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Determinants of asynchronous processing in vision

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When a stimulus oscillates in both colour and direction of motion, changes in colour must lag behind those in direction if they are to be seen as concurrent. It has been argued that this lag is the consequence of asynchronous visual processing, with colour being processed more rapidly than motion. This proposal is contentious: it has been criticized on the basis that the time-course of cortical activity may not correlate directly with that of perceptual experience. Here, we demonstrate that the extent of the apparent asynchrony can vary according to the prevailing stimulus conditions. The apparent asynchrony is greatest if the stimulus is composed of opponent directions of motion and is reduced if the angular difference between the directions is reduced. This pattern of results suggests that asynchronous neural activity arises, in part, as a consequence of differential levels of inhibition within relatively independent cortical structures.

Keywords: perceptual binding; neural latency; inhibition; contingent adaptation

1. INTRODUCTION

It is generally accepted that the visual cortex contains relatively independent anatomical structures that are specialized for processing different stimulus attributes, such as colour and motion (Zeki 1978; Livingstone & Hubel 1988; Felleman & Van Essen 1991). However some argument persists as to whether such specialization is a general property of cortical vision or unique to motion processing (Lennie 1998). In either case, the situation seems to pose a question for which we have no adequate answer: How does activity within multiple and distributed cortical structures result in a unified visual experience?

A recent suggestion is that our conscious experience of different stimulus attributes, such as colour and motion, is independently mediated by multiple cortical structures (Moutoussis & Zeki 1997*a*,*b*; Bartels & Zeki 1998; Zeki & Bartels 1998). This does not mean that we fail to experience a unified visual awareness. The implication is merely that our experience of different visual attributes is mediated by activity within multiple cortical regions and that there is no need for this activity to interact with that of other cortical regions before a given attribute can be experienced (Moutoussis & Zeki 1997*b*). There are two lines of evidence that suggest this. First, damage to various parts of the brain can result in selective visual deficits. For instance, it is possible to have a preserved ability to perceive colour without being able to perceive motion (Zihl *et al.* 1983). Conversely, it is also possible to have a preserved ability to perceive motion without being able to see in colour (Cowey & Heywood 1997).

A second line of evidence has developed through consideration of the temporal properties of visual processing. Given that distinct cortical structures appear to be specialized for processing different stimulus attributes, it seemed reasonable to propose that the time taken to process the different stimulus attributes might differ. Furthermore, if processing within a relatively independent cortical structure is sufficient to produce a conscious visual experience, the differing times required to process different stimulus attributes might have a direct consequence in perceptual experience. Events that occur at the same physical time might be experienced as having occurred at separate times, and events that occur at different times might be experienced as being simultaneous (Moutoussis & Zeki 1997*a*,*b*; Bartels & Zeki 1998; Zeki & Bartels 1998).

In an effort to test this hypothesis, Moutoussis & Zeki (1997*a*) used a stimulus that oscillated in colour (red and green) and direction of motion (up and down). The relative phase of the changes in colour and direction was manipulated and subjects were required to indicate which colour was coexistent with upward motion. Surprisingly, subjects were most likely to report that a colour was moving in a given direction when the change in colour lagged behind the change in direction by *ca.* 80 ms (as described in figure 1). Moutoussis & Zeki (1997*a*) argued that this was indicative of a processing asynchrony that has a direct consequence in perceptual experience.

The conclusions drawn by Moutoussis & Zeki (1997*a*) have been questioned on the basis that their data were derived from an analysis of subjective report (Johnston & Nishida 2001). It has been argued that neural processing time may not correlate directly with the perceived time of occurrence (Dennett & Kinsbourne 1992; Johnston & Nishida 2001). It is therefore unclear if data of the form described by Moutoussis & Zeki (1997*a*) are indicative of asynchronous neural processing, or if they arise as a consequence of subsequent interpretive processes.

To address this concern, Arnold *et al.* (2001) made use of an indirect measure of visual processing—the colour-contingent motion after-effect. After looking at a given direction of motion, a subsequently viewed stationary object can appear to move in the opposite direction. This phenomenon can be made to be contingent on another stimulus attribute, such as colour. For example, if a clock-

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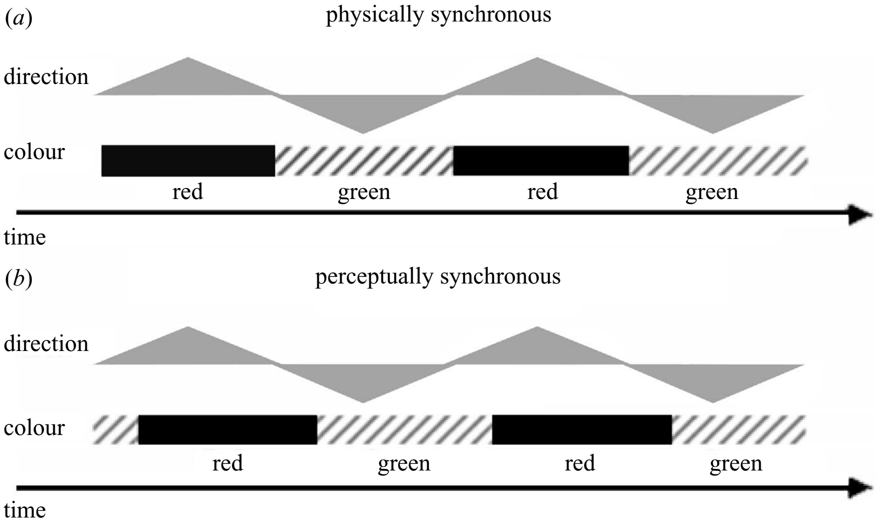

Figure 1. When Moutoussis & Zeki (1997*a*) made use of a stimulus that oscillated in colour (green–red) and direction of motion (up–down), a given direction was perceived to maximally correlate with a colour state when the changes in colour lagged behind those in direction by *ca.* 80 ms. Here, the situation where changes in direction and colour are physically synchronous (*a*) is depicted and contrasted with the situation where the changes are perceptually synchronous (*b*).

wise rotation is paired with the colour green and an anticlockwise rotation with the colour red then subsequently viewed stationary green objects can appear to rotate anticlockwise, whereas stationary red objects can appear to rotate clockwise (Favreau *et al.* 1972).

If changes in colour are processed more rapidly than those of the direction of motion, when alternating colours and directions are displayed, the perceptual correlation between the two stimulus attributes should differ systematically from the physical. This prediction was supported by the experiments of Arnold *et al.* (2001). When, during a period of adaptation, a given direction of motion was sequentially paired with two colours for equal periods of time, such that no physical correlation existed, a robust colour-contingent motion after-effect was induced. This is consistent with the premise that colour is processed more rapidly than motion. Further results indicated a processing advantage of a similar magnitude to the perceptual advantage demonstrated by Moutoussis & Zeki (1997*a*).

Although the convergence of data from Moutoussis & Zeki (1997*a*) and Arnold *et al.* (2001) appears to suggest a processing advantage for colour over motion, the possibility remains contentious. The main reason for this is that an asynchrony of this form appears to contradict physiological evidence suggesting that, if anything, motion should be processed faster than colour (Schiller & Malpeli 1978; ffytche *et al.* 1995; Munk *et al.* 1995). However, two phenomena might account for some of the findings. First, during exposure to a preferred stimulus a cortical neuron's response varies over time. The cell typically responds with a rapid increase in firing followed by a gradual decline (Maffei *et al.* 1973). If the firing rate of a motion-sensitive mechanism determines the degree to which its activity becomes associated with that of other mechanisms, a differential response across time could induce a perceptual contingency in the absence of a physical correlation that is dependent not on asynchronous processing, but rather on variation in the response magnitude (Johnston & Nishida 2001).

Although a differential magnitude of response might provide an explanation for the findings of Arnold *et al.* (2001), it is not clear why this should have an impact on temporal order judgments of the form used by Moutoussis & Zeki (1997*a*). This raises the question of whether the qualitative and quantitative similarity between the results of Arnold *et al.* (2001) and Moutoussis & Zeki (1997*a*) is merely coincidental. Although this is possible, it seems unlikely.

A second phenomenon that might account for both the results by Moutoussis & Zeki (1997*a*) and Arnold *et al.* (2001) is direction-selective inhibition. Following exposure to a given direction of motion, the activity of neurons that prefer other directions can become transiently suppressed. The magnitude of the suppression is dependent on the relative difference in direction of motion and can be maximal for opposing directions (Barlow & Levick 1965; Snowden *et al.* 1991). Inhibition is also a robust phenomenon in colour-sensitive mechanisms (Daw 1968). However, if a stimulus consisting of two directions of motion and colour states were to elicit a relatively greater degree of inhibition between motion-sensitive than between colour-sensitive neurons, neural responses that follow changes in direction of motion might become delayed relative to those that follow changes in colour.

If the apparent processing asynchrony between colour and motion arises as a consequence of differential levels of inhibition in relatively independent cortical structures, it should be possible to manipulate the extent of the apparent asynchrony by manipulating the magnitude of inhibitory interactions in one of the structures. For instance, the magnitude of the inhibitory interaction between successive motions is dependent on the angular difference between the two directions of motion (Barlow & Levick 1965). Thus, it is predicted that when oscillations in colour and direction of motion are viewed, the magnitude of the perceptual asynchrony will vary as a function of the angular difference between the two directions of motion.

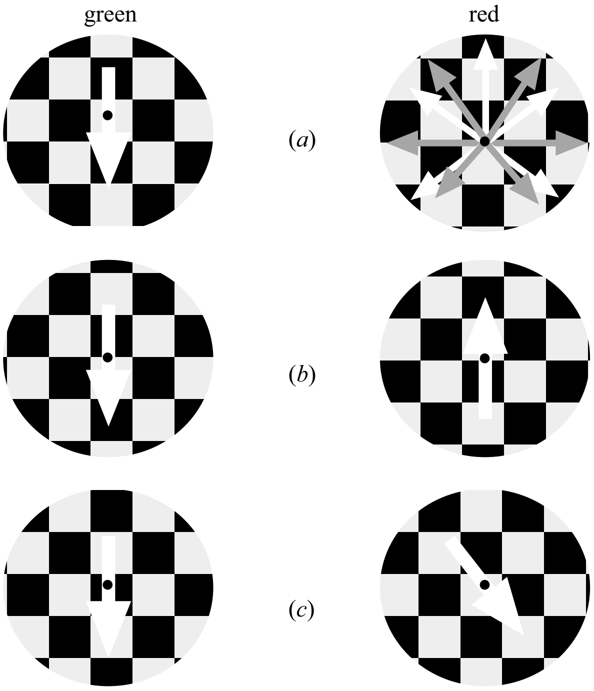

Figure 2. Depiction of the stimuli used. All stimuli had a diameter of 14°. The peak luminance of the red-contrast-modulated stimulus was 19 cd m^{-2}. The peak luminance of the green-contrast-modulated stimulus was made isoluminant with the red for each subject using the minimum motion technique of Anstis & Cavanagh (1983). The chromaticity coordinates (CIE 1931) for the red and green stimuli were ($x = 0.61$, $y = 0.34$) and ($x = 0.28$, $y = 0.595$), respectively. The central fixation point had an approximate diameter of 0.2°. The stimulus conditions experienced by the authors (*a*) and the naive subjects (*b*,*c*) are depicted. The stimuli were displayed on a 19 inch Sony Trinitron Multiscan 400PS monitor with a refresh rate of 100 Hz and were driven by a VSG 2/3 (Cambridge Research Systems). The stimulus was viewed binocularly in darkened conditions from 57 cm and the head was placed in a head rest. All subjects had normal or corrected-to-normal visual acuity and colour vision.

2. METHODS AND RESULTS

We tested this prediction by using a stimulus that oscillated in both colour and direction of motion. The stimulus, depicted in figure 2, had a diameter of 14° and the individual checks within the stimulus were 0.8° square. The stimulus drifted at 16° s^{-1} and the period of the oscillations in both direction and colour was 1 s. In each trial, one of the two directions of motion, the standard, was downwards, and the other direction of motion was one of 11 possible alternatives. Only two directions of motion were presented within any run of trials.

A run of trials consisted of the presentation of 10 phasic relationships four times each in pseudo-random order. At a phasic relationship of 0°, the standard direction of motion would always be red–black and the other green–black. At a phasic relationship of 180° this situation was reversed. The phasic relationships experienced ranged from 0° to 324° in steps of 36° (which corresponds to steps of 100 ms). In each trial, the stimulus commenced at a random point in the stimulus cycle and the trial persisted until the subject indicated a response. The two authors completed four trial runs for each comparator direction of motion. One of four judgments was made throughout each trial run. Subjects reported the perceived direction of motion during the red or green–black colour state or the perceived colour while the stimulus drifted in the standard or other direction. Each trial could then be interpreted as providing a response that indicated if the red–black colour state was perceived to be moving in the standard direction.

Data derived from each trial run were analysed to determine the percentage of times that red was perceived to be moving downwards at each phasic relationship. The centroid of this distribution was then determined. Doing this provided four estimates of the point at which colour and motion were perceived to correlate maximally in the presence of each of the 11 alternative directions of motion. For both authors, the average of these estimates and the standard error between them are plotted in figure 3*a* for each direction of motion pairing. The distribution is markedly peaked. The magnitude of the apparent asynchrony is greatest when the stimulus is composed of opposing directions of motion and least when the two directions differ only slightly.

To demonstrate the robustness of this finding, eight naive subjects completed four trial runs each. Again, the standard direction was 180° (downwards)—in two trial runs, the stimulus alternated between drifting in opposing directions of motion, and in the other two runs, the stimulus alternated between drifting towards 180° and 143.1°. Completing two trial runs for each motion pairing made it possible to obtain two judgments from each subject within separate trial runs. For half of the subjects, the perceived direction of motion while the stimulus was red–black or green–black was required. The other subjects indicated the perceived colour of the stimulus while the stimulus drifted downwards or in the alternate direction of motion.

For each subject, analysis of these trial runs provided two estimates of the perceived point of maximal correlation between colour and motion for each direction of motion pairing. The average of the two estimates was used as the dependent measure for each direction of motion. When the stimulus was composed of opposing directions of motion, on average, colour and motion were perceived to correlate maximally when changes in colour lagged behind those in direction by 93.3 ± 15.0 ms. When the stimulus alternated between drifting towards 180° and 143.1°, the maximal correlation was observed when changes in colour lagged those in direction by 56.2 ± 13.5 ms. This indicates that reducing the difference between the directions of motion from 180° to 36.9° diminished the magnitude of the perceptual asynchrony by 39.8%. The difference between the two conditions is depicted in figure 3*b* and was highly significant (paired *t*-test, $t_7 = 4.17$, $p < 0.005$).

3. DISCUSSION

Several prominent papers have recently sought to examine the temporal properties of neural processing (Nijhawan 1994; Whitney & Murakami 1998; Eagleman & Sejnowski 2000). The motivation for this is the desire to ascertain how our subjective visual experience might be related to the underlying neural processing. The

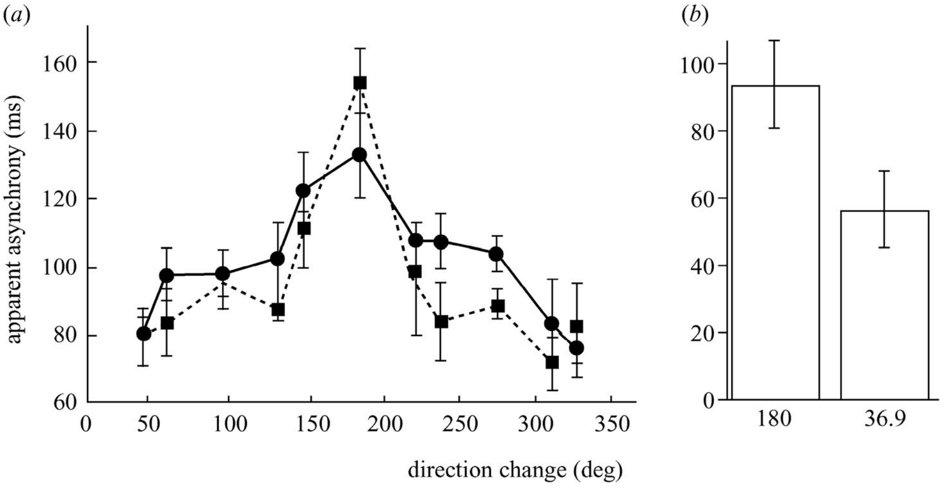

Figure 3. Average perceptual asynchrony as a function of direction change for the authors (circles, D.H.A.; squares, C.W.G.C.) (*a*), and for naive subjects (*b*). In each trial, subjects indicated either the perceived colour while the stimulus was observed to drift in a given direction or the perceived direction of drift while the stimulus was a specific colour. Ten phasic relationships between colour and motion state were each sampled four times during a trial run. These responses were fitted to a polar plot, indicating the number of times that green was perceived to be moving downwards at each phasic relationship. The centroid of this distribution was determined according to the equation $\phi_c = \tan^{-1}\left(\sum_{i=1}^{N} M_i \sin\phi_i / \sum_{i=1}^{N} M_i \cos\phi_i\right)$, where $\phi_1 = 0°$, $\phi_2 = 36°\ldots$, $\phi_N = 324°$, M_i is the number of times that red was reported to be moving downwards, and ϕ_c is the phase of centroid. For the two experienced observers, trial runs were completed under 11 different conditions. The stimulus oscillated between drifting in two directions. One of the two directions was always downwards (180°). The other direction was one of 11 possible alternatives ranging from 0° to 323.1°. The magnitude of the direction change between the two directions of motion therefore ranged from 36.9° to 323.1°. This provided four estimates of the point of maximal perceptual correlation between colour and motion state for each of the 11 magnitudes of direction change (*a*). Naive subjects completed trials in only two conditions, an angular difference of 180° and an angular difference of 36.9° (*b*).

simplest relationship would seem to be one in which our awareness of an event is directly related to activity within an identified cortical structure. If this were the case, the time-course of our visual awareness should be dictated by the time-course of activity within specialized cortical structures (Moutoussis & Zeki 1997*a*). The contrasting perspective is that perceptual awareness only arises following the intervention of subsequent interpretive processes, giving visual awareness a postdictive (Dennett & Kinsbourne 1992; Eagleman & Sejnowski 2000) rather than a contemporary (Whitney & Murakami 1998) or even a predictive (Nijhawan 1994) character.

An explicit assumption of the theory put forward by Moutoussis & Zeki (1997*a*) is that visual awareness is directly and invariantly related to activity within identified cortical structures. A focal point of evidence that led to the proposal was the observation of asynchronous perceptual awareness. Here, we have shown that the perceptual asynchrony between colour and motion depends on the prevailing stimulus conditions, suggesting that differential levels of inhibition within relatively independent cortical structures might delay the integration of motion relative to colour.

The implications of this may surprise those who argue that visual experience requires the mediation of interpretive processes. The central motivation for proposals of this kind is the apparent need to resolve ambiguities in the time-course of neural activity. For instance, it has been argued that because image properties, such as luminance, contrast and speed, can have an impact on the time-course of neural activity (Bolz *et al.* 1982; Gawne *et al.* 1996; Carandini *et al.* 1997; Maunsell *et al.* 1999), it is necessary to impose a period of delay between neural activation and perceptual representation in which any temporal ambiguity can be resolved (Dennett & Kinsbourne 1992; Eagleman & Sejnowski 2000). By contrast, we have shown that stimulus conditions (the angular difference between presented directions of motion) that are intended to have specific neural consequences (differential levels of inhibition), also have direct perceptual consequences (differential degrees of temporal asynchrony). Thus, if a mechanism of some form exists that is supposed to correct for ambiguities of this kind, it appears to be surprisingly fallible.

The present findings suggest that direction-selective inhibition may have a causal role in the production of a perceptual asynchrony. However, they also suggest that an additional factor may be relevant. If an induced neural asynchrony were the sole cause of this phenomenon, the asynchrony might be expected to disappear once the contrasted directions of motion were sufficiently similar. By contrast, while reduced, a robust perceptual asynchrony was still evident in the presence of a relatively slight angular difference in direction of motion.

It is possible that the persistent asynchrony is a consequence of a general processing advantage for colour relative to motion (Moutoussis & Zeki 1997*a*,*b*; Bartels & Zeki 1998; Zeki & Bartels 1998). Alternatively, it has been argued that the asynchrony might be a consequence of activity within a neural system that is specialized for determining the temporal order of events (Johnston & Nishida 2001). This proposal poses some interesting philosophical questions and empirical challenges. As James (1890) observed, a succession of feelings is not a feeling of succession. Consideration of this is pertinent because, as discussed by Johnston & Nishida (2001), temporal order judgments of the form required here necessitate a sensation of succession. How then does this sensation arise?

Moutoussis & Zeki (1997*a*) have proposed that activity within individual cortical structures is sufficient to precipitate conscious perceptual experiences (Zeki & Bartels 1999). If the hypothesis is correct, the relative independence of cortical structures that seems to permit distinctive patterns of processing may also prompt qualitatively different sensations of succession. Instead of a specialized temporal coding system (Johnston & Nishida 2001), our temporal awareness would be mediated independently by multiple cortical structures. This possibility may prove to be a productive focus for further attempts to clarify the causes of the perceptual asynchrony between colour and motion. Certainly, this proposal does not explain how the multiple sensations of succession might be introspected and contrasted so that a temporal order judgment could be made. To do so seems to require self-awareness and, although at this point we do not know how this might arise, assuming a singular temporal processing system does not clarify the issue.

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