Motion transparency promotes synchronous perceptual binding

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Abstract

While identified regions of human extrastriate visual cortex are functionally specialized for processing different attributes of an object, the cognitive and neural mechanisms by which these attributes are dynamically bound into integrated percepts are still largely mysterious. Here, we report that perceptual organization influences the dynamics of binding. Specifically, the perception of motion transparency promotes the synchronous perceptual binding of colour and motion, which otherwise exhibits considerable asynchronies. In addition, we demonstrate that perceptual asynchrony can be reinstated by manipulating stereoscopic disparity or speed within the stimulus. Our findings suggest that the phenomenology of colour–motion binding parallels the known physiology of motion processing in area MT of primate visual cortex, supporting the view that the dynamics of perceptual binding is a direct reflection of the time course of the underlying neural processing.

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1. Introduction

Our visual system is continually interpreting a kaleidoscopic array of colours and forms in motion that we generally perceive in terms of unified objects. The architecture of human extrastriate visual cortex appears to be highly modular, in that different attributes of an object are analyzed by dedicated and anatomically distinct sub-systems (Zeki, 1993). Modularity creates a binding problem: attributes such as colour and motion are processed in different areas of the brain but must be associated with, or bound to, a common object. Intriguingly, the perceptual binding of colour and motion has consistently been found to be asynchronous, with colour appearing to be processed more rapidly than motion (Arnold, Clifford, & Wenderoth, 2001; Arnold & Clifford, 2002; Bedell, Chang, Ogmen, & Patel, 2003; Moutoussis & Zeki, 1997a, 1997b; Nishida & Johnston, 2002).

The interpretation of this finding remains controversial. For example, while some studies have sought to explain asynchronous binding of colour and motion on the basis of neural response latencies and temporal profiles (Arnold et al., 2001; Arnold & Clifford, 2002; Bedell et al., 2003; Moutoussis & Zeki, 1997a, 1997b; Zeki & Bartels, 1998), others have invoked a scheme of temporal markers in which representation of the timing of events is abstracted away from the precise timing of the underlying neural activity (Nishida & Johnston, 2002).

The temporal marker theory maintains that it is correspondence between representations of salient temporal features rather than differences in neural response latencies that underlies the asynchronous perception of visual attributes such as colour and motion (Nishida & Johnston, 2002). While acknowledging that there must generally be a strong correlation between the subjective time...
course of events as it appears to the observer and the times at which representations of those events are established in the observer’s brain. Nishida and Johnston argue that to equate these two time courses in the case of colour–motion asynchrony is not justified. Instead, they argue that perceptual asynchrony is introduced through the meta-analysis of salient temporal features by a neural mechanism dedicated to coding the timing of events. The view that the subjective time course of visual experience is the product of analysis beyond the temporal processing of the content of the events themselves has been influential in philosophical and psychophysical discussions of perceived timing. As Nishida and Johnston point out, their position is close to that taken by Dennett and Kinsbourne (1992) in the multiple drafts theory of subjective timing and Eagleman and Sejnowski (2000) in their postdictive theory of visual awareness.

Following the methods introduced by Moutoussis and Zeki (1997a), we investigated perceptual binding in stimuli alternating periodically in direction of motion (left–right) and either chromatic (red–green) or achromatic (black–white) colour. Both attributes alternated with the same period (500ms), but the relative phase of the two alternations was varied from trial to trial (Fig. 1A). We found that perceptual asynchrony is virtually eliminated under conditions of motion transparency, when two patterns appear to slide over one another in the same depth plane. Disrupting this percept by introducing conflicting stereoscopic disparity or speed cues reinstates the perceptual asynchrony. This pattern of data complements the known physiology of motion processing in area MT, suggesting that the dynamics of perceptual binding is a direct reflection of the time course of the underlying neural processing (Arnold et al., 2001; Arnold & Clifford, 2002; Bedell et al., 2003; Moutoussis & Zeki, 1997a, 1997b; Zeki & Bartels, 1998).

2. General methods

A total of four experiments were conducted. We first give details of general methods under the headings Subjects, Procedure and Stimulus and then describe variations from these employed in individual experiments.

2.1. Subjects

A total of five subjects were used across all experimental conditions. Subjects CC and JP were authors of the paper. Subjects SD, ER and WL were experienced psychophysical observers naive to the purposes of the study. In Experiments 1 and 3 there were four subjects: CC, JP, ER and WL. In Experiment 4 there were three subjects: CC, JP and SD. In Experiment 2 there were two subjects: CC and JP.

Fig. 1. Measuring perceptual asynchrony. (A) Space–time trajectory of a single dot alternating in direction of motion and contrast polarity with the same period (500ms), for three relative phases of contrast and direction changes. 0°: contrast and direction changes are physically synchronous, such that the dot is white when moving to the left and black when moving to the right. 90°: contrast and direction changes are one quarter of a cycle out of phase, such that the dot changes colour mid way between direction changes. 180°: contrast and direction changes are again physically synchronous, but now the dot is black when moving to the left and white when moving to the right. (B) Subjects were required to indicate the predominant perceptual pairing in a stimulus composed of 96 dots each following the same duty cycle. The proportion of trials on which white was paired with leftward motion at each of 30 relative phases of contrast and motion changes (four trials at each) is plotted for subject CC in two conditions. When all stimulus dots started at the same initial phase in the duty cycle (phase coherence = 1.0), perceptual pairing of white with leftwards motion at each of 30 relative phases of contrast and motion changes was centred on a phase of 92.4°, corresponding to a perceptual asynchrony of 128ms. This corresponds to a situation in which the white dots in a 90° stimulus would consistently be reported as moving to the left, even though the dots actually changed contrast mid way between direction changes. The direction of the asynchrony is such that, in a perceptually synchronous stimulus, the phase of the contrast changes lags the phase of the direction changes. Thus, it is as though contrast is perceived more rapidly than motion. (C) When each stimulus dot started at a random initial phase in the same duty cycle (phase coherence = 0.0), perceptual pairing was centred on a phase of 15.0°, corresponding to a perceptual asynchrony of only 21ms. This corresponds to a situation in which the white dots in a 0° stimulus would consistently be correctly reported as moving to the left.

2.2. Procedure

Subjects were required to indicate in a forced-choice judgment the predominant perceptual pairing of colour with direction of motion in a stimulus alternating periodically in direction of motion and colour. Both attributes alternated with the same period (500ms), but the relative phase of the two alternations was varied from trial to trial. In each condition, each subject performed four trials at each of 30 relative phases of contrast and
motion changes—a total of 120 trials per data point. Conditions within each experiment were interleaved in pseudo-random order.

To control for the possibility of more rapid processing of the attended attribute (Sternberg & Knoll, 1973), subjects answered different questions in separate runs of trials (e.g., “Which way is white going?”; “What colour is moving rightwards?”). These reports were then recoded so as to represent the proportion of times that white was paired with leftwards motion as a function of the relative phase of the colour and motion changes. If the pairing was veridical, this distribution would be centred on physical synchrony (0° 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 motion processing (Moutoussis & Zeki, 1997a), as illustrated in Fig. 1B and C. For each individual subject’s data, an estimate of the associated standard error was computed using non-parametric bootstrapping (Efron & Tibshirani, 1993).

2.3. Stimulus

The stimulus consisted of 96 dots alternating periodically in direction of motion (left–right) and either chromatic (red–green) or achromatic (black–white) colour. Both attributes alternated with the same period (500 ms), but the relative phase of the two alternations was varied from trial to trial. The stimulus subtended 10×10° of visual angle at the viewing distance of 55 cm. All dots moved at a speed of 16°/s, except in Experiment 4 where dot speed was manipulated as the independent variable. The background was a uniform grey of luminance 63 Cd m−2 and CIE chromaticity coordinates (0.28, 0.30). The dots (size: 0.14 × 0.14”) could either be black (0 Cd m−2) and white (126 Cd m−2) or red (luminance: 26 Cd m−2; chromaticity: 0.63, 0.34) and green (luminance: 26 Cd m−2; chromaticity: 0.28, 0.62). 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; 120 Hz refresh rate).

3. Experiment 1

Previous studies of the perceptual asynchrony of colour and motion (Moutoussis & Zeki, 1997a, 1997b) have used stimuli whose elements all change colour simultaneously (e.g., from black to white) and change direction of motion simultaneously (e.g., from left to right), producing perceptually salient temporal markers (Nishida & Johnston, 2002). If perceptual asynchrony is due to a characteristic difference in the latency of processing of these two attributes then it should be unaffected by randomizing the initial phase in the duty cycle of each stimulus element. Note that randomizing the phase relationship between elements can be achieved while leaving the within-element phase relationship of colour and motion the same across all elements (Fig. 2A).

3.1. Experiment 1: methods

Using dots as stimulus elements, we investigated two novel conditions in addition to the condition with no phase difference between elements (phase coherence = 1.0). In the first, all dots change in a given attribute at the same time, but half of the dots start at one phase in the duty cycle and half start at the opposite phase (phase coherence = 0.5). In the second, all dots start at a random phase in the duty cycle (phase coherence = 0.0). While for a phase coherence of 0.5 the synchronous temporal changes in the stimulus are still perceptually salient, for a phase coherence of zero the
changes are uniformly distributed across stimulus frames, effectively eliminating temporal markers. In these two conditions, both stimulus colours and both directions of motion are present at all times and the percept is one of motion transparency (Kanai, Paffen, Gernino, & Verstraten, 2004) such that dots moving in a given direction are perceptually grouped together, overriding the perception of individual dot trajectories alternating in direction of motion. To see example stimuli go to www.psych.usyd.edu.au/staff/colinc/HTML/transparency.htm.

For each of the three phase coherences we investigated two direction change conditions, 180° and 90°. In the 180° direction change condition, dots alternated between rightwards and leftwards motion. For the 90° direction change condition, absolute direction was randomized from trial to trial to avoid directional adaptation and subjects were told to base their reports on vertical and horizontal motion rather than left and right.

3.2. Experiment 1: results

For a phase coherence of 1.0, a robust perceptual asynchrony is observed that depends on the angular change in direction between alternating motions (Arnold & Clifford, 2002, Bedell et al., 2003). Data from four subjects shows that colour appears to lead motion by an average of 98 ± 19 ms for 180° direction changes and 46 ± 15 ms for 90° changes. A within-subjects analysis of variance of shows significant main effects of direction change condition (F₁ = 11.1; p = 0.04) and phase coherence (F₂ = 21.7; p = 0.002) as well as a significant interaction (F₂ = 13.7; p = 0.006). Post-hoc contrasts show that the main effects are entirely accounted for by the interaction, such that reducing phase coherence from 1.0 to 0.5 markedly reduces perceptual asynchrony and eliminates the difference between 180° and 90° direction change conditions (Fig. 2B). Note that the elimination of this difference cannot be due to a floor effect as there is no a priori reason why the perceptual asynchrony could not be negative (with motion appearing to lead colour). Reducing phase coherence further, to zero, had no significant effect on the pattern of results. Within-subject variability in measurements of asynchrony was also lower for phase coherences of 0.0 and 0.5 than 1.0 by an average of 49 ± 10% (t₁ = 3.14; p = 0.03), indicating increased reliability under the former stimulus conditions.

3.3. Experiment 1: discussion

These data are not consistent with a fixed difference in the latency of processing colour and motion or with the temporal marker account of perceptual asynchrony (Nishida & Johnston, 2002). However, the reduction in perceptual asynchrony does appear to correlate with the perception of motion transparency evident in the stimuli with phase coherences of 0.0 and 0.5. Even though each individual stimulus element alternates in direction of motion with a period of 500 ms, the percept is of two groups of dots sliding transparently across one another.

We investigated the apparent link between motion transparency and synchronous perceptual binding in three further experiments, enabling us to relate the phenomenology of colour–motion binding to the known neurophysiology of motion processing in the primate visual cortex. Stimuli with a phase coherence of 0.5 were used throughout.

4. Experiment 2

We divided the stimulus into strips parallel to the element motion (Fig. 3A). When the strips are wide, their alternating colour and direction of motion cause them to segment perceptually. When the strips are sufficiently narrow, however, the similar elements in non-adjacent strips group together and appear as transparent sheets of moving dots (van Doorn & Koenderink, 1982). Perceptual asynchrony decreases monotonically as strip width is reduced (Fig. 3B). This effect is observed for both black–white and red–green stimuli, demonstrating that the asynchrony is not an artifact of contrast polarity changes during motion (Anstis, 1970).

5. Experiment 3

We introduced stereoscopic disparity of ±0.4° between alternate strips (Fig. 3C) by viewing through a mirror stereoscope (which reduced luminance uniformly by 30%). When strip width is sufficiently narrow, the stimulus appears as two planes of dots separated in depth. However, perceptual asynchrony remains substantial even at the narrowest strip widths (Fig. 3D). This reinstatement of perceptual asynchrony with disparity is specific to disparity between strips. When dots from each strip are randomly allocated to one of two depth planes then transparent motion is perceived in both planes and the pattern of results is the same as in the previous experiment where all dots were coplanar.

6. Experiment 4

We varied the speeds of the two sets of dots in the original spatially homogeneous stimulus. When the speeds were similar, the stimulus appeared as two transparent sheets of dots, each sheet appearing to move in a constant direction. When speed differences were large, and at least one set of dots was moving relatively slowly
(8°/s or less), perceptual grouping by direction of motion gave way to grouping by speed and the stimulus was perceived as two sets of dots each alternating back and forth in direction. In these conditions, perceptual asynchrony tended to increase monotonically with the difference in speed between the two sets of dots, such that it was smallest when the dots were grouped perceptually on the basis of direction and largest when they were grouped by speed (Fig. 4). When the speed of both sets of dots was at least 16°/s the percept was consistently one of motion transparency and there was little or no perceptual asynchrony.

7. Discussion

The dependence of perceptual asynchrony on the angular difference between alternating directions of motion when phase coherence is 1.0 poses a problem for temporal marker accounts, since it is not clear why the position of a temporal marker signalling a given direction of motion should depend on the magnitude of the preceding direction change. Instead, it is consistent with a delayed response to motion following direction change due to direction-selective inhibitory mechanisms (Arnold & Clifford, 2002, Bedell et al., 2003). According to this account, the perceptual lag of motion relative to colour is greater for 180° than 90° direction changes because of opponent motion inhibition, as observed in area MT (Snowden, Treue, Erickson, & Andersen, 1991).

Under conditions of motion transparency, opponent inhibition attenuates the maintained response of MT neurons to their preferred direction (Qian & Andersen, 1994, Snowden et al., 1991). The response, although attenuated, is constant over time as long as the preferred direction of motion is present within the receptive field. There are no longer temporal alternations between responses to the two directions of motion. Thus, we would expect the reduction of phase coherence from 1.0 to 0.5 (and below) to eliminate delays in responding to the new direction of motion following a direction change and hence eliminate the apparent perceptual lag of motion relative to colour.

Phase coherence determines whether the stimuli used here appear as coherent or transparent. Stimuli of different phase coherence were constructed to be identical at the level of individual dots, so spatial pooling of similar motion signals is required to differentiate coherent from transparent motion. While neurons in V1 show little or no difference in their response to coherent versus transparent motion, marked response differences are evident in MT (Qian & Andersen, 1994; Snowden et al., 1991) where receptive fields are larger (Albright & Desimone, 1996).
Indeed, it is probably because both directions of motion occur within a single MT receptive field, but not within a single V1 receptive field, that the stimulus appears transparent (Qian & Andersen, 1994, Qian, Andersen, & Adelson, 1994a, Qian, Andersen, & Adelson, 1994b). Consequently, the spatial resolution necessary for accurate binding of colour and motion for individual dots in transparent motion has been lost by the time visual information reaches MT. Thus, if the mechanisms of motion transparency facilitate perceptual binding, the mechanism of this facilitation would appear to involve the feedback of information from MT to cortical areas with higher spatial resolution such as V1. Such feedback connections have been shown to exist anatomically (Shipp & Zeki, 1989), and have been proposed to be involved in perceptual binding (Hochstein & Ahissar, 2002) and in gating the contents of visual awareness (Pascual-Leone & Walsh, 2001).

When the stimulus is divided into strips, perceptual asynchrony decreases as the strips become narrower and perceptual segmentation gives way to the perception of motion transparency. If more than one strip falls within the receptive field of an MT neuron then that neuron will respond to the stimulus in essentially the same way as to transparent motion (Qian & Andersen, 1994; Snowden et al., 1991). In our experiment, the critical strip width is about 2°, roughly the receptive field size of a foveal MT neuron in the primate (Albright & Desimone, 1987).

When stereoscopic disparity is introduced between alternate strips, perceptual asynchrony is reinstated. Perceptually, the effect of adding stereoscopic disparity between strips is to introduce depth separation between the two surfaces, as distinct from the coplanar transparent surfaces seen in the absence of disparity. That transparency based on stereoscopic disparity and motion transparency should give such different results is surprising given that interactions between different motions have previously been found to be essentially independent of disparity differences (Watamaniuk & McKee, 1995). However, many MT neurons are selective for disparity as well as for motion (Bradley & Andersen, 1998; Bradley, Qian, & Andersen, 1995; Maunsell & Van Essen, 1983). A stimulus containing opposite directions
of motion in the same depth plane will elicit a maintained response from an MT neuron as long as the preferred direction of motion is present within the receptive field (Qian & Andersen, 1994; Snowden et al., 1991). When stereoscopic disparity differences are introduced between strips, the disparity tuning of MT neurons causes the direction of motion signalled by the neuronal sub-population selective for each disparity to alternate over time. Opponent inhibition between neurons tuned to similar disparities (Bradley et al., 1995, Bradley & Andersen, 1998) introduces delays in responding to the new direction of motion following a direction change, producing the apparent perceptual lag of motion relative to colour.

The effect of introducing a speed difference between the two sets of dots in a stimulus of phase coherence 0.5 can similarly be related to MT physiology. The responses of neurons in MT typically show selectivity for speed (Perrone & Thiele, 2001). Dots moving at similar speeds will stimulate overlapping populations of MT neurons while dots moving at very different speeds will not. Thus, introducing speed differences into the stimulus will introduce temporal alternations into the direction of motion represented by the sub-population of MT neurons responding to each speed. Opponent inhibition between these temporally alternating neuronal responses will produce a perceptual lag of motion relative to colour.

Previous psychophysical evidence has shown that there is a limited number of speed-tuned global motion channels in human vision, perhaps as few as two (Edwards, Badcock, & Smith, 1998). Our data are consistent with this observation. Speed differences between the two sets of dots failed to abolish the perception of transparency when both speeds were at least 16°/s, presumably because both sets of dots stimulated the same directional neurons tuned to a similar range of speeds. In this case, activity amongst these neurons would be maintained across alternations in direction of the dots and no perceptual asynchrony would be expected (Fig. 4B–D).

A novel form of perceptual transparency, temporal transparency, has recently been reported in the context of binding colour and orientation. When a stimulus alternates between orthogonal gratings of different colours at rates approaching 20 Hz, the two gratings appear transparently superposed (Holcombe, 2001; Holcombe & Cavanagh, 2001). When perceptual asynchrony between alternations in colour and orientation is measured, the results depend upon alternation frequency (Clifford, Arnold, & Pearson, 2003). It is only when stimulus alternation frequency is within the range of temporal transparency that binding of colour and orientation is essentially synchronous. At slower alternation rates (Clifford et al., 2003, Moutoussis & Zeki, 1997b), colour appears to lead orientation by 50–60 ms. Thus, it appears that the promotion of synchronous binding through transparency might generalize beyond motion transparency to include temporal transparency. Specifically, we suggest that synchronous perceptual binding is enhanced whenever rapid alternation between stimulus attributes gives rise to a maintained perceptual representation.

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