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Perceptual pairing of colour and motion

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Abstract

Observers often pair colours with earlier periods of motion. This observation has prompted the proposal that changes in colour are processed *faster* and perceived as occurring *before* physically coincident changes in direction—a brain-time account. Alternatively, it has been proposed that the sudden onset of a surface, or a direction reversal within a persistent surface, can trigger an analysis that determines the perceptual properties of the surface. Hypothetically, this analysis persists for some period of time and the consequences are perceived as having occurred when the analysis commenced—a post-dictive account. Hypotheses based upon these alternate accounts are contrasted in a series of experiments. It is shown that the optimal conditions for pairing specific combinations of colour and motion arise when colour changes are delayed relative to direction changes. In these conditions observers can pair more rapid oscillations of colour and motion and perceptual pairings are more systematic relative to when the changes in colour and direction are physically synchronous. It is also shown that, when pairing colour and motion, the sudden onset of a moving surface does not have the same consequences as a direction reversal within a persistent surface. These findings are consistent with the brain-time, but are inconsistent with the post-dictive, account of perceptual asynchrony.

When are changes perceived as having occurred? One perspective, which I will refer to as the brain-time theory of perception, suggests that the apparent timing of stimulus changes are related to when analyses are *concluded* within distinct and relatively independent regions of the brain (Bartels & Zeki, 1998; Zeki, 2002). Alternatively, it has been suggested that stimulus changes might be perceived as having occurred at the point in time at which an analysis *commenced*. This form of analysis has been described as post-dictive because perceptual experience is supposedly delayed so that the visual system can take into account information that becomes available after an event has occurred before committing to a visual interpretation of the past event (Eagleman & Sejnowski,

2000; Moradi & Shimojo, 2004; Rao, Eagleman, & Sejnowski, 2001).

A recent series of psychophysical experiments seemed to provide evidence in favour of the brain time theory of perception (Moutoussis & Zeki, 1997a, 1997b). In these experiments, observers were exposed to stimuli that contained combinations of two attributes that each oscillated at the same rate between different states, such as colour (red/green) and direction of motion (up/down). The relative timing of the oscillations was manipulated and observers were required to indicate the predominant perceptual pairings. It was found that observers were most likely to pair colours and motions when the changes in direction *preceded* the changes in colour (Moutoussis & Zeki, 1997a, 1997b). This is consistent with the proposal that the brain takes longer to process changes in direction as opposed to changes in colour and that

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this influences *when* the different changes are perceived as having occurred—the brain time theory of perception (Bartels & Zeki, 1998; Zeki, 2002).

More recently it has been suggested that the apparent perceptual asynchrony between colour and motion occurs because of a post-dictive analysis (Moradi & Shimojo, 2004). According to this interpretation when a new surface appears, or when a persistent surface reverses direction at rates of less than ∼8 Hz, an analysis of the surface's properties is triggered—including colour (Moradi & Shimojo, 2004). This analysis persists for some period of time, but it is assumed that the consequences of the analysis are experienced as having occurred at the point in time at which the analysis commenced. During the analysis, the colour of the surface could change—say from red to green. The analysis would then encompass a brief instance of red and a more prolonged instance of green. As a consequence, the perceived colour of the new surface would be green—thereby inappropriately pairing a later colour state with an earlier period of motion (Moradi & Shimojo, 2004). The potential for inappropriate perceptual pairing created by this theoretical process is exacerbated by the assumption that colour is not treated uniformly during the period of analysis. Instead, it is assumed that the perceptual outcome is biased in favour of the later periods of the analysis (Moradi & Shimojo, 2004; see Fig. 1 for a graphical description).

It is not clear how the post-dictive proposal described above might account for some existing data. For instance, an apparent perceptual asynchrony between colour and motion can be observed when the two attributes are spatially separated (Moutoussis & Zeki, 1997b). In one study, the stimulus was split into two halves. Colour oscillations were shown to one side of a central fixation point and motion oscillations appeared on the other. In this study, as in earlier experiments when the two attributes were spatially superimposed (Moutoussis & Zeki, 1997a), observers paired motions with physically *lagging* colours.

The post-dictive account of perceptual asynchrony presumes that the phenomenon arises because the sudden onset of a moving surface, or a reversal in direction, triggers an analysis of the surface's properties—including colour (Moradi & Shimojo, 2004). This proposal seems reasonable in that we might expect the sudden onset of a surface to trigger an analysis of that surface's properties. However, the observation that a perceptual asynchrony can be observed when the two attributes are spatially separated may seem problematic. In this context, a reversal in the direction of one surface would have to trigger an analysis of a different surface. While this proposition may seem improbable, perhaps an interaction between the two surfaces is facilitated by spatial proximity or by the fact that the observer must simultaneously monitor both surfaces.
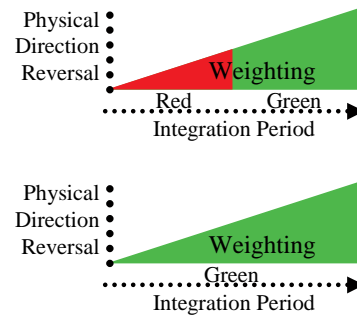

Fig. 1. Schematics depicting the theoretical post-diction and temporal averaging account of colour/motion perceptual asynchrony. It is assumed that physical direction reversals (depicted as vertical dotted lines), or the sudden appearance of a moving surface, can trigger a process of temporal averaging that determines the apparent colour of the moving surface. This account is post-dictive as it is also assumed that the colour determined during this process is experienced as having persisted from when the analysis commenced. It is further assumed that colour is not treated equally during the period of analysis. Instead, the outcome of the analysis is biased in favour of the colour present during the later stages of analysis. Because of this, the apparent colour of the moving surfaces determined by the processes depicted above and below will be green—even though the surface depicted above is red during the first half of the analysis. Note that while a process of this form could cause inappropriate perceptual pairings of colour and motion, according to this perspective pairing should be veridical when a single colour persists throughout the period of analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

The post-dictive account of perceptual asynchrony between colour and motion depends upon post-dictive analyses being triggered by the sudden appearance of a moving surface or by direction reversals (at rates less than ∼8 Hz) within a persistent surface (Moradi & Shimojo, 2004). Accordingly, the sudden appearance of a moving surface and direction reversals within a persistent surface should have similar consequences—both events should bias observers to pair colour with later instances of motion.

Other evidence, consistent with the brain time theory of perception (Bartels & Zeki, 1998; Zeki, 2002), suggests that direction reversals and the sudden onset of a new surface should have quite different consequences. Both Arnold and Clifford (2002) and Bedell, Chung, Ogmen, and Patel (2003) have shown that the magnitude of the perceptual asynchrony between colour and motion varies as a function of the angular difference between the contrasted directions. The asynchrony is greatest if opposite directions are contrasted and decreases as the angular difference between the oscillating directions is reduced (Arnold, Clifford, & Wenderoth, 2001; Bedell et al., 2003). These findings suggest that an opponent direction can transiently suppress neural responses to, and therefore the perceptual experience of, subsequent motions. According to this perspective, the sudden onset

of a new surface and reversals of direction within a persistent surface should have quite different consequences. The latter situation should impose a perceptual delay of successive motions. In the former situation, however, no transient suppression of motion would be expected. According to this perspective an additional prediction could also be posed—intermittent motions interspersed by periods of opponent motion should be paired with later motions that are interspersed by blank periods.

The post-dictive (Moradi & Shimojo, 2004) and brain time (Arnold et al., 2001; Bartels & Zeki, 1998; Bedell et al., 2003; Zeki, 2002) accounts of perceptual asynchrony make different predictions concerning the consequences of the sudden onset of a new surface and reversals of direction within a persistent surface. However, this is not the only point where the two accounts provide competing hypotheses. According to the post-dictive account, perceptual pairing of colours and motions should be most accurate when the period of post-dictive analysis encompasses just one colour (see Fig. 1). If the period of analysis is initiated by a direction reversal, this should occur when changes in colour and direction are physically synchronous. In contrast, according to the brain time account this situation should be sub-optimal as observers will perceive colour changes *before* they perceive changes in direction. Instead, perceptual pairing of colour and motion should be optimal (in that a specific colour should be most systematically paired with a specific direction) when changes in colour *lag* changes in direction by ∼100 ms.

The competing hypotheses, based upon the brain time and post-dictive accounts of perceptual asynchrony, that have been described above are contrasted in the following series of experiments. The following hypotheses will be tested:

According to the post-dictive account. (a) Perceptual pairing of colour and motion should be optimal when changes in colour and direction are physically synchronous (Experiments 1 and 3). (b) Perceptual pairing of colours with intermittent motion should be consistent whether the intermittent motion is interspersed by blank periods or by periods of opponent motion (Experiment 2).

According to the brain time account. (a) Perceptual pairing of colour and motion should be optimal when changes in colour *lag* changes in direction by ∼100 ms (Experiments 1 and 3). (b) Intermittent motion should be paired with relatively later colours when the intermittent motion is interspersed by periods of opponent motion rather than by blank intervals (Experiment 2). (c) Intermittent motions interspersed by periods of opponent motion should be paired with relatively later motions that are interspersed by blank periods (Experiment 2).

1. Methods

1.1. General methods

All stimuli were displayed on a 19″ Sony Trinitron Multiscan 500PS monitor with a refresh rate of 100 Hz driven by a VSG 2/5 (Cambridge Research Systems). Stimuli in Experiments 1 and 2 consisted of groups of four luminance-modulated gratings. The width and height of the individual gratings subtended 1.88° of visual angle and were centred 1.88° above or below and 1.88° to the left or right of a central fixation point. The stimulus used in Experiment 3 consisted of a single luminance-modulated grating with a width and height of 7.52° that was centred upon a central fixation point. All gratings contained drifting motion (10 deg/s).

2. Experiment 1

The first experiment is essentially a replication of earlier experiments (Arnold & Clifford, 2002; Bedell et al., 2003; Clifford, Spehar, & Pearson, 2004; Moutoussis & Zeki, 1997a, 1997b). This will provide a behavioural measure to which later experimental conditions can be contrasted and permit an exploration of the relative timing between colour and motion changes that is optimal for pairing specific combinations of colour and motion.

2.1. Methods

Four observers participated in Experiment 1, the author and three observers who were naïve as to the purposes of the study. All observers had normal, or corrected to normal, visual acuity and colour vision. Observers viewed stimuli binocularly, in darkened conditions, from 57 cm while their head was placed in a headrest.

The observers viewed groups of four vertical sinusoidal luminance-modulated gratings (spatial frequency 1cpd) that oscillated between different colour and motion states (i.e., red/green and left/rightward drift). As depicted in Fig. 2, the relative timing of the oscillations was manipulated. Two observers were required to indicate if leftward motion was always paired with red, whereas the other observers indicated if red was always paired with leftwards motion. Having half the observers respond to one question, and then reversing the question for the other observers, helped to ensure that the results of the experiment would not be influenced by any systematic tendency to monitor one stimulus attribute before switching to attend to the alternate attribute—a strategy that could bias temporal judgments (Clifford, Arnold, & Pearson, 2003; Enns & Oriet, 2004).

The perceptual tasks used in this experiment differ from tasks used previously in similar experiments (Arnold et al., 2001; Bedell et al., 2003; Clifford et al.,
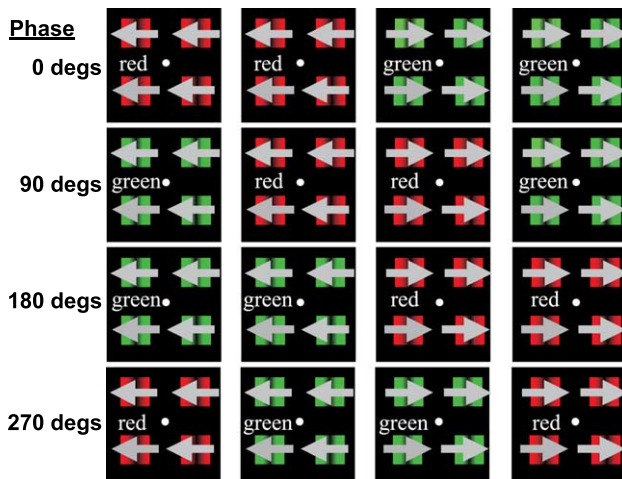
Fig. 2. Schematic depicting some of the phasic relationships between colour and motion oscillations sampled during Experiment 1. Each row depicts a full stimulus cycle (800 ms, so each square depicts 200 ms) that could be shown during a stimulus presentation. The relationship between colour and motion was manipulated by delaying colour changes relative to direction changes. At a phasic relationship of 0°, colour is not delayed and red is always paired with leftward motion. At a phasic relationship of 180°, colour changes are delayed by 400 ms so leftward motion is never paired with red. At phasic relationships of 90° and 270°, colour changes are delayed by 200 and 600 ms, respectively, so leftward motion is paired for equal periods of time with green and then red (90°) or with red and then green (270°). During a trial, the stimulus cycle persisted until the observer indicated if they thought that red was always paired with the colour red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

2003; Moutoussis & Zeki, 1997a, 1997b). In these experiments, observers were required to indicate a predominant perceptual pairing—i.e., while the stimulus is green in which direction is it moving? In comparison, the judgment used here has a considerable advantage—it is relatively easy. If a given direction of motion is seen to be first red and then green, the observer does not have to make a difficult decision as to which of the two colours the movement was paired with for longer. In this situation it would be apparent that the movement had not always been paired with either colour.

During each trial, the stimulus alternated between drifting towards the left and right (10 deg/s) and between being red-black (peak red CIE 1931; $X = 0.60$, $Y = 0.34$, $Z = 14.5$) and green-black (peak green CIE 1931; $X = 0.28$, $Y = 0.595$, $Z = 14.5$). The period of the oscillations between different colours and different motions was 0.8 s. As depicted in Fig. 2, during a run of trials the relative phase of the oscillations was manipulated. At a phasic relationship of 0°, leftward motions were always paired with red and rightward motions with green. This situation was reversed at a phasic relationship of 180°. At a phasic relationship of 90°, leftward motions were paired (for equal durations) first with green and then with red. This situation was reversed at a phasic relationship of 270°.

During a run of trials, 10 phasic relationships were each sampled on 8 occasions—so each observer saw 80 individual trials. Each stimulus presentation commenced at a random point within the stimulus cycle and persisted until the observer indicated a response. During each trial, the observer indicated if they felt that leftward motion was always paired with red by pressing one of two response levers. A run of trials therefore provided a distribution of perceived coincidence between leftward motion and the red colour state as a function of the physical coincidence between the two attributes. Centroids, a measure of central tendency, were fitted to these distributions to provide estimates of perceptual coincidence between colour and motion. Each observer completed a single run of trials providing four estimates of perceptual coincidence.
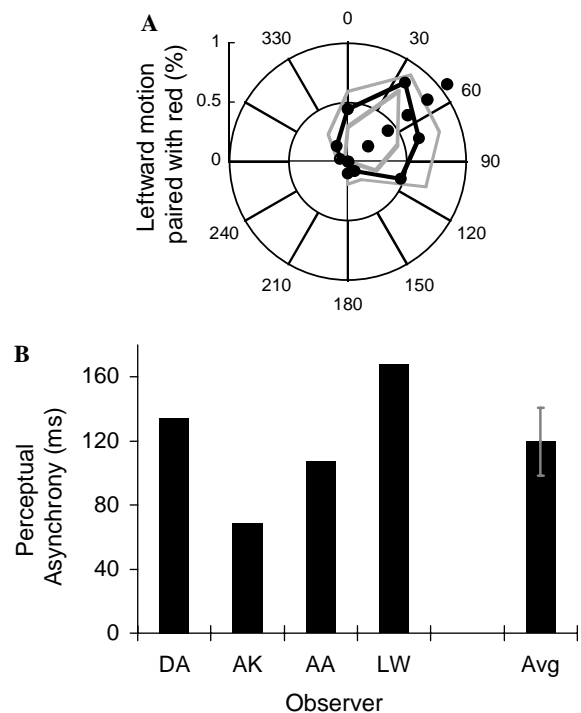

Fig. 3. (A) Polar plot depicting the average percentage of times that observers reported that leftward motion was always paired with red as a function of the physical relationship between the two attributes (bold black line). Each data point (black circles) shows the average performance during four trial runs completed by different observers. Grey lines show ±1 standard error between performances at each phasic relationship during different trial runs. A centroid (dotted black line) is fitted to the distribution to provide an estimate of the phasic relationship at which red and leftward motions were perceptually coincident. In this case the centroid is rotated by ~51.75°, indicating that the two attributes appeared coincident when changes in colour lagged changes in direction by ~115 ms. This differs from the average estimate that is reported in the results as statistical analysis was based upon multiple estimates determined during trial runs completed by each observer. (B) Bar graph showing estimates of perceptual coincidence between colour and motion for four observers. The average of the four estimates is also shown. The error bar shows ±1 standard error between the four estimates.

2.2. Results

As depicted in Fig. 3B, analysis of the four estimates of central tendency suggest that colours were perceived as being coincident with motions when changes in colour *lagged* changes in direction by 120 ± 21 ms ($t_3 = 5.681$, $p = 0.011$). Task performance was also more systematic when colour changes lagged changes in direction. Fig. 3A depicts the average responses of all observers as a function of the relative timing between changes in colour and direction. When changes in colour and direction were physically synchronous (a phasic relationship of 0°) observers reported that leftward motion was coincident with red on just 44% of trials. This performance does not differ significantly from chance ($t_3 = 0.40$, $p = 0.716$). In contrast, observers systematically reported that leftward motion was coincident with red when the changes in colour lagged changes in direction by 80 ms (on 82% of occasions, $t_3 = 3.94$, $p = 0.03$).

2.3. Discussion

The results of Experiment 1 are consistent with many previous studies that have shown that colours and motions can appear to be coincident when changes in colour physically *lag* changes in direction (Adams & Mamassian, 2004; Arnold et al., 2001; Aymoz & Viviani, 2004; Bedell et al., 2003; Clifford et al., 2003; Moutoussis & Zeki, 1997a, 1997b; Nishida & Johnston, 2002; Paul & Schyns, 2003).

The results of Experiment 1 also show that the optimal conditions for pairing specific combinations of colour and motion arise when colour changes *lag* direction changes as opposed to when the changes are physically synchronous. This observation is consistent with the brain time account of perceptual asynchrony, but seems to be inconsistent with the post-dictive.

The brain time and post-dictive accounts of perceptual asynchrony also provide competing hypotheses concerning the consequences of direction reversals and the sudden onset of a new surface. These shall be tested in Experiment 2.

3. Experiment 2

3.1. Methods

The same observers who had participated in Experiment 1 also participated in Experiment 2.

The stimulus configuration used in Experiment 2 was similar to that used in Experiment 1. Two of the four gratings within the stimulus, the standard gratings, were horizontal, achromatic and contained intermittent upward motions. The intermittent upward motions appeared at a frequency of 1.2 Hz and persisted for 400 ms. The upward motions could be interspersed by
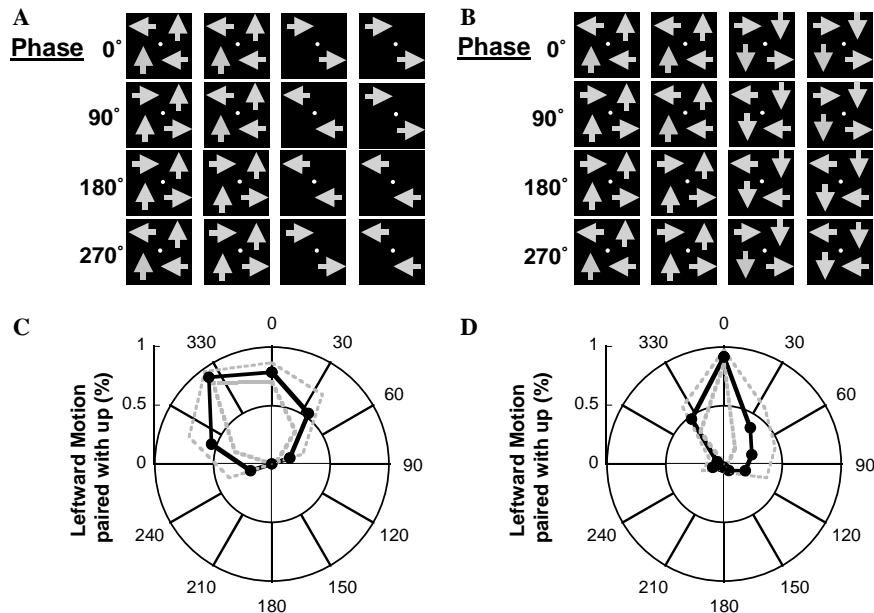

Fig. 4. (A,B) Schematics depicting some of the relationships between comparison left/right oscillations and standard intermittent upward motions interspersed by blank periods (A) or by periods of movement in the opposite direction (B). Details concerning these schematics are similar to that shown and described in Fig. 2, however here left/right direction changes are delayed relative to the appearance of upward motion. Phasic relationships of 0°, 90°, 180°, and 270° are depicted. (C,D) Polar plots depicting the average percentage of times that observers reported that upward motions interspersed by blank intervals (C) or by periods of opponent motion (D) were always paired with leftward motions as a function of the physical relationship between the two directions. Specific details concerning these plots are similar to those relating to Fig. 3A.
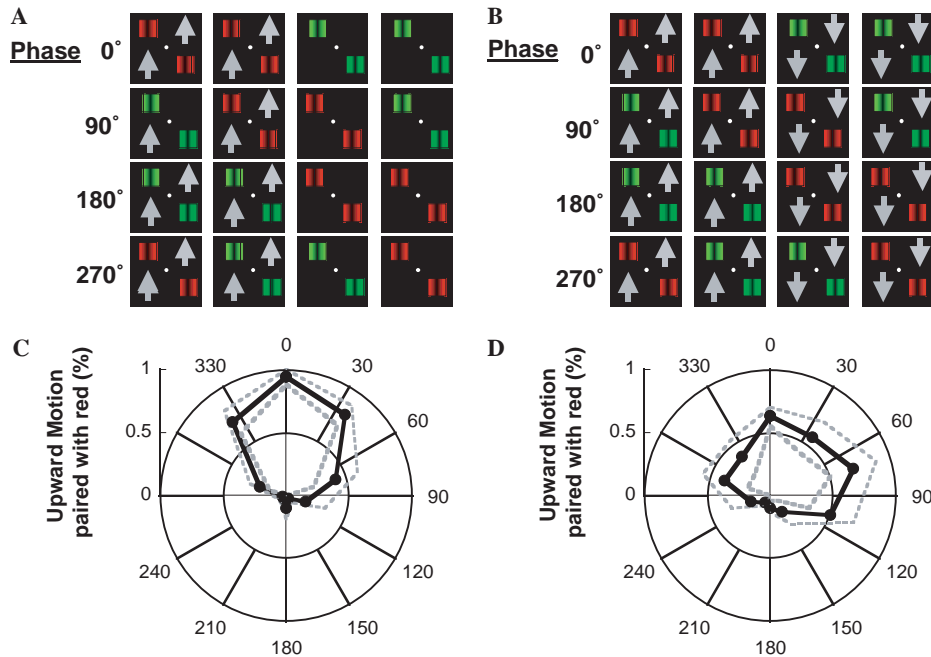
Fig. 5. (A,B) Schematic depicting some of the relationships between comparison red/green oscillations and standard intermittent upward motions interspersed by blank periods (A) or by periods of movement in the opposite direction (B). Details concerning these schematics are similar to those depicted and described in Fig. 2. Phasic relationships of 0°, 90°, 180° and 270° are depicted. (C,D) Polar plots depicting the average percentage of times that observers reported that upward motions interspersed by blank intervals (C) or by periods of opponent motion (D) were always paired with red as a function of the physical relationship between the two attributes. Specific details concerning these plots are similar to those relating to Fig. 3A. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this paper.)

periods of downward motion (up/down oscillations—Figs. 4B and 5B) or by blank intervals during which the grating would disappear (intermittent upward motion—Figs. 4A and 5A). The positions of these standard gratings were determined at random on a trial-by-trial basis.

The other gratings within the stimulus, the comparison gratings, were vertical and contained either oscillations in colour (red/green oscillations—Figs. 5A and B) or direction of motion (left/right oscillations—Figs. 4A and B). These oscillations had a period of 0.8 s. During a run of trials, only one type of standard stimulus was presented (either intermittent upward motions or up/down oscillations) and one type of comparison stimulus (left/right oscillations or red/green oscillations). The comparison gratings that contained colour oscillations also contained persistent leftward drift.

If the comparison gratings contained left/right oscillations, half of the observers were required to indicate if upward motion was always paired with leftward motion whereas the other observers were instructed to indicate if leftward motion was always paired with upward motion (Figs. 4A and B). If the comparison gratings contained red/green oscillations, half the observers were required to indicate if upward motion was always paired with red whereas the other observers were required to respond to the reversed question (Figs. 5A and B). Each stimulus presentation commenced at a random point

within the stimulus cycle and persisted until the observer indicated a response by pressing one of two response levers.

As depicted in Figs. 4 and 5, the relative timing of the oscillations within the standard and comparison gratings was manipulated. The details of these manipulations are similar to the manipulation used in the first experiment and they produced distributions of perceived coincidence between upward motions within the standard gratings and either leftward motions or red-black colour states within the comparison gratings. Centroids were fitted to these distributions to provide estimates of perceived coincidence. Each observer completed four runs of trials. This provided four estimates of perceived coincidence between each of: intermittent upward motions and leftward motions within left/right oscillations (Fig. 4A), upward motions within up/down oscillations and leftward motions within left/right oscillations (Fig. 4B), intermittent upward motions and instances of red-black within red/green oscillations (Fig. 5A), and upward motions within up/down oscillations and intermittent instances of red-black within red/green oscillations (Fig. 5B).

3.2. Results

Fig. 6 shows the average temporal offsets at which upward motions were perceived as being coincident with
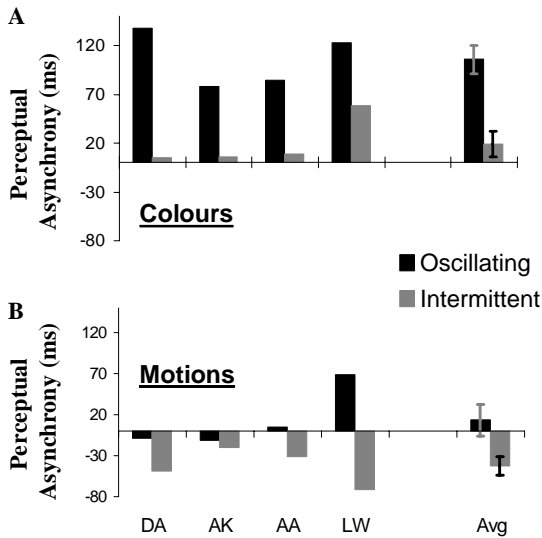
Fig. 6. (A) Bar graph depicting the temporal relationships at which leftward motions within left/right oscillations were perceptually coincident with upward motions interspersed by either periods of downwards motion (oscillating, shown in black) or blank intervals (intermittent, shown in grey). (B) Bar graph depicting the temporal relationships at which intervals of red-black within red-black/green-black oscillations were perceptually coincident with upward motions either interspersed by periods of downward motion (oscillating, shown in black) or by blank intervals (intermittent, shown in grey). (A,B) Both graphs depict four individual estimates for each combination of standard and comparison stimulus. In addition, the average of each set of four estimates is shown. Error bars show ±1 standard error between four estimates.

spatially offset instances of red-black (Fig. 6A) or with spatially offset leftward motions (Fig. 6B).

Upward motions within up/down oscillations were paired with later (~106 ms) instances of red-black within red/green oscillations (configuration Fig. 5B, results Fig. 5B, $t_3 = 7.315$, $p = 0.005$). However, intermittent upward motions were paired with physically synchronous instances of red (configuration Fig. 5A, results Fig. 6A, $t_3 = 1.495$, $p = 0.232$).

Upward motions within up/down oscillations were paired with physically synchronous leftward motions within left/right oscillations (configuration Fig. 4B, results Fig. 6B; $t_3 = 0.7$, $p = 0.534$). However, intermittent upward motions were paired with preceding (~43 ms) leftward motions within left/right oscillations ($t_3 = 3.846$, $p = 0.031$).

3.3. Discussion

Consistent with previous observations (Moutoussis & Zeki, 1997b), the results of Experiment 2 show that observers pair motions within oscillations between opponent directions with later colours within spatially offset colour oscillations. However, intermittent motions interspersed by blank intervals are paired with physically synchronous colours. Therefore, the intermittent sud-

den onset of a moving surface promotes veridical pairing of colour and motion whereas direction reversals within a persistent moving surface biases observers to pair motions with later colours.

Again, consistent with previous observations (Moutoussis & Zeki, 1997a), the results of Experiment 2 show that pairing of intermittent and spatially offset motions is veridical when both motions are interspersed with periods of motion in the opposite direction. However, when an intermittent motion is interspersed by blank intervals, it is paired with earlier motions that are interspersed with periods of opponent motion.

The results of Experiment 2 clearly demonstrate that, when pairing colours and motions, reversals in direction have very different consequences to the intermittent sudden onset of a moving surface. Reversals in direction prompt observers to pair motions with later colours, but the intermittent onset of a moving surface does not. These observations are not consistent with the premise that the perceptual asynchrony between colour and motion is caused by some form of post-dictive analysis triggered by either the sudden onset of a moving surface or by direction reversals within a persistent surface (Moradi & Shimojo, 2004).

In light of this evidence it could be claimed that, while direction reversals trigger post-dictive analyses of other attended or proximate surfaces, the intermittent appearance of a moving surface does not.[1] Some pertinent questions would then arise—why is the sudden appearance of a moving surface an unreliable trigger of post-dictive analyses (for an example where the sudden appearance of a moving surface hypothetically triggers a post-dictive analysis, see Experiment 5 in Moradi & Shimojo, 2004) and when could we *predict* that a post-dictive analysis would occur. It does not seem satisfactory to infer the presence or absence of post-dictive analyses by the presence or absence of perceptual synchrony. In contrast, the brain-time account of perceptual asynchrony *predicts* that perceptual pairing will be similarly influenced whenever processing time is influenced.

The results of Experiment 2 are consistent with the suggestion that changing processing time can influence perceptual pairing. The suggestion is that neural responses to, and therefore perceptual experience of, motion can be transiently delayed by exposure to earlier periods of movement in the opposite direction (Arnold & Clifford, 2002; Bedell et al., 2003). Not only did observers pair intermittent motions with delayed colours when the intermittent motion was interspersed by periods of opponent motion, they also paired intermittent motions interspersed by periods of opponent motion

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[1] I am indebted to Farshad Moradi for this suggestion.

with delayed motions interspersed by blank intervals—a motion/motion perceptual asynchrony.

It is possible that observers may treat the intermittent appearance of a moving surface as an intermittent appearance of luminance-contrast. If there were little difference between detecting changes in luminance or chromatic contrasts, the veridical pairing of intermittent motions and colours would be anticipated. However, intermittent motions and colours are not interchangeable. In Experiments 1 and 2, observers paired oscillating motions with colours that were delayed by ~100 ms. In Experiment 2, observers paired intermittent motions with oscillating motions that were delayed by ~42 ms. This seems to suggest that the dynamics of perceptual pairing depend upon the specific combinations of attributes that are being contrasted.

Another implication of the results of Experiment 2 is that presenting colour changes after changes in direction should facilitate the perceptual pairing of colour and motion. The results of Experiment 1 have already shown that this is true when colours and motions oscillate at a fixed frequency (1.25 Hz). Another way to test this proposition is to determine the maximal rates at which observers can pair instances of colour and motion. This issue will be assessed in Experiment 3.

4. Experiment 3

4.1. Methods

Five observers participated in Experiment 3, the first author and four observers who were naïve as to the purpose of the study. All observers had normal, or corrected to normal, visual acuity and colour vision.

Observers viewed a vertical sinusoidal luminance-modulated grating (spatial frequency 1cpd) that oscillated between different colour and motion states (i.e., red-black/green-black and left/rightward drift). During each individual trial, the oscillations in colour and direction could be physically synchronous or made perceptually synchronous by introducing a lag between the direction reversals and colour changes (120 ms—the average perceptual asynchrony estimated in Experiment 1). The colour red could be coupled with leftward or rightward motion, determined at random on a trial-by-trial basis. During a run of trials the period of the oscillations was manipulated according to the method of constant stimuli (200, 400, 600, 800 or 1000 ms corresponding to frequencies of 5, 2.5, 1.67, 1.25 or 1 Hz). A run of trials consisted of the presentation of each of the 5 different periods on 15 occasions for both physically and perceptually synchronous stimuli (150 individual trials). Each stimulus presentation commenced at a random point within the stimulus cycle and observers were required to indicate with which direction the colour red was
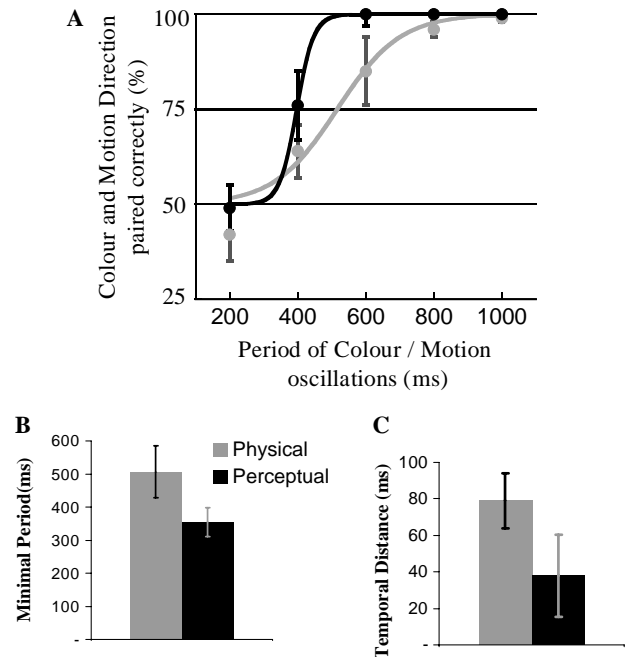

Fig. 7. (A) Psychometric functions fitted to the averaged data for all observers for each style of stimulus presentation. Error bars show ±1 standard error between the 5 individual estimates that contribute to each data point. The fitted functions are provided primarily for illustrative purposes as the statistical analysis was based upon estimates determined from single trial runs for each observer. (B) Bar graph depicting the average minimal period at which observers could accurately pair colour and motion when changes in colour and motion were either physically (grey) or perceptually (black) synchronous. Error bars show ±1 standard error between the five individual estimates of the minimal period. (C) Bar graph depicting the average temporal distance between the 75% and 87.5% points on psychometric functions calculated from trial runs in which colour and motion changes were either physically (grey) or perceptually (black) synchronous. This measure provides an estimate of task difficulty. Error bars show ±1 standard error between five individual estimates.

paired. The trial persisted until the observer indicated a response by pressing one of two response levers.

Each observer completed a single run of trials—producing a distribution showing the percentage of trials, for each style of stimulus presentation, in which observers correctly paired the colour red with the appropriate direction of motion.[2] Psychometric functions, like those depicted below in Fig. 7A, were fitted to distributions determined for each observer during a single run of trials. The 75% points of the functions were taken as estimates of the minimal period at which observers could accurately pair colour and motion. Distances between

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[2] Note that when colour changes lagged direction changes by 120 ms and the period of the oscillations was 200 ms, red was arbitrarily considered as being *correctly* paired with the direction with which it was paired for just 80 ms as opposed to the colour with which it was paired with for 120 ms. In all other circumstances red was paired predominantly with a specific direction and this pairing was taken as being *correct*.

the 75% and 87.5% points were taken as estimates of task difficulty.

4.2. Results

As depicted in Fig. 7B, observers could pair colour and motion at more rapid rates of alternation when colour changes *lagged* changes in direction as opposed to when the changes were physically synchronous (periods of $\sim 355 \pm 44$ ms and $\sim 507 \pm 79$ ms, corresponding to oscillation rates of 2.82 as opposed to 1.97 Hz; $t_4 = 2.945$, $p = 0.042$). As depicted in Fig. 7C, observers also found that the pairing task was easier when colour changes *lagged* changes in direction as opposed to when the changes were physically synchronous ($t_4 = 2.789$, $p = 0.049$).

4.3. Discussion

The results of Experiment 3 are consistent with the results of Experiment 1, in that both sets of results demonstrate that delaying colour changes relative to changes in direction can facilitate perceptual pairing of colour and motion. While this observation is consistent with the brain-time account of perceptual asynchrony, they appear to be inconsistent with the post-dictive account.

One suggestion that could resolve the apparent discrepancy between the post-dictive account and the results of Experiments 1 and 3 is that there might be a delay between detection of the triggering event and the period of post-dictive analysis that follows. For instance, a post-dictive analysis might be triggered by the detection of a direction reversal within a motion processing structure (like V5) but the post-dictive analysis within a colour processing structure (perhaps V4) may not begin until sometime later.[3]

This suggestion differs from earlier post-dictive hypotheses (Eagleman & Sejnowski, 2000; Rao et al., 2001). One of the major computational advantages of the initial suggestions was that time consuming neural analyses would have little or no impact upon timing judgments. In contrast, the proposal outlined above suggests that systematic temporal errors would occur as a direct consequence of a time consuming neural process—the delay between a direction reversal being detected and the beginning of a post-dictive analysis. This proposal therefore appears to lack the functional advantages of earlier post-dictive hypotheses (Eagleman & Sejnowski, 2000; Rao et al., 2001) and seems to diminish the differences between this and the brain time account.

It should be noted that in Experiment 3, observers were only able to successfully pair colours and motions at fairly slow rates of oscillation: 2.82 Hz if colour changes lagged changes in direction and 1.97 Hz if the changes were coincident.[4] This performance contrasts with the performance of observers in a similar task where observers were able to pair colours and motions at rates of up to 8.33 Hz (Moradi & Shimojo, 2004). This discrepancy is probably due to the specifics of the stimuli used in the different studies.

The stimuli used in Experiment 3 consisted of sinusoidal luminance-modulated gratings that periodically appeared to change both in colour and direction of drift. In contrast, the stimuli used by Moradi and Shimojo (2004) consisted of multiple, temporally interleaved fields of differently coloured dots moving in different directions. At very rapid rates of oscillation (~ 8.33 Hz) this stimulus did not appear to periodically change direction but rather to consist of two persistent surfaces moving in different directions—an example of motion transparency. It has been shown previously that perception of motion transparency can promote accurate pairings of colour and motion (Clifford et al., 2004).

When a field of dots oscillate between different directions and different colour states, observers tend to pair motions with physically delayed colours—the typical perceptual asynchrony between colour and motion. Experiments demonstrating this finding have used a stimulus wherein all the dots change colour and direction at the same times (Arnold & Clifford, 2002; Bedell et al., 2003; Clifford et al., 2004). However, when the relative phase of the individual dot oscillations was randomised (such that the characteristics of the oscillation of each dot was unchanged but occurred at different times) observers tended to perceive two transparent surfaces moving in different directions and pairings of colour and motion were veridical (Clifford et al., 2004). The phenomenology of motion transparency parallels the known physiology of motion processing in macaque MT (Clifford et al., 2004; Qian & Anderson, 1994; Qian, Anderson, & Adelson, 1994a, Qian, Anderson, & Adelson, 1994b). Findings relating motion transparency to perceptual pairings of colour and motion therefore pose an important caveat: observers will only mis-bind colour with later instances of motion when a persistent surface appears to change direction (Clifford et al., 2004; Moradi & Shimojo, 2004). Presumably perceived direc-

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[3] I am indebted to Farshad Moradi for this suggestion.

[4] At very rapid rates of oscillation, observers can sometimes surmise the direction of drift while the stimulus is red because one side of the grating bars look red-ish. This happens when the rate of oscillation prevents the grating from drifting through a full cycle of the spatial waveform—so some regions of the stimulus will only ever be coloured red or black. While this provides a cue that can be used to complete the task, there is no sensation of motion. This is very different to situations where rapid oscillations can induce a percept of multiple transparent surfaces (Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004). Transparency was never observed at any rate of oscillation with this stimulus.

tion changes require an analysis involving the human analogue of MT and are subject to the dynamics of motion processing at this level of analysis—including opponent inhibition (Clifford et al., 2004).

5. General discussion

Competing hypotheses based upon the brain-time and post-dictive accounts of perceptual asynchrony have been contrasted in a series of experiments.

The post-dictive account was used to predict that: (1) perceptual pairing of colour and motion should be optimal when changes in colour and direction were physically synchronous, and (2) that both the sudden appearance of a new surface and direction reversals within a persistent surface should bias observers to pair colours with earlier instances of motion. The first hypothesis was contradicted by the findings that pairing of colours and motions was facilitated by inducing a lag between changes in direction and colour at a fixed (800 ms, Experiment 1) and at variable (200–1000 ms, Experiment 3) periods of oscillation. The second hypothesis was contradicted by the finding that reversals in direction prompt observers to pair motions with later colours, but the intermittent onset of a moving surface does not (Experiment 2).

All the hypotheses based upon the brain-time account of perceptual asynchrony were supported by experimental results in this study. It was hypothesised and demonstrated that colour and motion pairing could be facilitated by inducing a lag between changes in direction and colour (Experiments 1 and 3). It was also hypothesised and demonstrated that while direction reversals within a persistent surface would bias observers to pair colours with earlier instances of motion, the intermittent appearance of a moving surface would not (Experiment 2). Additionally, it was hypothesised and demonstrated that intermittent motions interspersed by blank periods would be paired with later motions that are interspersed with periods of opponent motion.

In general, the results of this study refute the post-dictive account of perceptual asynchrony (Moradi & Shimojo, 2004) while providing support for the brain-time account (Bartels & Zeki, 1998; Zeki, 2002). This should not, however, be misconstrued as support for the existence of a fixed latency between the analyses of colour and motion. The hypothesis allows for the possibility of variable processing times.

Ample evidence has shown that the extent of the temporal asynchrony between colour and motion is variable. Manipulations known to influence the time course of sensory processing can also influence the magnitude of the apparent asynchrony (Adams & Mamassian, 2004; Arnold & Clifford, 2002; Bedell et al., 2003; Paul & Schyns, 2003). This is not inconsistent with the brain-time account. The major implications of the brain-time theory of perception are that stimulus changes are perceived when analyses are *concluded* in specific regions of the brain and that the times at which changes are perceptually experienced will influence *when* the changes seem to occur. This does not imply that any analysis can occur instantaneously. Rather, analyses are likely to require variable periods of time to complete—reflecting the computational demands of the specific analyses that are required (see Bedell et al., 2003 and Ogmen, Patel, Bedell, & Camuz, 2004 for similar arguments).

It should be noted that data in this paper were derived from judgments of relative timing and show that perceptual pairings of events are not necessarily veridical in relation to relative physical timing. These data do not shed any light on a related question: *when* relative to physical event times are changes perceived as having occurred? Although the brain time account suggests that sensory processing shapes *when* events are perceived as having occurred (Bartels & Zeki, 1998; Zeki, 2002), it is possible that events are not perceived as having occurred when specific analyses are concluded in the brain, but are instead experienced as having occurred at an earlier epoch (Libet, 1985; Libet, Gleason, Wright, & Pearl, 1983; although see van de Grind, 2002 for a critical commentary). The functional significance of this backwards time referral would be to facilitate an accurate sense of timing, so that events are perceived as having occurred at an earlier epoch that is more likely to coincide with the physical timing of the event—thereby mitigating any influence of sensory processing.

Relative timing failures, like those described here, do not allow us to discount the possibility of backward time referral (Libet, 1985; Libet et al., 1983) because the judgments are relative and not absolute—we cannot possibly say *when* observers experienced changes as having occurred in relation to the physical timing of the changes. However, relative timing failures do show that, like other proposed methods of temporal compensation for the demands of sensory processing (Eagleman & Sejnowski, 2000; Moradi & Shimojo, 2004; Rao et al., 2001), if backward time referral occurs the process of compensation must be fallible and presumably apparent relative timing can still be influenced by the time course of sensory processing.

Although data in this paper are consistent with the brain-time theory of perception (Bartels & Zeki, 1998; Zeki, 2002), the hypothesis will probably remain a focus of debate for some time to come. Any alternate account will have to address the rapidly growing number of findings that are consistent with the brain-time theory. In addition to the present findings, these include the systematic effects of the angular difference between contrasted directions of motion (Arnold & Clifford, 2002; Bedell et al., 2003), the effects of attention (Paul & Schyns, 2003) and the salience of the contrasted stimulus

attributes (Adams & Mamassian, 2004). Alternate accounts would also have to explain why timing judgments are influenced by stimulus intensity (Arden & Weale, 1954; Roufs, 1963). While all these findings are consistent with the brain-time theory, they tend to be inconsistent with alternate accounts (Moradi & Shimojo, 2004; Nishida & Johnston, 2002).

6. Conclusions

An increasing body of evidence is consistent with the hypothesis that stimulus changes are perceived when analyses are completed within relatively independent regions of the brain and that the timing of perceptual experiences influences when changes seem to occur (Bartels & Zeki, 1998; Zeki, 2002). The implication of this is that any process of perceptual binding must be subject to the temporal limitations of sensory processing. If processing is delayed, illusory temporal conjunctions can be formed. If neural processes attempt to compensate for the temporal limitations of sensory processing (Eagleman & Sejnowski, 2000; Libet, 1985; Libet et al., 1983; Moradi & Shimojo, 2004; Rao et al., 2001), it seems that the compensation must be fallible.

While the results of experiments in this paper are consistent with the brain-time theory of perception (Bartels & Zeki, 1998; Zeki, 2002), a cautionary note should be sounded—the brain-time theory does not explain *how* relative timing judgments are made. Human observers are able to determine the relative timings of a remarkable variety of different events. To some degree observers can judge the timing of a visual relative to another visual (Moutoussis & Zeki, 1997a, 1997b), auditory (Fujisaki, Shimojo, Kashino, & Nishida, 1994), or haptic (Vogels, 2004) event. Subjectively, it seems that the other *event* can be entirely mental and abstracted—like the sensation of reaching seven while mentally counting from one to ten. The fact that these judgments can be made dictates that the necessary information is encoded. It is possible that this information is encoded in an undiscovered, specialised mechanism that compares representations of temporal features (Nishida & Johnston, 2002). Alternatively, event timing may be encoded implicitly as the point in time at which some brain state is established (Bartels & Zeki, 1998; Johnston & Nishida, 2001; Zeki, 2002). However, even if this were true, we would still need to explain how establishing a brain state in a specific region can facilitate timing judgments involving events encoded in different regions of the brain.

References

Adams, W. J., & Mamassian, P. (2004). The effects of task and saliency on latencies for colour and motion processing. *Proceedings of the Royal Society of London B, 271*, 139–146.

Arden, G. B., & Weale, R. A. (1954). Variations of the latent period of vision. *Proceedings of the Royal Society of London B, 142*, 258–267.

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

Arnold, D. H., Clifford, C. W. G., & Wenderoth, P. (2001). Asynchronous processing in vision: Colour leads motion. *Current Biology, 11*, 594–600.

Aymoz, C., & Viviani, P. (2004). Perceptual asynchronies for biological and non-biological visual events. *Vision Research, 44*, 1547–1563.

Bartels, A., & Zeki, S. (1998). The theory of multistage integration in the visual brain. *Proceedings of the Royal Society of London B, 265*, 2327–2332.

Bedell, H. E., Chung, S. T. L., Ogmen, H., & Patel, S. S. (2003). Color and motion: Which is the tortoise and which is the hare? *Vision Research, 43*, 2403–2412.

Clifford, C. W. G., Arnold, D. H., & Pearson, J. (2003). A paradox of temporal perception revealed by a stimulus oscillating in colour and orientation. *Vision Research, 43*, 2245–2253.

Clifford, C. W. G., Spehar, B., & Pearson, J. (2004). Motion transparency promotes synchronous perceptual binding. *Vision Research*, 44.

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

Enns, J. T., & Oriet, C. (2004). Perceptual asynchrony: Modularity of consciousness or object updating? Vision Sciences Society abstracts.

Fujisaki, W., Shimojo, S., Kashino, M., & Nishida, S. (1994). Recalibration of audiovisual simultaneity. *Nature Neuroscience, 7*, 773–778.

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

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

Libet, B. (1985). Unconscious cerebral initiative and the role of conscious will in voluntary action. *The Behavioural and Brain Sciences, 8*, 529–566.

Libet, B., Gleason, C. A., Wright, E. W., & Pearl, D. K. (1983). Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential): The unconscious initiation of a freely voluntary act. *Brain, 106*, 623–642.

Moradi, F., & Shimojo, S. (2004). Perceptual-binding and persistent surface segregation. *Vision Research, 44*, 2885–2899.

Moutoussis, K., & Zeki, S. (1997a). A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society of London 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 B, 264*, 1407–1414.

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

Ogmen, H., Patel, S. S., Bedell, H. E., & Camuz, K. (2004). Differential latencies and the dynamics of the position computation process for moving targets, assessed with the flash-lag effect. *Vision Reseach, 44*, 2109–2128.

Paul, L., & Schyns, P. G. (2003). Attention enhances feature integration. *Vision Research, 43*, 1793–1798.

Qian, N., & Anderson, R. A. (1994). Transparent motion perception as detection of unbalanced motion signals. II. Physiology. *Journal of Neuroscience, 14*, 7367–7380.

Qian, N., Anderson, R. A., & Adelson, E. H. (1994a). Transparent motion perception as detection of unbalanced motion signals. I. Psychophysics. *Journal of Neuroscience, 14*, 7357–7366.

Qian, N., Anderson, R. A., & Adelson, E. H. (1994b). Transparent motion perception as detection of unbalanced motion signals. III. Modeling. *Journal of Neuroscience, 14*, 7381–7392.

Rao, R. P. N., Eagleman, D. M., & Sejnowski, T. J. (2001). Optimal smoothing in visual motion perception. *Neural Computation, 13*, 1243–1253.

Roufs, J. A. (1963). Perception lag as a function of stimulus luminance. *Vision Research, 3*, 81–91.

van de Grind, W. (2002). Physical, neural and mental timing. *Consciousness and Cognition, 11*, 241–264.

Vogels, I. M. (2004). Detection of temporal delays in visual-haptic interfaces. *Human Factors, 46*, 118–134.

Zeki, S. (2002). The disunity of consciousness. *Trends in Cognitive Sciences, 13*, 173–196.