Synchronous and asynchronous perceptual bindings of colour and motion following identical stimulations

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ABSTRACT

When a moving surface alternates in colour and direction, perceptual couplings of colour and motion can differ from their physical correspondence. Periods of motion tend to be perceptually bound with physically delayed colours – a colour/motion perceptual asynchrony. This can be eliminated by motion transparency. Here we show that the colour/motion perceptual asynchrony is not invariably eliminated by motion transparency. Nor is it an inevitable consequence given a particular physical input. Instead, it can emerge when moving surfaces are perceived as alternating in direction, even if those surfaces seem transparent, and it is eliminated when surfaces are perceived as moving invariably. For a given observer either situation can result from exposure to a common input. Our findings suggest that neural events that promote the perception of motion reversals are causal of the colour/motion perceptual asynchrony. Moreover, they suggest that motion transparency and coherence can be signalled simultaneously by subpopulations of direction-selective neurons, with this conflict instantaneously resolved by a competitive winner-takes-all interaction, which can instantiate or eliminate colour/motion perceptual asynchrony.

1. Introduction

When a visual stimulus alternates in colour and motion direction, instances of motion can bind perceptually with physically delayed colours (by ~100 ms, see Moutoussis & Zeki, 1997a, 1997b). The magnitude of this perceptual asynchrony is not fixed, as it tends to scale with the magnitude of differences between successive motion directions (Arnold & Clifford, 2002; Bedell, Chung, Ogmen, & Patel, 2003). More striking still, the effect can be eliminated altogether in the presence of motion transparency (Clifford, Spehar, & Pearson, 2004; Moradi & Shimojo, 2004).

Motion transparency has been achieved in studies of colour/motion perceptual asynchrony by either rapidly alternating different fields of dots (Moradi & Shimojo, 2004), or by desynchronising direction reversals of individual elements within multi-element displays (Clifford et al., 2004). In the former case, the authors proposed that the colour/motion perceptual asynchrony was eliminated by transparency as perceptual bindings of colour and motion were skewed in strength toward early stages of motion analysis. Holcombe (2009) made a similar suggestion – that the colour/motion asynchrony arises because perceptual binding favours early instances of colour. Both accounts predict that the optimal conditions for perceptually binding colour and motion would be when alternations in colour and direction are physically

synchronous. Arnold (2005), however, showed that bindings could be identified more readily when colour changes are physically delayed relative to direction reversals. This suggests that neural analyses of motion are delayed relative to colour when the colour/motion perceptual asynchrony is experienced (also see Arnold, Clifford, & Wenderoth, 2001).

Clifford et al. (2004) attributed the advent of transparency to the continual presence of a common motion signal within spatio-temporally defined RFs. These authors further suggested that the characteristics of the relevant RFs were consistent with the response properties of cells in the human analogue of MT (Qian, Anderson, & Adelson, 1994a, 1994b). Specifically, these authors suggested that transparency would be promoted, and colour/motion perceptual asynchrony eliminated, when a persistent motion signal was present within spatial regions subtending ~2 degrees of visual angle (dva) at the retinae. This implies that motion transparency will be contingent on the physical properties of input.

To further investigate the importance of continual motion signals within defined spatial regions, we constructed a stimulus that had two groups of elements alternating between opposite directions in counter-phase. The most important feature of these stimuli was that the individual elements in the two groups of moving elements had a fixed minimal separation at points of motion reversal (see Fig. 1). We did this because in previous investigations moving elements promoting

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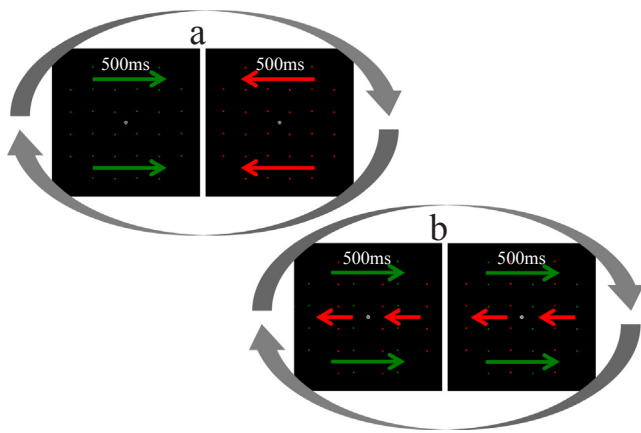
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Fig. 1. Depiction of an in phase stimulus presentation (a) and an anti phase stimulus presentation (b). In each type of presentation individual elements translate horizontally at a fixed linear speed, alternating in direction (left/right) and in colour (red/green) every 500 ms. For in phase presentations, all elements move in the same direction and are the same colour at any given time. For anti phase presentations, half the elements move left while others move right, and half the elements are red while other are green, and these statuses reverse every 500 ms. Here a colour/motion phasic relationship of 0 is depicted; so all dots moving left are red (and green right). Different subsets of dots are red in each half of the duty cycle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

transparency were either interspersed (Clifford et al., 2004; Moradi & Shimojo, 2004), or were separated by an average extent, but with some portions physically abutting (Clifford et al., 2004; also see Kanai, Paffen, Gerbino, & Verstraten, 2004). Having a fixed separation between counter-phased reversing elements will allow us to precisely control the size of spatial regions that contain a continual direction signal, allowing for a more precise estimate of the impact of this manipulation.

To preface our results, in Experiment 1 we find a lawful reduction of colour/motion perceptual asynchrony as the minimal separation of counter-phased moving elements is reduced at points of direction reversal. Asynchrony is greatest when elements are widely separated (3 dva), eliminated when elements abut, and intermediate for an intermediate separation (1.5 dva). We felt this last observation might be due to the stimulus sometimes being experienced as two invariant transparent surfaces, and sometimes as two changing surfaces. So we conducted Experiment 2 using the same stimuli, with participants reporting on both their perceptual bindings and on the appearance of motion signals (invariant 'streaming' or intermittently 'reversing'). Analyses of these data confirmed our suspicions, that a common physical input can sometimes elicit the impression of two surfaces moving persistently in opposite directions, which eliminates the colour/motion perceptual asynchrony, and sometimes as two surfaces which each intermittently reverse, which instigates the asynchrony.

2. Experiment 1 – Minimal element separations at points of direction reversal

2.1. Methods

2.1.1. Participants

Twenty participants (12 females, Mage = 21 years, SD = 5) volunteered to participate. These included the authors and 18 undergraduate psychology students, who were naïve as to the purpose of the experiment and were awarded course credit for participation. All participants reported having normal colour vision and normal, or corrected-to-normal, visual acuity. All participants provided informed consent to participate, and were free to withdraw from the study at any time without penalty. All experiments were granted ethical approval from the University of Queensland Ethics Committee, and were carried

out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.1.2. Apparatus

Stimuli were presented on a 20″ SyncMaster 1100p-Plus monitor, and generated by a Cambridge Research Systems ViSaGe stimulus generator driven by custom Matlab R2007b (The MathWorks, Natick, MA) software. The monitor had a resolution of 1024 × 768 pixels and a refresh rate of 120 Hz. Participants viewed stimuli binocularly in a quiet darkened room from a distance of 57 cm, with their head positioned in a chin rest.

2.1.3. Stimuli and design

Stimuli were comprised of a field of 100 moving coloured Gaussians, presented against a black background. Participants fixated a central black and white bull's-eye configuration, with a diameter subtending 0.44 dva. Each Gaussian had a diameter of 0.25 dva, a spatial constant of ~0.04 dva, and they translated linearly, left or right at a speed of 6 dva/s. Gaussians were coloured red (peak CIE 1931; x = 0.62, y = 0.34, Y = 18) or green (peak CIE 1931: x = 0.28, y = 0.62 Y = 18). Individual Gaussians cycled between being red and green, and between translating to left and right, according to a square-wave duty cycle, with a period of 1000 ms (see Fig. 1). Stimuli were seen through an invisible 20 dva circular aperture, which allowed between 30 and 35 individual Gaussians to be visible at any one time. The surrounding display was black. While peak red and green luminance values were equated, colour changes may have been associated with subjective brightness changes. We are unconcerned by this as a qualitatively similar perceptual asynchrony can be elicited by a stimulus that alternates in luminance contrast polarity relative to background (see Clifford et al., 2004).

Gaussian elements were putatively centered about the central fixation point, with each element vertically and horizontally separated, according to a 10 × 10 grid-like formation. All elements traversed 3 dva between direction reversals (see Fig. 1). In one condition (In-phase: see Figs. 1 and 2d and Supplemental Movie 1) all Gaussians moved in unison and had a uniform vertical and horizontal separation of 3 dva throughout the animation. In other conditions alternate Gaussians moved in anti phase (if the first was moving left, the next would be moving right, and vice versa; see Fig. 1). In these cases even numbered Gaussians within the putative grid formation were shifted down (by 0.44 dva), to ensure elements never overlapped.

In the *0 dva Anti-phase* condition (see Fig. 2a), even and odd numbered Gaussians abutted at the start of each direction cycle (vertically aligned), and were vertically and horizontally separated from the next pair of elements by 6 dva. Odd numbered elements initially moved left, and even numbered elements right, in each animation duty cycle, ensuring that even and odd numbered elements always abutted at points of direction reversal (see Fig. 2a and Supplemental Movie 2).

In the *1.5 dva Anti-phase* condition (see Fig. 2b and Supplemental Movie 3), even numbered Gaussians were positioned 1.5 dva right of odd numbered elements to the left, and 4.5 dva to the left of odd numbered elements to the right at the start of each animation duty cycle. As Odd numbered elements initially moved right, and even numbered elements left, in each animation duty cycle, this ensured that even and odd numbered elements were minimally horizontally separated by 1.5 dva at each point of direction reversal. In the *3 dva Anti-phase* condition (see Fig. 2c and Supplemental Movie 4), elements were arranged in a grid-like formation at the start of each duty cycle, vertically and horizontally separated by ~3 dva. This ensured that all elements were separated by ~3 dva at each point of direction reversal (see Fig. 2c).

Time shifts of direction relative to colour changes were manipulated during blocks of trials according to a method of constant stimuli. Direction reversals varied between being physically synchronous and being offset by up to 950 ms, in steps of 50 ms – resulting in 20 phasic