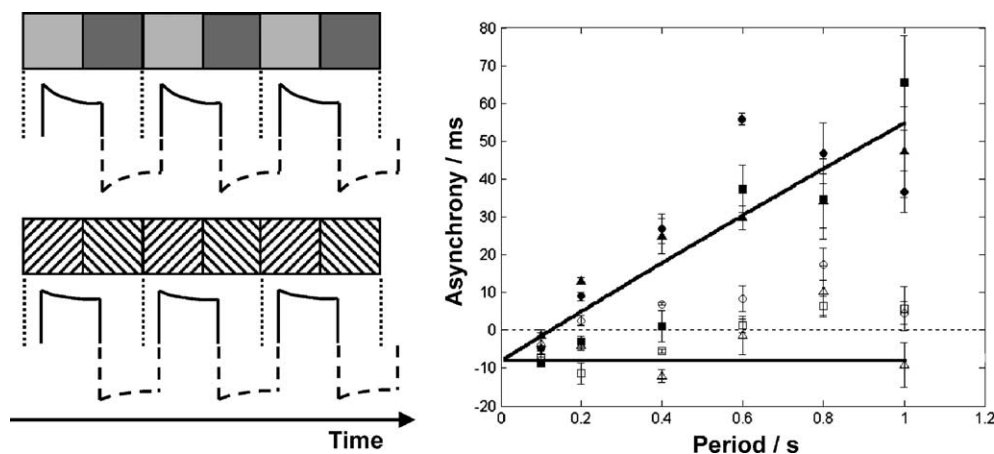

Fig. 5. Model of the effect of stimulus oscillation period on perceptual asynchrony measured using the pairing and simultaneity tasks. The neural response to colour and orientation are each modelled as rising rapidly to a peak with a characteristic latency following a change in the relevant attribute and then decaying exponentially over time. Simultaneity judgements are modelled as depending on the differential latency of the peak responses to colour and motion, while pairing judgements depend upon the sign of the cross-correlation of the two temporal response profiles. Data for the pairing (filled symbols) and simultaneity (open symbols) tasks are redrawn from Fig. 3. Bold lines show the model predictions for a differential latency of −8 ms and a decay constant ratio of 0.77, such that the colour response reaches a peak with a *longer* latency but decays *faster* than the response to orientation.

1997b; Nishida & Johnston, 2002), or between spatially separated colour and orientation changes (Holcombe & Cavanagh, 2001), suggest that high temporal precision can be retained only when overlapping populations of neurons are involved in coding the two relevant attributes. When responses must be compared between cortical areas, or between spatially distinct regions of a single topographically organized cortical area, a degree of temporal resolution appears to be lost.

The suggestions that: (1) different aspects of the temporal response profile might underlie different aspects of perception; and (2) high temporal precision between visual attributes can be retained only when overlapping populations of neurons are involved in their coding, are in accord with the intriguing hypothesis that single neurons in the primate visual system can simultaneously carry information about colour and spatial pattern using separable temporal codes (McClurkin & Optican, 1996; McClurkin, Zarbock, & Optican, 1996). Electrophysiological recordings from neurons in the visual cortex of the rhesus monkey were found to approximate a multiplex code under which each neuron's temporal response profile was the product of separable temporal codes for colour and pattern. This led to the proposal that: (1) the psychological separateness of colour and pattern arises not from encoding by separate populations of neurons but from encoding by separable temporal codes within the responses of single neurons; (2) the binding of colour and form may occur by virtue of their codes being multiplexed on the same neurons (McClurkin & Optican, 1996).

Whatever the mechanisms underlying perceptual judgements in the pairing task, the existence, at long oscillation periods, of a perceptual asynchrony between colour and orientation suggests that there must be a degree of independence in their processing. Establishing whether this involves analysis by functionally specialized cortical regions at some level of the visual processing hierarchy (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Moutoussis & Zeki, 1997b; Zeki, 1973) or multiple interactions within a more homogeneous population of neurons (Lennie, 1998; McClurkin & Optican, 1996; McClurkin et al., 1996) will require electrophysiological investigation using stimuli whose visual attributes oscillate over time.

Appendix A

The neural response to colour and orientation are each modelled as rising rapidly to a peak with a characteristic latency following a change in the relevant attribute and then decaying exponentially over time. Simultaneity judgements are modelled as depending on the differential latency of the peak responses to colour and motion, while pairing judgements depend upon the sign of the cross-correlation of the two temporal response profiles.

Calculation of the relative phase of colour and orientation change at which the cross-correlation of the two temporal response profiles is zero is simplified greatly by the observation that the effect of differential latency can be considered separately from the effect of rapid adaptation. We can simply calculate the cross-correlation as though the differential latency were zero and then add in the differential latency.

The situation in which the cross-correlation is zero is illustrated in Fig. 6. The response, $R(t)$, to the two stimulus attributes is given by:

$$R_i(t) = \exp\left(\frac{-t}{\tau_i}\right); \quad i = 1, 2$$

where τ denotes the decay time constant of the response. The cross-correlation of the two response profiles is zero when:

$$\int_0^Q R_1(t)R_2(t)\,dt = 0$$

where Q is the duration of one quarter of a cycle of the stimulus oscillation. It can be seen from Fig. 6 that this condition is satisfied when:
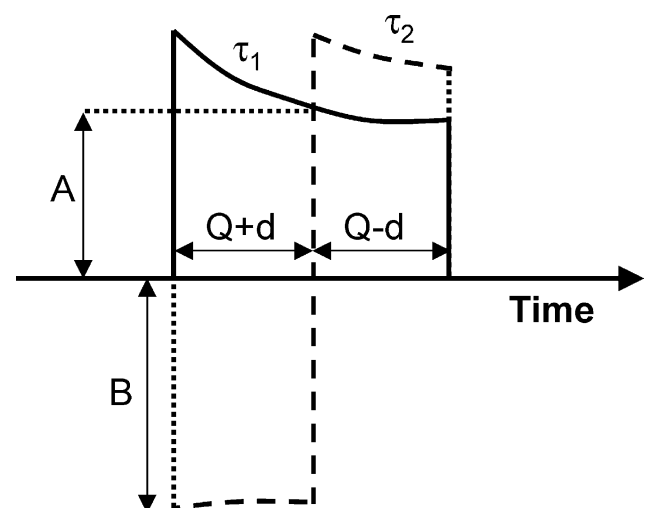

Fig. 6. Illustration of the situation in which the cross-correlation of two temporal response profiles is zero. The time constants of rapid neural adaptation for the two profiles are denoted by τ_1 and τ_2. Q is the duration of one quarter of a cycle of the stimulus oscillation and d is the perceptual asynchrony between stimulus attributes.

$$\int_0^{Q+d} \exp\left(\frac{-t}{\tau_1}\right) B \exp\left(\frac{-t}{\tau_2}\right) dt$$
$$= \int_0^{Q-d} A \exp\left(\frac{-t}{\tau_1}\right) \exp\left(\frac{-t}{\tau_2}\right) dt$$

where d is the perceptual asynchrony between stimulus attributes for which we must solve. The values of A and B are given by:

$$A = \exp\left(-\frac{(Q+d)}{\tau_1}\right)$$

and

$$B = \exp\left(-\frac{(Q-d)}{\tau_2}\right).$$

The integral equation solves to:

$$\exp(-ad) = \frac{\left(1 + \exp\left(\frac{-2Q}{\tau_1}\right)\right)\exp\left(\frac{-Q}{\tau_2}\right)}{\left(1 + \exp\left(\frac{-2Q}{\tau_2}\right)\right)\exp\left(\frac{-Q}{\tau_1}\right)}$$

where a is given by:

$$a = \frac{\tau_1 + \tau_2}{\tau_1 \tau_2}.$$

Letting $\tau_2 = k\tau_1$ gives:

$$\exp(-ad) = \frac{\left(1 + \exp\left(\frac{-2Q}{\tau_1}\right)\right)\exp\left(\frac{-Q(1-k)}{k\tau_1}\right)}{\left(1 + \exp\left(\frac{-2Q}{k\tau_1}\right)\right)}$$

where k is the ratio of the decay time constants.

Solving for d in the limit that the decay time constants are long relative to the oscillation period (i.e., τ_1, $\tau_2 \gg Q$) shows that the model pairing asynchrony depends on the ratio of the decay time constants, k, and increases linearly with oscillation period, Q:

$$d \propto Q\left(\frac{1-k}{1+k}\right).$$

The predicted perceptual asynchrony increases with the deviation from unity of the ratio of the decay time constants but is independent of the absolute magnitude of those time constants. The linear dependence of asynchrony on oscillation period shows that rapid adaptation has the effect of introducing a fixed phase shift into the model predictions. The fixed phase effect of rapid adaptation coupled with the fixed time effect of differential latency allows the model to capture the main features of the psychophysical pairing data. The simulations whose results are shown in Fig. 5 were performed with a differential latency of −8 ms and a decay constant ratio of 0.77, such that the colour response reaches a peak with a *longer* latency but decays *faster* than the response to orientation.

References

Anstis, S. M., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In J. Mollon, & R. T. Sharpe (Eds.), *Colour vision: physiology and psychophysics* (pp. 156–166). London: Academic.

Arnold, D. H., & Clifford, C. W. G. (2002). Determinants of asynchronous processing in vision. *Proceedings of the Royal Society of London Series B, 269*, 579–583.

Arnold, D. H., Clifford, C. W. G., & Wenderoth, P. (2001). Asynchronous processing in vision: colour leads motion. *Current Biology, 11*, 596–600.

Bair, W., Cavanaugh, J. R., Smith, M. A., & Movshon, J. A. (2002). The timing of response onset and offset in macaque visual neurons. *Journal of Neuroscience, 22*, 3189–3205.

Barbur, J. L., Wolf, J., & Lennie, P. (1998). Visual processing levels revealed by response latencies to changes in different visual attributes. *Proceedings of the Royal Society of London Series B, 265*, 2321–2325.

Buracas, G. T., Zador, A. M., DeWeese, M. R., & Albright, T. D. (1998). Efficient discrimination of temporal patterns by motion-sensitive neurons in primate visual cortex. *Neuron, 20*, 959–969.

Clifford, C. W. G., Spehar, B., Solomon, S. G., Martin, P. R., & Zaidi, Q. (2003). Interactions between colour and luminance in the perception of orientation. *Journal of Vision, 3*, 106–115.

Dennett, D. C., & Kinsbourne, M. (1992). Time and the observer: the where and when of consciousness in the brain. *Behavioral and Brain Sciences, 15*, 183–247.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology (London), 357*, 241–265.

DeValois, R. L., Abramov, I., & Jacobs, G. H. (1966). Analysis of response patterns of LGN cells. *Journal of the Optical Society of America, 56*, 966–977.

DeValois, R. L., Cottaris, N. P., Elfar, S. D., Mahon, L. E., & Wilson, J. A. (2000). Some transformations of color information from geniculate nucleus to striate cortex. *PNAS, 97*, 4997–5002.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science, 287*, 2036–2038.

Gawne, T. J., Kjaer, T. W., & Richmond, B. J. (1996). Latency: another potential code for feature binding in striate cortex. *Journal of Neurophysiology, 76*, 1356–1360.

Gur, M., & Akri, V. (1992). Isoluminant stimuli may not expose the full contribution of color to visual functioning: spatial contrast sensitivity measurements indicate interaction between color and luminance processing. *Vision Research, 32*, 1253–1262.

Gur, M., & Snodderly, D. M. (1997). A dissociation between brain activity and perception: chromatically opponent cortical neurons signal chromatic flicker that is not perceived. *Vision Research, 37*, 377–382.

Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P., & Tootell, R. B. H. (1998). Retinotopy and color sensitivity in human visual cortical area V8.

Holcombe, A. O. (2001). A purely temporal transparency mechanism in the visual system. *Perception, 30*, 1311–1320.

Holcombe, A. O., & Cavanagh, P. (2001). Early binding of feature pairs for visual perception. *Nature Neuroscience, 4*, 127–128.

James, W. (1890). *The principles of psychology*. New York: Dover Press.

Jeannerod, M. (1992). The where in the brain determines the when in the mind. *Behavioral and Brain Sciences, 15*, 212–213.

Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience, 4*, 409–416.

Johnston, A., & Nishida, S. (2001). Time perception: brain time or event time? *Current Biology, 11*, R427–R430.

Lennie, P. (1998). Single units and visual cortical organization. *Perception, 27*, 889–935.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience, 10*, 649–669.

McClurkin, J. W., & Optican, L. M. (1996). Primate striate and prestriate cortical neurons during discrimination I. Simultaneous temporal encoding of information about colour and pattern. *Journal of Neurophysiology, 75*, 481–495.

McClurkin, J. W., Optican, L. M., Richmond, B. J., & Gawne, T. J. (1991). Concurrent processing and complexity of temporally encoded neuronal messages in visual perception. *Science, 253*, 675–677.

McClurkin, J. W., Zarbock, J. A., & Optican, L. M. (1996). Primate striate and prestriate cortical neurons during discrimination II. Separable temporal codes for colour and pattern. *Journal of Neurophysiology, 75*, 496–507.

Moutoussis, K., & Zeki, S. (1997a). A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society of London Series B, 264*, 393–399.

Moutoussis, K., & Zeki, S. (1997b). Functional segregation and temporal hierarchy of the visual perceptive systems. *Proceedings of the Royal Society of London Series B, 264*, 1407–1414.

Muller, J. R., Metha, A. B., Krauskopf, J., & Lennie, P. (1999). Rapid adaptation in visual cortex to the structure of images. *Science, 285*, 1405–1408.

Nishida, S., & Johnston, A. (2002). Marker correspondence, not processing latency, determines temporal binding of visual attributes. *Current Biology, 12*, 359–368.

Patel, S. S., Chung, S. T. L., Bedell, H. E., & Ogmen, H. (2002). Colour and motion: which is the tortoise and which is the hare? *Journal of Vision, 2*, 746a.

Raiguel, S. E., Xiao, D.-K., Marcar, V. L., & Orban, G. A. (1999). Response latency of macaque area MT/V5 neurons and its relationship to stimulus parameters. *Journal of Neurophysiology, 82*, 1944–1956.

Reeves, A., & Sperling, G. (1986). Attention gating in short-term visual memory. *Psychological Review, 93*, 180–206.

Rinner, O., & Gegenfurtner, K. R. (2000). Time course of chromatic adaptation for color appearance and discrimination. *Vision Research, 40*, 1813–1826.

Salinas, E., & Abbott, L. F. (1994). Vector reconstruction from firing rates. *Journal of Computational Neuroscience, 1*, 89–107.

Schmolesky, M. T., Wang, Y., Hanes, D. P., Thomson, K. G., Leufgeb, S., Schall, J. D., & Leventhal, A. G. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology, 79*, 3272–3278.

Shadlen, M. N., & Movshon, J. A. (1999). Synchrony unbound: a critical evaluation of the temporal binding hypothesis. *Neuron, 24*, 67–77.

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience, 18*, 555–586.

Stelmach, L. B., & Herdman, C. M. (1991). Directed attention and perception of temporal order. *Journal of Experimental Psychology: Human Perception and Performance, 17*, 539–550.

Sternberg, S., & Knoll, R. L. (1973). The perception of temporal order: fundamental issues and a general model. In S. Kornblum (Ed.), *Attention and performance IV* (pp. 629–685). New York: Academic Press.

Suzuki, S., & Grabowecky, M. (2002). Overlapping features can be parsed on the basis of rapid temporal cues that produce stable emergent percepts. *Vision Research, 42*, 2669–2692.

Swindale, N. V. (1998). Orientation tuning curves: empirical description and estimation of parameters. *Biological Cybernetics, 78*, 45–56.

Thorell, L. G., DeValois, R. L., & Albrecht, D. G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research, 24*, 751–769.

Viviani, P., & Aymoz, C. (2001). Colour, form and movement are not perceived simultaneously. *Vision Research, 41*, 2909–2918.

Zeki, S. M. (1973). Colour coding in rhesus monkey prestriate cortex. *Brain Research, 27*, 422–427.

Zeki, S., & Bartels, A. (1998). The asynchrony of consciousness. *Proceedings of the Royal Society of London Series B, 265*, 1583–1585.