

Marker Correspondence, Not Processing Latency, Determines Temporal Binding of Visual Attributes

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Summary

Background: When simultaneous visual events appear to occur at different times, the discrepancy has generally been ascribed to time differences in neural transmission or cortical processing that lead to asynchronous awareness of the events.

Results: We found, however, that an apparent delay of changes in motion direction relative to synchronous color changes occurs only for rapid alternations, and this delay is not accompanied by a difference in reaction time. We also found that perceptual asynchrony depends on the temporal structure of the stimuli (*transitions* [first-order temporal change] versus *turning points* [second-order temporal change]) rather than the attribute type (color versus motion).

Conclusions: We propose that the perception of the relative time of events is based on the relationship of representations of temporal pattern that we term time markers. We conclude that the perceptual asynchrony effects studied here do not reflect differential neural delays for different attributes; rather, they arise from a faulty correspondence match between color transitions and position transitions (motion), which in turn results from a difficulty in detecting turning points (direction reversals) and a preference for matching markers of the same type.

Background

Visual perception cannot be instantaneous. Signal transmission and information processing by sluggish neural components inevitably introduces a certain degree of temporal delay between retinal stimulation and the cortical awareness of events. Furthermore, the time required for visual processing is likely to depend on stimulus properties and the cortical-coding mechanisms involved. This provides a challenging problem for

the visual system: to correctly perceive the temporal relationships between visual events [1].

How does the brain represent when events occur? This question can be addressed experimentally by studying perceived simultaneity. Simultaneous visual events can appear to occur at different times if they differ in their stimulus intensity [2, 3], temporal continuity [4], or share of attention [5]. These observations have generally been regarded as indicating time differences in neural transmission or cortical processing, leading to asynchronous awareness of the events. Recently, a striking visual phenomenon, color-motion asynchrony [6], was added to the list of simultaneity illusions. When a green pattern moving upward and a red pattern moving downward are alternated every 250 ms, most observers find it difficult to tell which direction and color are shown together. On the other hand, when the direction change occurs about 100 ms earlier than the color change, the observers reliably bind the two attributes (e.g., red and downward direction), confidently reporting that the events appear to occur simultaneously (Figure 1A). As in the case of other simultaneity illusions, this subjective delay of motion change has been interpreted as indicating that the conscious perception of motion requires more time than color, due to processing time differences in modules specialized for each attribute (Figure 1B). This interpretation has led to an intriguing hypothesis that different visual attributes are processed asynchronously in separate cortical areas and are perceived asynchronously without compensation [6–8].

However, explanations of simultaneity illusions in terms of neural-processing delays have a logical pitfall in that they implicitly equate two time courses that need to be distinguished [9–12]. One is a physical time course, which indicates the time at which the observer's brain establishes neural representations of the events. The time at which explicit descriptions of external events are finally made available is thought to be related to the time at which the observer becomes aware of the events [13]. The other is a subjective time course, the sequence of events as they appear to the observer. Although there must be a strong correlation between these two time courses, whether they exactly match each other on a micro time scale remains controversial [9, 14, 15]. In the case of color-motion asynchrony, it is doubtful that equating these two time courses is justified. It is difficult to identify when the neural processing of a color-change event or a direction-change event starts and finishes in a distributed, continuously changing pattern of neural activity. Even if brain events clearly signal the times at which representations of external events are established, to utilize this information, there must also be a mechanism to encode these signals. In order to judge the temporal order of two arbitrary neural events, the brain must have a mechanism to compare them and anatomical connections of high temporal fidelity between the neurons to be compared. This meta-analysis of neural processing places a high combinatorial burden on the brain. In any case, the time taken to establish a

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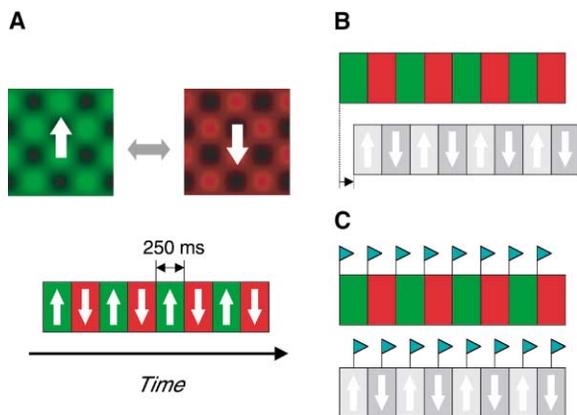


Figure 1. Perceptual Asynchrony of Motion and Color

(A) Perceptual asynchrony of motion and color [6, 7]. When a green pattern moving upward and a red pattern moving downward alternate with the indicated time course, it is hard to judge which color and direction are shown together. For motion and color to be seen in phase, the direction change has to lead the color change by about 100 ms for an interchange interval of 250 ms. The stimulus pattern we used in the experiments was a pair of luminance-modulated plaid patterns.

(B) Conventional account of the apparent motion delay in terms of perceptual processing lag [6–8]. Motion takes longer to be consciously perceived than color.

(C) New account in terms of correspondence matching of transitions. Marker flags indicate transitions in the two sequences. The observers cannot perform the required task to match direction reversals with color transitions due to difficulty in detecting the time of direction reversals (turning points/second-order temporal changes) at rapid alternations. They instead use more salient position transitions (first-order temporal changes) as features (time markers) for cross-attribute binding.

representation of an external event will depend upon many factors and should prove to be an unreliable estimate of the real time of events. The event-time from “brain-time” theory is fraught with difficulties [9–12].

The interpretation of color-motion asynchrony in terms of processing delay is not compatible with a number of our experimental findings described below. We propose an alternative account of color-motion asynchrony (Figure 1C). Our results suggest that there is not a substantial difference in the time it takes for the brain to establish representations of color change and motion direction change. The visual system, however, cannot directly compare these physical time courses; instead, it has separate mechanisms for temporal judgments. In David Marr’s [16] theory of low-level image description, the primal sketch, spatially localized tokens representing elements of a spatial pattern are used as the input to grouping processes (now often called mid-level visual processes), which combine tokens of the same type to form coherent regions in what Marr called the full primal sketch. Here, we extend this idea to temporal processing and use the term temporal marker to refer to temporally localized representations of salient temporal features. We propose that color-motion asynchrony results from the action of mid-level temporal grouping processes. To be specific, our hypothesis ascribes this simultaneity illusion to biased cross-attribute linkage of time markers of the same temporal type: *transitions* (first-order temporal changes) in the color-change sequence map to

transitions in the motion sequence in place of *turning points* (second-order temporal changes). The introduction of color-motion asynchrony at high alternation rates results from a change in correspondence matching brought about by temporal limitations on encoding higher-order temporal change and linking tokens of different types.

An analogy may help clarify the distinction we would like to draw between the brain-time explanation of asynchrony we wish to challenge and the temporal correspondence explanation we wish to develop. In the brain-time theory, we can think of the specialized modules of the brain as singers in an Internet chorus. In Britain, a Japanese singer will appear to be delayed due to a transmission time lag. The brain-time theory proposes that there is no compensation for these delays, and the result is apparent asynchrony. Our alternative proposal is that all the singers are in the same place (no significant transmission delays), but time judgments are based on the temporal direction of links between corresponding key features. For the sake of the analogy, let’s say verbs are the key marked features. Then, a listener will suffer the illusion that the Japanese singer appears to be delayed, because, in Japanese, the verb is toward the end of the sentence.

Results

Alternation Rate Dependency

The first line of evidence against the interpretation of color-motion asynchrony in terms of processing latency differences is that color-motion asynchrony depends critically on the rate of stimulus change (Figure 2). We found that robust perceptual asynchrony occurred for stimulus changes at a rate of once every 250 ms, which was close to the values used in the original report [6]. When the alternation rate was slowed down, however, the apparent asynchrony was gradually reduced and almost disappeared at a rate of once every 2000 ms. Subjects could accurately judge the temporal order of a color change and a direction change for nonrepetitive single changes. The observation that the asynchrony effect is rate dependent not only accounts for why we are not normally aware of color-motion asynchrony but also raises questions about the idea that the illusion reflects a processing time difference between color and motion, which, at least in its simplest version, would predict apparent motion delay regardless of the rate of alternation.

However, we are assuming that processing time delays are fixed. One might argue that the observed effects of alternation rate can be explained if the hypothetical differential processing delays of the two attributes are only seen at high alternation rates. Subjects, however, could accurately judge the order of occurrence between a single change and a change embedded in a rapid sequence of alternations, whether the judgment was within or between attributes (asymmetric temporal order judgment: Figure 3). This result does not support a differential rate dependency of processing time. Crucially, it shows that the apparent delay at high alternation rates is not due to the alternation rate per se. This effectively voids any simple explanation for color-motion asyn-

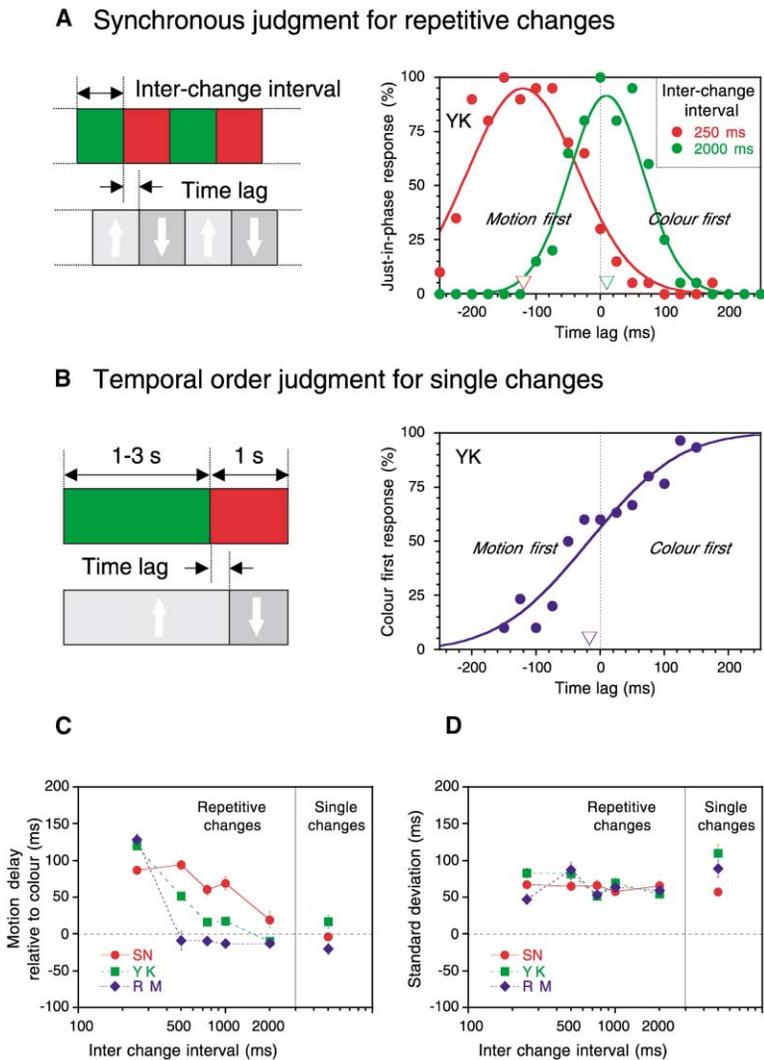


Figure 2. Rapid Alternation Is Critical for Perceptual Color-Motion Asynchrony

(A) Subjects judged whether the oscillation of color and that of direction were perfectly in phase. The percentages of the in-phase responses, obtained for subject Y.K. with the interchange interval of 250 and 2000 ms, are plotted as a function of the time lag. The triangle indicates the point of perceptual synchrony, estimated from the peak of the best-fit Gaussian function. It is largely shifted to the left (i.e., apparent motion delay) for the interval of 250 ms, but it is close to the physical synchrony point for the interval of 2000 ms.

(B) Subjects made a temporal order judgment between a single change of color and direction. The percentage of the color-first responses is plotted as a function of the time lag. The triangle indicates the point of perceptual simultaneity at which the color-first response was 50% in the best-fit cumulative Gaussian function.

(C) Perceptual delay of motion relative to color estimated from the synchronous judgment of repetitive changes plotted as a function of the interchange intervals, together with the delay estimated from the temporal order judgment of single changes. Different symbols indicate different subjects. Although a large perceptual delay for motion was found for rapid repetitive changes, it disappeared for slow repetitive changes and for single changes.

(D) The standard deviation plotted in the same format. In spite of the systematic change in delay, the response variability remained nearly constant. The error bars in (C) and (D) represent a 95% confidence interval estimated by a bootstrap technique.

chony based in the temporal tuning characteristics of low-level visual mechanisms. The apparent delay occurs as a consequence of the requirement to make a comparison across two different sequences at high alternation rates. Note also that, for alternations significantly faster than once every 250 ms, the judgment of the motion-color temporal relationship is almost impossible, even when the alternations themselves are clearly visible. A similar failure of attribute association was reported for luminance-orientation or color-orientation binding when the two attributes changed in separate objects [17], but the temporal limits on color-direction binding are fairly low even when the changes are instantiated in the same objects. These observations indicate that, except in a few cases in which two attributes are presumably coded in combination explicitly by early stages [17], cross-attribute temporal binding requires not only the detection of changes in two attributes, but also an extra attention-demanding, time-limited comparison process.

Reaction Time Inconsistency

The second line of counterevidence against the processing delay hypothesis is that the subjective asynchrony in the temporal binding of color and motion is not

accompanied by a corresponding difference in reaction time. In this experiment, subjects were asked to press a button as soon as a target (motion direction or color) appeared in a pseudorandom stimulus sequence in which stimuli were selected from one of three distracters (Figure 4A). Button-press latencies were found to be almost identical for motion and color under the stimulus conditions we used (cf. [18–21]). To measure subjective time differences in a situation in which we know the processing time of attribute change (as measured by reaction time) is, to a first approximation, identical, we presented the same motion direction target sequence together with a pseudorandom color test sequence in which colors were selected from one of four alternatives (Figure 4B). Subjects had to report the color displayed in the test sequence when the target direction was presented. It was found that the probability of apparent concurrence peaked for the test color presented 65–95 ms after the target direction. Under the reversed condition (color targets), the probability of concurrence peaked for the motion test presented 99–113 ms before the color target, indicating a perceptual delay that cannot be ascribed to slow attention shifts from target to test [22]. The results indicate that, under conditions in

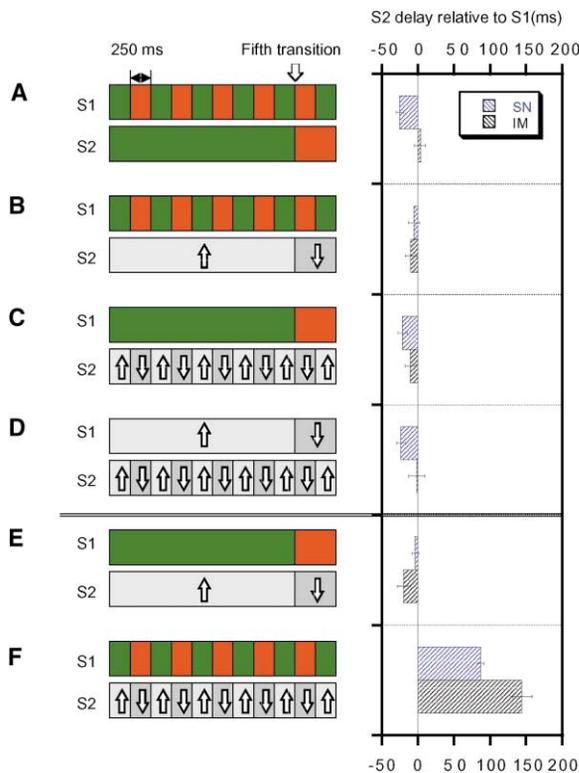


Figure 3. Alternation Rate, Per Se, Had Little Effect on the Temporal Order Judgment

(A–D) Subjects made an asymmetric order judgment between a single isolated change and a change embedded in a rapid alternation sequence (a fifth change to red or to downward) for various combinations of color and motion changes. For each condition, the right graph indicates the apparent delay of the second stimulus (S2) relative to the first stimulus (S1), estimated from the point of perceptual simultaneity.

(E and F) Some of these delays should indicate large positive values if the disagreement between (E) accurate temporal order judgment for single changes and (F) large apparent motion delay for rapid changes reflects rate dependency of the processing delays. The results, however, did not support this prediction, showing fairly accurate temporal order judgments for any combinations of slow and rapid changes. The error bar represents a 95% confidence interval.

which there was no difference in response latency to targets, subjective simultaneity required a very substantial motion sequence advance relative to the color sequence, even though both tasks required identification of the same target stimulus appearing in the same stimulus sequence (Figure 4C).

If we accept that the subjective judgement of perceptual asynchrony measured here, which can be as large as 100 ms, reflects neural-processing time differences, then it is difficult to understand why it is not reflected in reaction time. The possibility that delayed motion perception is completely compensated for by fast post-perception processing is not only anatomically unlikely, but it is also incompatible with the finding that response latencies were nearly identical for single changes of color and motion. This is because, when perceptual asynchrony does not occur, such compensation should make response latencies much shorter for motion than for color.

Task Dependency

The asymmetric temporal order judgement task (Figure 3) shows that rapid direction changes do not always appear to be delayed. Here, we introduce a performance measure of the perceived time of stimulus alternation that provides confirmatory evidence of this. In these experiments, we used synchronous motor tasks that reflect the subjective temporal relationship between visual stimuli and motor responses. In one experiment, subjects were asked to press a button and hold it down during the downward phase of a repetitive 2 Hz direction alternation. It was found that subjects' button responses for motion change lagged the true point of simultaneity by around 100 ms (Figure 5). Subjects' button presses were approximately synchronous for color changes regardless of the alternation rate. Also, some subjects' button presses synchronized with the direction changes at slow alternation rates. All of this is consistent with the data from the perceptual judgment tasks. These results appear to suggest that temporal relationships were judged veridically for button presses, color changes, and direction changes at the low alternation rate, although rapid direction changes appeared delayed relative to these events.

However, although this response delay to motion change appeared to reflect the perceptual delay as described above, it vanished when we switched to a slightly different task. In the second experiment, we found that subjects could accurately synchronize the unseen movement of a computer mouse with the movement of the visual stimulus when asked to move the mouse forward and backward in time with the upward-downward movement. This synchronization would be impossible if perception of the motion direction change sequence was substantially delayed. To explain synchronization of mouse movement with these rapid direction changes, one might propose that the proprioceptive perception of the rapid direction changes of the mouse was also delayed, but, if so, this argument should also apply in the case of the button-press experiment, which also requires a repetitive response to the same predictable movement and in which we reported an approximately 100-ms motion direction change delay.

The difference in the results between the two synchrony tasks may appear counterintuitive, but it seems to agree with the phenomenology of the tasks. For rapid direction changes, although alternation of two directions is seen, there is no subjective transient signal that clearly indicates the time of the direction change. We suspect this is why the subjects could make a forward mouse movement in synchrony with the phase of upward motion but could not press a button in time with the beginning of a direction change. We think that subjects cannot reliably encode the time of direction changes due to a lack of salient features that mark the change events, and this failure in turn leads to perceptual asynchrony.

Transitions versus Turning Points

We have ascribed errors in judging the temporal relationship of color and direction changes to the temporal structure of these changes and the need to compare two alternating sequences, rather than processing time

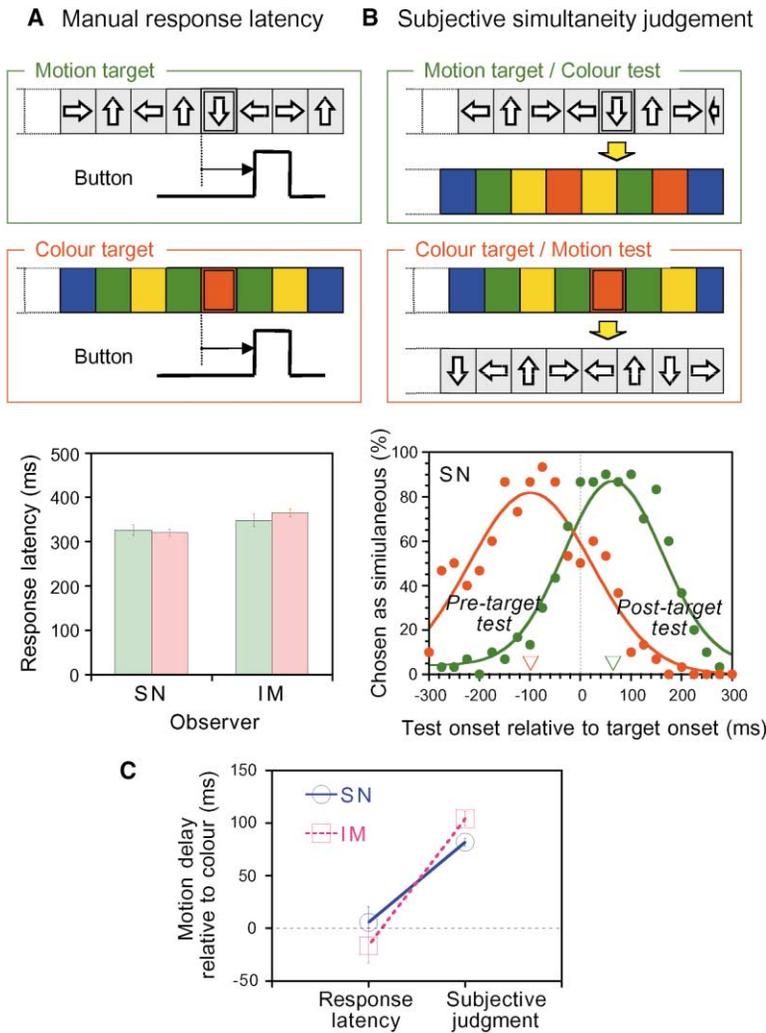


Figure 4. Dissociation of Reaction Time and Perceptual Simultaneity

(A) Comparison of manual reaction latency between motion and color. Subjects were required to press a mouse button immediately if a target (red color or downward motion) appeared in a pseudorandom stimulus sequence. The results indicate that the response latencies were almost equal for motion (green bar) and color (red bar).

(B) Subjective simultaneity judgment between motion and color. The same target stimulus sequence that was used for the latency measurement was presented on one side of the display, and a test sequence was presented on the other side. Subjects had to decide which test stimulus was concurrent with the target. In the bottom graph, the abscissa shows the time of test onset relative to target onset (negative for the test ahead of the target), and the ordinate is the probability that the subject chose a stimulus as concurrent. The smooth curve is the best-fit Gaussian function, whose peak, indicated by a triangle, is the estimate of the subjective point of simultaneity. The results indicate the apparent motion delay relative to color for both the motion target condition (green) and color target condition (red).

(C) Comparison of the magnitudes of perceptual motion delay obtained in the two tasks. The error bars in (A) and (C) represent a 95% confidence interval.

differences for different attributes. Here, we characterize these changes in more detail. Whereas a color change is a first-order temporal change (first-order derivative of color with respect to time), direction reversal is a second-order temporal change (second-order derivative of spatial position with respect to time). In this paper, we use the terms transitions for first-order changes and turning points for second-order changes (to emphasize the difference between the meaning of first-order/second-order used here and the well-established first-order/second-order categorization distinguishing luminance- and, say, contrast-defined stimuli in the space and motion domains [23]). We consider only transitions and turning points of nontemporal attributes that can be defined at one point in time (e.g., luminance, color, and position), thus a transition requires measurements at just two points in time, while a turning point requires measurements at three points. When color changes and direction reversals are correctly marked and compared, accurate temporal judgments of color and motion change can be made. We assume that the visual system can use both transitions and turning points, but it tends to make a match between transitions, instead of between transitions and turning points, at

high temporal rates (Figure 1C). For rapid alternations, transitions of position (i.e., motion) become brief, facilitating their use as time markers in place of turning points, and are linked to transitions in the color sequence. This is, at least in part, we believe, because of temporal limits on the allocation of attention needed to link transitions and turning points. There is also considerable evidence showing that changes in speed (second-order changes) are poorly detected by the visual system [24–27]. Given that neural sensors specialized for temporal change exist only for transitions, but not for turning points, it is reasonable that the visual system can use only transitions at high temporal rates. This explanation of apparent asynchrony does not require any delay of the motion response relative to the color response. (Note that our notion of a time marker has no direct relationship with the visual marking mechanism proposed by Watson and Humphreys [28] for efficient selection of new events.)

If our hypothesis is correct, it is to be expected that perceptual asynchrony will depend on the temporal structure of stimulus sequences (transitions versus turning points) rather than their attribute type (color versus motion). To test this, we measured the point of percep-

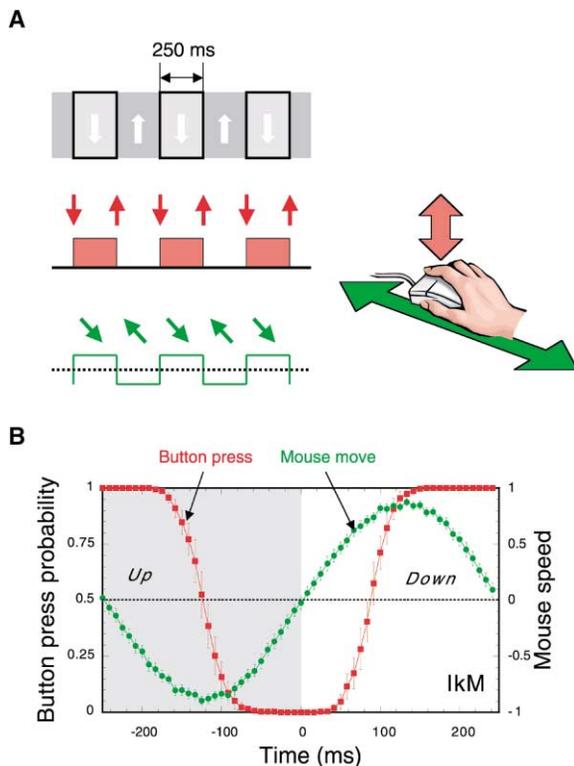


Figure 5. Synchronous Button Press and Mouse Movement to Rapid Stimulus Direction Changes

(A) The task was to synchronously press a button while the stimulus was downward, or to move a hand-held computer mouse forward and backward in synchrony with the stimulus movements. (B) Red squares and the left ordinate indicate the probability of button press for the phase of downward motion. Green circles and the right ordinate indicate the speed of mouse movement, with positive value being assigned for backward mouse movement to be matched with the downward stimulus motion. Both variables are plotted as functions of time within a direction alternation cycle of 500 ms. The stimulus direction changed from upward to downward at time zero. The time course of the button press probability indicates a response delay of about 100 ms, while the time course of the speed of the mouse movement indicates nearly perfect synchrony between the stimulus and response. The error bar represents a 95% confidence interval.

tual synchrony for all combinations of transitions and turning points of color and position using a cross-attribute matching task (Figure 6A). The transition of color (C1) was an abrupt change between two colors, and the turning point (C2) was the reversal of a gradual change between the two colors. The transition of position (P1) was an abrupt change between the two positions, which could be judged only by the jump direction, and the turning point (P2) was a motion direction reversal. As in the original demonstration of perceptual asynchrony of color and motion [6], we systematically varied the relative phase of the color and position changes, then asked the subjects to judge their temporal relationships. For instance, for the C2P1 stimuli, subjects judged whether the color was changing from red to gray or from gray to red when the position was top or bottom. According to our hypothesis, for the combination of transitions (C1P1) or turning points (C2P2), no perceptual delay

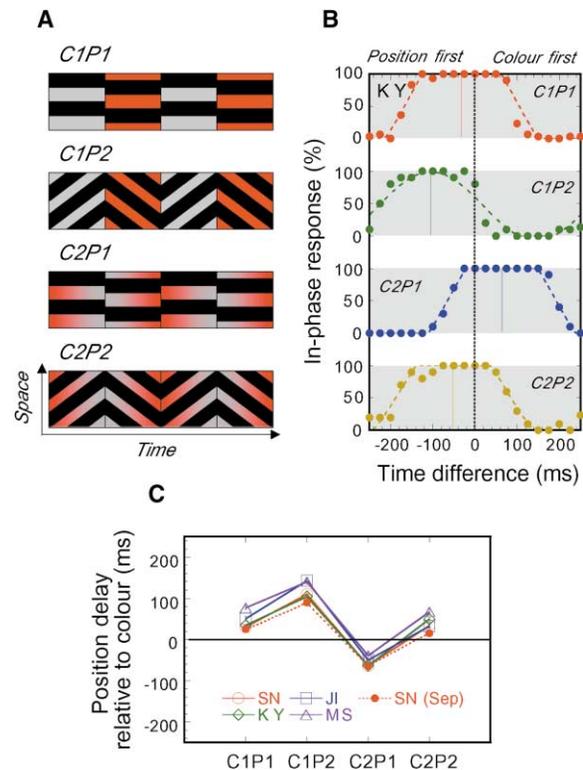


Figure 6. Temporal Matching Experiment for Combinations of Transitions and Turning Points of Color and Position

(A) The stimulus sequence in a space-time format for the C1P1, C1P2, C2P1, and C2P2 conditions, where C1P2, say, indicates a combination of color *transition* and position turning point (motion direction reversal). Subjects reported (forced choice) whether the stimulus was in phase (as illustrated) or out of phase. (B) The probability that a subject made an in-phase response for each stimulus as a function of the time difference of the attribute changes. The smooth curve is the best-fit truncated cosine function, the zero phase of which, indicated by a line segment, is the estimate of subjective point of simultaneity. (C) Perceptual delay for position change relative to color change estimated from temporal matching data for four subjects. The color and position changes were made within the same plaid patterns (filled symbols), or separately in two plaids (open symbols). The results indicate an apparent delay of turning points relative to transitions regardless of the types of stimulus attribute. The error bar represents a 95% confidence interval.

is expected, since, in both cases, the tasks could be accomplished by matching features of the same type. Apparent motion delay is expected for the combination of color transitions and position turning points (C1P2) as before. The critical prediction is that an apparent color-change delay should occur for the combination of color turning points and position transitions (C2P1). These predictions were indeed supported by the experiment (Figures 6B and 6C). This indicates that the key factor in perceptual asynchrony is the temporal properties of the stimuli, not the specialist neural system activated. Note that this result is an empirical justification of our characterization of motion reversal as a second-order change in position in this context rather than a first-order change in motion direction.

Closely examining Figure 6C, however, one can notice

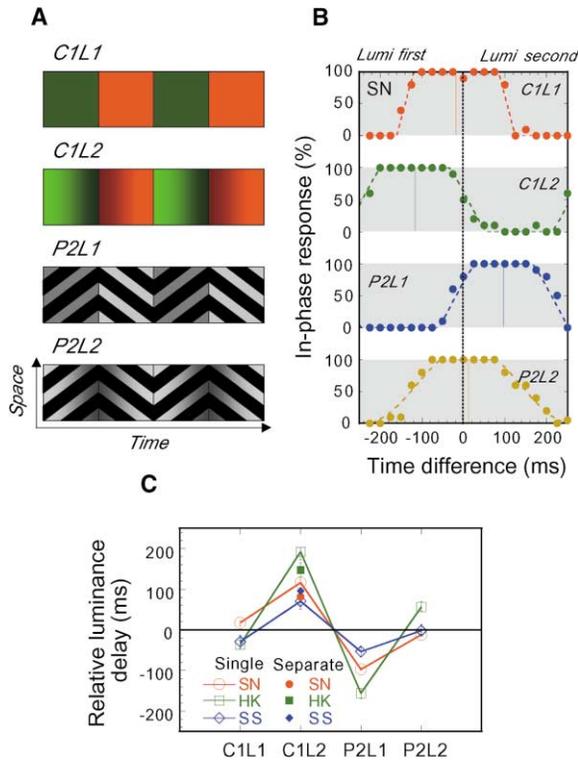


Figure 7. Temporal Matching Experiment for Combinations of Transitions and Turning Points of Luminance with Color Transitions or Position Turning Points

(A) The stimulus sequence for the C1L1, C1L2, P2L1, and P2L2 conditions, where C1L2, say, indicates a combination of a color transition and a luminance turning point. The luminance transition was an abrupt change in the plaid mean luminance, and the luminance turning point was a reversal between linear luminance increment and decrement. The range of luminance change was 5–15 cd/m².

(B and C) The results are shown in the same format as Figure 6. Again, the results indicate apparent delay of turning points relative to transitions regardless of the types of stimulus attribute.

that perceptual synchrony for C1P1 and C2P2 occurred at a point for which position (motion) changed slightly earlier than color. Bias in the same direction was found for C1P2 and C2P1. Although we cannot reject the possibility that this residual effect might reflect processing delays, attentional gating [22] could also account for the observed bias if the subjects always judged the timing of (less salient) color change using the timing of (more salient) position change as the reference. In fact, the bias was slightly reduced when the strategy to use the color changes as a reference was facilitated by changing color and position in separate objects (open symbols).

The importance of temporal structure was further supported by the results of experiments using luminance change. The results (Figure 7) suggest that abrupt transitions of luminance level appear to be almost synchronous with abrupt color transitions, while they appear to be largely ahead of motion direction changes. In contrast, luminance turning points (the point of change between linear luminance increments and decrements) appear to largely lag behind abrupt color transitions but

are almost synchronous with motion direction changes. The point of subjective simultaneity is thus strongly biased toward alignment of the same type of stimulus change regardless of the type of stimulus attribute.

By applying the same rule for cross-modality judgments, one can account for the results for synchronized behavioral responses (Figure 4). For the synchronous button press, the subjects were asked to synchronize transitions of finger/button position with turning points of visual stimulus position. For the mouse movement, on the other hand, they were asked to synchronize transitions of hand/mouse position with transitions of visual stimulus position. Thus, subjects' tendency to link changes of the same temporal type for both body and visual stimuli leads to asynchronous responses in the former case but synchronous responses in the latter case.

Discussion

Color-motion asynchrony does not indicate that the processing time for motion is longer than for color. Turning points (second-order temporal changes including motion direction change) generally appear delayed relative to transitions (first-order temporal changes including color changes) when they are compared in rapid alternation (Figures 6 and 7). One cannot ascribe this apparent delay to longer neural-processing times for turning points than those for transitions since direction changes were not subjectively delayed relative to color changes at slow alternation rates (Figure 2). The possibility that alternation rate itself changes the magnitude of the temporal delay was rejected (Figure 3). Also, motion change could appear to be delayed by about 100 ms without a consequential increase in manual response time (Figure 4).

We suggest that the apparent delay of turning points is a result of an error of subjective temporal judgment rather than a temporal asynchrony of visual awareness or temporal distortion of immediate visual experience. We recognize that relative information about segregated objects/events is not directly computed in parallel but requires the establishment of a perceptual strategy or perceptual routine to extract the information. To make a relative judgment, an event must be marked and identified as a reference for subsequent comparison with other events. The asynchrony effect arises because, at rapid alternation rates, it is difficult to mark and link turning points to transitions, but it is still possible to match the transitions in the two temporal sequences. In fact, the maximum delay was about a quarter cycle of the alternation (125 ms), as would be expected from this theory. Even turning points in rapid alternation can be accurately located when subjects pay attention to a single change in the sequence (Figure 3). Attending to a turning point might enhance its signal strength, influence feature selection, and/or allow subjects to infer the location of a missing turning point from adjacent transitions. In any case, problems in marking turning points at high alternation rates reflect, in part, constraints on the dynamic allocation of attention. At alternation rates higher than a few hertz, temporal judgments

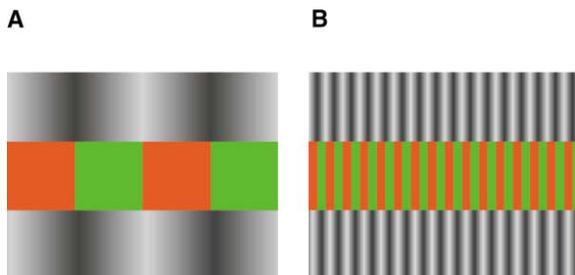


Figure 8. Spatial Analog of Perceptual Asynchrony

(A and B) In both (A) and (B), turning points (peaks and troughs of the triangular wave) and color transitions (border between red and green) are in phase between top and middle gratings, while the bottom grating was misaligned by an amount corresponding to a quarter cycle of (B). Alignment is easily judged for the low alternation rate (A) but is difficult for the high alternation rate (B).

become impossible even when the stimulus changes are still detectable (temporal crowding). This can be ascribed to a difficulty in marking salient transitions or a failure in using them properly for temporal binding. Our argument that asynchrony is based on temporal grouping can be neatly demonstrated using a spatial version of transition/turning point correspondence. The alignment of color transition edges (border between red and green) with luminance turning points (peaks and troughs of a triangular wave) is not difficult when the alternation cycle is low (Figure 8A), but the appropriate alignment is not unambiguously determined for high spatial alternations (Figure 8B) [29]. Which parts of the display appear aligned depends on how features are identified and matched, rather than how the spatial map of brightness and chromatic change is aligned. For Figure 8B, there seems to be a more natural alignment between the color pattern and the lower luminance pattern. In this case, color transitions are linked to luminance transitions rather than to luminance turning points. We believe that a similar principle governs temporal judgment, although matching between transitions prevails in temporal cases due to difficulty in detecting temporal turning points.

A recent report of temporally asymmetric binding of color and motion direction in contingent aftereffects [30] argues against our proposal that perceptual asynchrony cannot be ascribed to neural delay; however, this asymmetry could be attributed to a temporal response profile difference between the two attributes [11]. An intriguing reversal of subjective temporal order of the cutaneous stimuli delivered to each hand due to arm crossing [31] demonstrates a different type of temporal misjudgment (mislabeling) that also cannot be ascribed to neural delay. Our position is close to the multiple drafts model of subjective timing [9] and the postdiction theory of visual awareness [12, 15] in that the subjective time course of events is regarded as a result of the brain's interpretative processes.

What is the neural basis of the process of temporal judgment mediated by time markers? We conjecture that the brain encodes temporal relationships of events based on the temporal pattern of the neural activity elicited by those events. This view is distinct from the

neural-processing time theory in that we propose that the target neural activity used for temporal coding is time locked to events and dissociated from the encoding of the content of events. It does not need to be located at the cortical area that plays a major role in the analysis of the event content, nor need it reflect the time of establishment of the event representation. These specialist mechanisms for temporal analysis are expected to draw on neural events early in the processing hierarchy so as to mirror, as far as possible, the temporal order of external events (cf. [14]). Our hypothesis thus evades inherent problems involved in the processing time theory (see "Background"). The idea of special neural systems for temporal coding was suggested by visual motion processing, in which direction-sensitive neurons encode spatiotemporal relationships (e.g., something is moving from left to right), while other neural systems encode the detailed appearance (e.g., color, texture) of the object [32, 33]. Although the experimental evidence thus far does not clearly point to a mechanism for encoding the temporal relations, it is possible that spatiotemporal comparators analogous to local motion detectors [34–36] or global synchrony detectors [37] could encode this information. We speculate that the cross-attribute linkage between transitions could be implemented by a simple mechanism that computes cross-correlation of early neural responses, while the linkage between transitions and turning points may result from an attention-demanding feature matching mechanism. It is intriguing that cross-attribute temporal binding is similar to cross-attribute apparent motion in various respects, such as low temporal resolution, sensitivity to stimulus saliency, and strong influence of attention [38–42].

We believe that manual reaction time primarily reflects the objective time at which a decision by the perceptual system becomes available to the motor system; it is unlikely to be totally unrelated to the time taken to process task-relevant visual information. Our hypothesis accounts for why the response latency can be largely dissociated from the subjective judgment of simultaneity. Besides the present study, dissociations between these chronometric measures have been reported for comparisons across sensory modality [10, 43] and spatial frequency [10] and for spatial cueing [44]. Unlike in the present case, some previous studies [10, 44] show that temporal judgments tend to be more accurate than predicted from differences in response latency. This pattern of results is generally expected from our theory, since judgments based on time markers should be less affected by processing delays. Note, however, that subjective asynchrony occurs without a difference in stimulus temporal structure (e.g., [5, 43]), and, in many cases, the two temporal measures show positive correlations. Agreements are particularly high for luminance [3] and wavelength [18, 45] manipulations. We believe that this dependency reflects the temporal properties of peripheral neural responses that can affect both the temporal codes for subjective judgments and the total processing time of the system. Revealing the relationship between subjective temporal judgments and various response latencies will lead to greater insight into the neural basis of temporal judgments.

Conclusions

An apparent delay of changes in motion direction relative to synchronous color changes cannot be ascribed to a processing delay in neural systems specialized for motion. Perception of the relative time of events is based on the comparison of representations of temporal features (time markers). Since transitions (first-order temporal changes) become more salient than turning points (second-order temporal changes) at rapid alternation rates, the comparison process results in a correspondence match between transitions of color and position occurring at different times. This leads to a temporally biased linkage across stimulus modalities, which is perceived as temporal asynchrony.

Experimental Procedures

General

A pair of luminance-modulated plaid patterns were placed on either side of a fixation bull's-eye. The plaid size was $4^\circ \times 4^\circ$, and the gap between the two plaids was 4° . Each plaid consisted of two sinusoidal gratings of 1.4 c/° (unless otherwise noted), having 50% contrast and oriented $+45^\circ$ and -45° from the vertical. The plaid pattern was stationary or moved at $6^\circ/\text{s}$ (unless otherwise noted) within a stationary border. The mean luminance was either 5 cd/m^2 (green plaids), or an isoluminant value (other color plaids, and gray background,) as determined by the minimum motion technique [46]. The CIE (1931) chromaticity coordinates were $(x = 0.279, y = 0.598)$, $(x = 0.625, y = 0.343)$, $(x = 0.139, y = 0.055)$, $(x = 0.491, y = 0.446)$, and $(x = 0.285, y = 0.317)$, for green, red, blue, yellow, and gray, respectively. The stimulus pattern was displayed at a 120 Hz refresh rate on a color monitor driven by a VSG 2/3 (Cambridge Research Systems). The subject binocularly viewed the display in a dimly lit room at a distance of 71 cm. One of the authors (S.N.) and additional naïve subjects participated. They all had normal or corrected-to-normal visual acuity.

Synchronous Judgment for Repetitive Changes

In each trial of the experiment (Figure 2A), a stationary plaid presented on one side alternated in color between green and red, and a moving plaid presented on the opposite side alternated in its direction between upward and downward. (An auxiliary experiment indicated that changing color and direction within the same patterns did not alter the results.) The relative temporal phase was varied from trial to trial. The subject was asked to make a yes-no judgment about whether the two oscillations were perfectly in phase. "In phase" was defined as "when the color is red, the direction is downward." The stimulus was presented until the subject made a judgment. A total of 30 judgments were made for each phase ($n = 30$). The interchange interval (the alternation rate) was 250 ms (2 Hz), 500 ms (1 Hz), 750 ms (0.67 Hz), 1000 ms (0.5 Hz), or 2000 ms (0.25 Hz). The subject was instructed to observe several alternations before making a judgment.

Temporal Order Judgment for Single Changes

In each trial of the experiment (Figure 2B), a green stationary plaid was presented on one side, and an upward moving plaid was presented on the opposite side. After 1–3 s from the stimulus onset (this duration was randomly varied), the first plaid changed color to red, and the second plaid changed direction to downward. They disappeared 1 s after the change in color. The relative timing of the color and direction changes was varied from trial to trial. The subject was asked to judge which change occurred first. $n = 30$.

Asymmetric Temporal Order Judgment between Single and Repetitive Changes

In each trial of the experiment (Figure 3), a repetitive alternation of color or motion direction was presented on one side, and a single change of color or motion direction was presented on the opposite side. The repetitive stimulus was presented for five and half oscillations, with an interchange interval of 250 ms, starting and ending

with the green/upward phase. The single change from green to red (or from upward to downward) took place within 150 ms of the fifth change from green to red (or from upward to downward) in the repetitive sequence. The subject was asked to judge which of these two changes occurred first. No sign was presented to specify the fifth change; thus, the subject had to count the number of changes. $n = 30$.

Response Latency Measurement for Color/Motion Target

To appropriately measure the reaction time difference between color and motion under the temporal conditions for which a robust perceptual asynchrony effect is obtained (Figure 4A), we used a pseudorandom alternation of color or motion direction with an interchange interval of 250 ms. The time of appearance of the target could not be predicted. In each trial, one of three colors (green, blue, yellow) or one of three directions of motion (upward, leftward, rightward) appeared in a pseudorandom order in a pair of plaids. A target (red or downward) appeared once at the third from last position in the sequence (2–4 s after the onset of the sequence). The same stimulus could not appear consecutively. Subjects were required to press a mouse button immediately when they detected the target. The reaction time from the onset of the target to the button press was recorded. $n = 60$.

Subjective Simultaneity Judgment between Motion and Color in Pseudorandom Sequences

In each trial of the experiment (Figure 4B), the same target stimulus sequence that was used for the latency measurement was presented on one side of the display, and a test sequence was presented on the other side. In the test sequence, one of four colors or directions appeared in a pseudorandom order, with the restriction that the last four stimuli differed from one another. The test sequence was temporally offset relative to the target sequence by ΔT , which ranged from -225 to 0 ms. Subjects had to decide which of the four test stimuli was concurrent with the target. For a given ΔT , we could compute the four probabilities of choosing the test stimuli presented at $\Delta T - 250$ ms, ΔT ms, $\Delta T + 250$ ms and $\Delta T + 500$ ms. $n = 30$.

Synchronous Button Press and Mouse Movement

A pair of gray plaids were presented on both sides of the fixation point (Figure 5). They changed motion direction between upward and downward. The direction change interval was 250 ms. The subject was asked to synchronously press a button while the stimulus was downward, or to move a hand-held computer mouse forward and backward in synchrony with the stimulus movements. Since the subjects had to look at the stimulus in the monitor at all times, they could not see the movement of their hand, but they could hear the click upon the press of the button. During a trial, the state of button or speed of the mouse movement was recorded. Each trial lasted for 15 s, but the first 5 s was discarded in the analysis. For the button press response, the button press probability was computed for each trial, then averaged over trials. For the mouse movement response, the speed of the mouse movement was normalized by the fastest speed in the trial, then the mean speed was computed for each trial. A total of 20 trials were conducted for each task.

Temporal Matching for Combinations of Transitions and Turning Points of Color and Position

For each block, color and position were changed in a pair of plaids (consisting of 0.7 c/° gratings) with a given combination of type of changes (Figure 6). We varied the relative temporal phase of color and motion changes from trial to trial. Subjects made a two-alternative forced choice on the relative phase. The interchange interval was 250 ms. For the C1P1 stimuli, subjects judged whether the color was gray or red when the position was top or bottom (which could be judged only by the direction of a quarter-cycle jump of the plaid). For the C1P2 stimuli, subjects judged whether the color was gray or red when the motion direction was upward or downward ($8^\circ/\text{s}$). For the C2P1 stimuli, subjects judged whether the color was changing from red to gray or from gray to red when the position was top or bottom. For the C2P2 stimuli, subjects judged whether the color was changing from red to gray or from gray to red when

the motion direction was upward or downward. The stimulus was presented until the subjects made a judgment. $n = 20\text{--}30$. For the experiment shown in Figure 7, the method was similar except for the stimulus. The interchange interval was 250 ms for S.N. and 500 ms for the other subjects. $n = 10$.

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