V

TEMPORAL CHARACTERISTICS OF FEATURE AND OBJECT PERCEPTION

14 Perceptual Consequences of Timing Differences Within Parallel Feature-Processing Systems in Human Vision

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The transmission of information in sensory systems and within the brain occurs primarily via neural action potentials, which take time to generate and transmit. For example, the conduction velocities of mammalian unmyelinated retinal axons range approximately between 1 and 5 m/s, depending on the axon diameter. The conduction velocities of myelinated optic nerve axons also vary systematically with fiber diameter, ranging approximately between 5 and 30 m/s (Tolhurst & Lewis, 1992). As a result of the delays that are introduced by the elaboration and transmission of neural signals, information processing within the brain must always lag to a greater or lesser extent behind the real-world events that this brain information represents.

In this chapter, we will focus on the temporal aspects of information processing within the primate and human visual systems. The earliest stages of visual information processing in the retina depend to some extent on the characteristics of the visual stimulus. For example, the earliest responses that are recorded in the optic nerve vary inversely with the luminance of the visual stimulus (Lennie, 1981; Lee et al., 1990). These stimulus-dependent differences in neural response time carry forward to produce the initial responses to visual events in the lateral geniculate nucleus and visual cortex (e.g., Maunsell & Gibson, 1992; Maunsell et al., 1999).

Two additional properties of the primate visual system generate additional difficulties for the timing of visual events. First, evidence exists that visual information is encoded and transmitted from the retina to the visual cortex in two (or three; see Dacey & Lee, 1994; Hendry & Reid, 2000) parallel pathways, with overlapping but different temporal characteristics (Maunsell & Gibson, 1992; Schmolesky et al., 1998; Maunsell et al., 1999). And, second, visual information processing in the brain appears to be largely modular. That is, information about many aspects of the visual stimulus (e.g., color, motion, depth, etc.) is processed in specialized brain centers (e.g., Zeki & Shipp, 1988; Livingstone & Hubel, 1988; van Essen et al., 1992; Tootell et al., 1996; however, for a different view see Lennie, 1998), each of which may require a different amount of time to complete its analysis. Although the various brain areas are richly interconnected (van Essen et al., 1992; Tootell et al., 1996), it is unclear to what extent the vision-related events that result from modular processing within different areas in the brain are synchronized.

Uniform neural conduction and processing delays should cause sensory events to be registered or perceived at some fixed time after they actually occur. Clearly, such delays are detrimental for accurate interaction with the physical world, much of which must occur "online" in real time. One general strategy to alleviate this problem is motor prediction (Kerzel & Gegenfurtner, 2003), that is, the generation of motor programs and responses to stimuli based on the recent previous record of sensory information. The accuracy of this approach can be monitored by the sensory feedback that results from motor events (cf. von Holst & Mittelstädt, 1950), such as the retinal position and velocity signals that occur during ocular tracking of visual targets or during manual reaching responses to moving stimuli (Goodale et al., 1986; Barnes & Asselman, 1991; Saunders & Knill, 2003).

Even more problematic are the *differential* timing errors that would be expected to result from the unequal conduction and processing delays within specialized neural streams and within brain areas that preferentially encode and process different characteristics of a stimulus. These differential processing delays raise the possibility that different stimulus attributes could reach perception at different times, which would be expected to lead to interesting, annoying, and sometimes dangerous errors in perception. One well-known illusion of this type is the *Pulfrich stereo-phenomenon*, wherein a longer conduction latency from one eye (as the result of unequal target luminance in the two eyes or of unilateral optic nerve pathology, e.g., Lit, 1960; Julesz & White, 1969; Rushton, 1975) produces substantial distortions of perceived stereoscopic depth during object or observer motion.

The goal of this chapter is to consider two visual illusions—the flash-lag phenomenon and color–motion perceptual asynchrony—that have been attributed by some authors to differences in relative neural timing. We will refer to this explanation based on a difference in neural timing as the *differential-latency hypothesis*. First, we will provide a brief description of the phenomenology associated with each illusion. Next, we will examine the influence of stimulus parameters and of the observer's task on each illusion. Finally, we will present a qualitative model to account for both illusions, which represents essentially an elaborated version of the differential-latency hypothesis.

14.1 The Flash-Lag Effect

The flash-lag effect (FLE) is the perception that a briefly flashed target is at an erroneous location with respect to a continuously moving target. In particular, the flashed target typically appears to lag spatially behind the moving target when both are presented simultaneously at the same spatial location (for reviews, see Krekelberg & Lappe, 2001; Nijhawan, 2002; Öğmen et al., 2004b). Most investigators agree that the FLE requires the image of the moving target to traverse across the retina (Brenner et al., 2001; Nijhawan, 2001; but also see Cai et al., 2000), although it appears to be immaterial whether motion of the retinal image results from object or eye motion (Mateeff & Hohnsbein, 1988; Nijhawan, 2001; van Beers et al., 2001). The spatial magnitude of the FLE increases linearly with the velocity of the moving target (Nijhawan, 1994; Krekelberg & Lappe, 2000), which implies that the FLE corresponds to a constant temporal delay of the flashed stimulus with respect to the moving target. This interpretation is consistent with the earliest explanations of the FLE in terms of a difference in the "sensation time" or "perception time" between the flashed and moving targets (e.g., Metzger, 1932). Our version of this differential-latency hypothesis assumes that the relative delay in determining the position of a moving compared to a flashed target is associated primarily with the characteristics of different neural streams that are hypothesized to process moving versus nonmoving (in this instance, flashed) stimuli. However, we do not assume that the delay in each processing stream is fixed but rather, as discussed below, that it varies systematically with characteristics of the target and the observer's task. As summarized, for example, in Krekelberg and Lappe (2001), Nijhawan (2002), and Öğmen et al. (2004b), a number of competing explanations have been proposed previously for the FLE.

The FLE still occurs when the flashed target occurs concurrently with the onset of motion (Khurana & Nijhawan, 1995; Eagleman & Sejnowski, 2000a; Patel et al., 2000). Initially, this result may be surprising, as a moving and a flashed target are physically indistinguishable right at the onset of motion. However, a moving target has been reported to become visible only after it traverses the earliest portion of its trajectory, presumably because of spatiotemporal interactions that are inherent in the early phases of motion processing. This phenomenon, known as the *Fröhlich effect*, could conceivably account for the presence of a flash lag when the flash is presented concurrently with the beginning of target motion (Eagleman & Sejnowski, 2000a). However, this possibility is not supported by findings that the Fröhlich effect can be substantially smaller than the FLE that occurs at the onset of motion (Whitney & Cavanagh, 2000; Müsseler et al., 2002; Kreegipuu & Allik, 2003).

The magnitude of the FLE depends on the retinal eccentricity of the targets (Baldo et al., 2002), and possibly also on whether the spatial position and timing of the flashed target are predictable (Khurana et al., 2000; Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000b; Baldo et al., 2002; Namba & Baldo, 2004). For parafoveal flashed and moving targets that are approximately the same luminance, a typical magnitude of the FLE is 40–80 ms (e.g., Whitney et al., 2000; Krekelberg & Lappe, 2001).

Altering the detectability of the flashed and moving stimuli results in systematic changes in the temporal magnitude of the measured FLE. For example, making the flashed target dimmer increases the FLE, and making the flashed target brighter reduces the FLE (Purushothaman et al., 1998; Lappe & Krekelberg, 1998; Öğmen et al., 2004b). If the flash is very bright and the moving stimulus is dim, the flash lag can reverse to a flash lead (see figure 14.1; see also Purushothaman et al., 1998; Patel et al., 2000). The existence of a flash lead casts substantial doubt on several proposed explanations for the FLE—for example, those that require the position of the moving target to be sampled only *after* the flash is perceived (cf. Öğmen et al., 2004b).

The changes in the FLE with target luminance can be accounted for on the basis of latency changes in the visual system that occur with variations in the stimulus intensity. As noted above, physiological recordings indicate that the latency of visual responses increases systematically as the luminance of the stimulus is reduced (Lennie, 1981; Lee et al., 1990; Maunsell & Gibson, 1992; Maunsell et al., 1999). In addition to the Pulfrich stereo-phenomenon, another piece of psychophysical

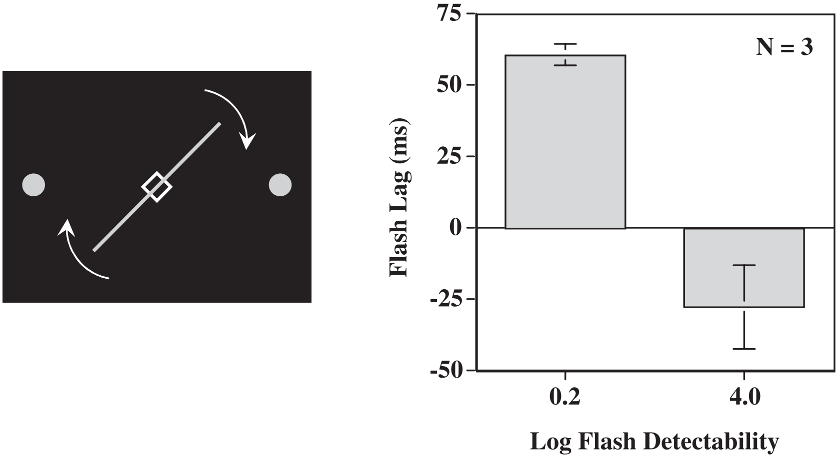


Figure 14.1
The flash-lag effect (FLE) can be determined as the temporal offset, with respect to the instant of *physical* alignment between a pair of briefly flashed dots and a rotating line, that yields the perception that the dots and line are in spatial alignment (left). The measured FLE changes from approximately a 60-ms lag (flashes presented *before* physical alignment with the moving line) to approximately a 25-ms lead (flashes presented *after* physical alignment with the moving line) when the luminance of the flashes increases from 0.2 to 4.0 log units above their detection threshold (right). The luminance of the rotating line was 0.5 log units above its detection threshold. (Data are the average of three observers ±1 *SE*, replotted from Öğmen et al., 2004b)

evidence for the dependence of visual processing latency on stimulus luminance is the *Hess effect*, wherein the dimmer of two moving stimuli is perceived to lag behind the brighter one, even though both stimuli are physically aligned. According to Williams and Lit (1983), the Hess effect corresponds to a delay of approximately 50 ms when the luminance of two relatively dim photopic moving stimuli differs by 2 log units.

14.2 Perceived Color–Motion Asynchrony

More recently, experiments using stimuli that change periodically in color and direction of motion have led to the inference that a temporal asynchrony exists between the processing of color and motion information in the brain (Moutoussis & Zeki, 1997a, 1997b; Zeki & Moutoussis, 1997). Consider the stimulus pictured in figure 14.2A, which is modeled after the stimulus used in the initial report of this phenomenon (Moutoussis & Zeki, 1997a). In order for the squares to be perceived as uniformly red when moving upward and uniformly green when moving downward, the change from upward to downward motion has to precede the change in color by between 80 and 140 ms (Moutoussis & Zeki, 1997a, 1997b; Zeki & Moutoussis, 1997; Arnold & Clifford, 2002; Nishida & Johnston, 2002; Bedell et al., 2003). Moutoussis and Zeki (1997a, 1997b) interpreted this result to mean that the neural processing of motion information lags behind the processing of color by this amount of time. Using a similar paradigm, the processing of stimulus orientation also was inferred to lag behind the processing of color (Moutoussis & Zeki, 1997b).

Altering the characteristics of the stimuli can substantially change the outcome of these temporal asynchrony experiments. For example, if the direction of motion change is less than 180°, then a much smaller temporal advance of the motion stimulus is required for stimulus color and motion to be perceived in correspondence. In particular, when the change in direction of motion is 45°, both Arnold and Clifford (2002) and Bedell et al. (2003) have reported that the apparent temporal asynchrony decreased from approximately 140 to 80 ms.

Changing the observers' task can cause the apparent temporal asynchrony between color and motion to vanish almost completely. Nishida and Johnston (2002) presented their observers with a stimulus on one side of fixation that changed in color from green to red and a second stimulus on the opposite side of fixation that changed in direction of motion from upward to downward. Both stimuli changed just once during each trial. Observers performed a temporal order judgment, by reporting whether the change in color or the change in direction of motion occurred first. The results indicate virtually no perceptual asynchrony when the color and direction of stimulus motion changed physically at the same time.[1]

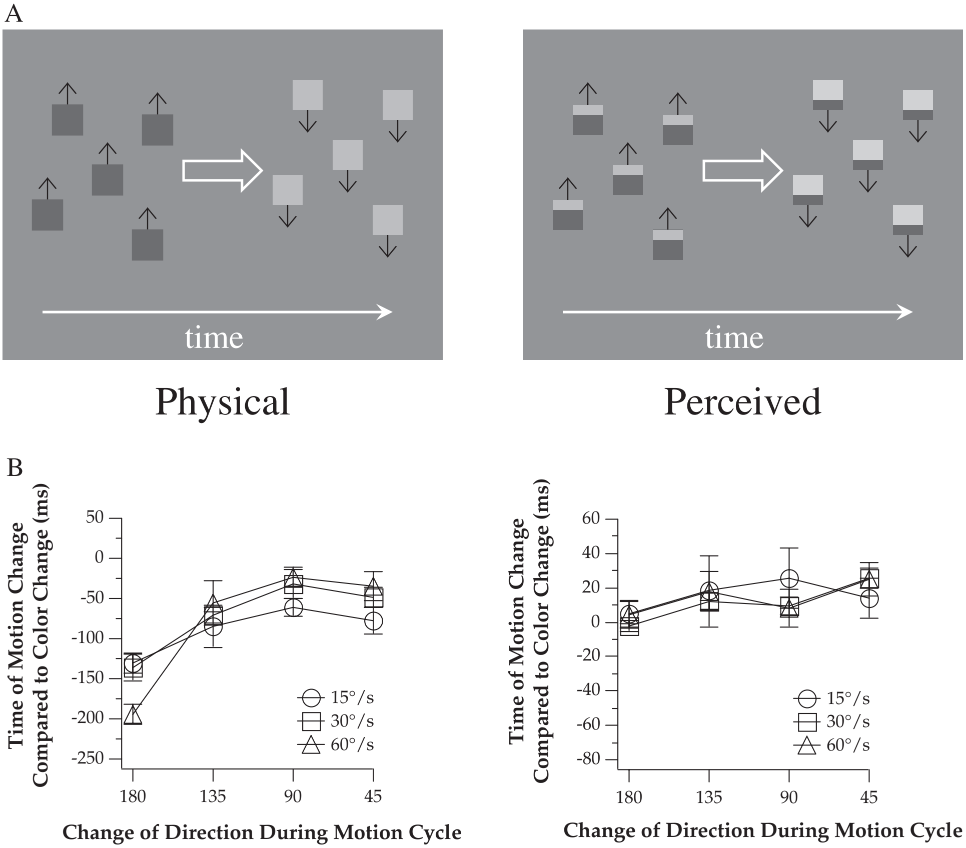
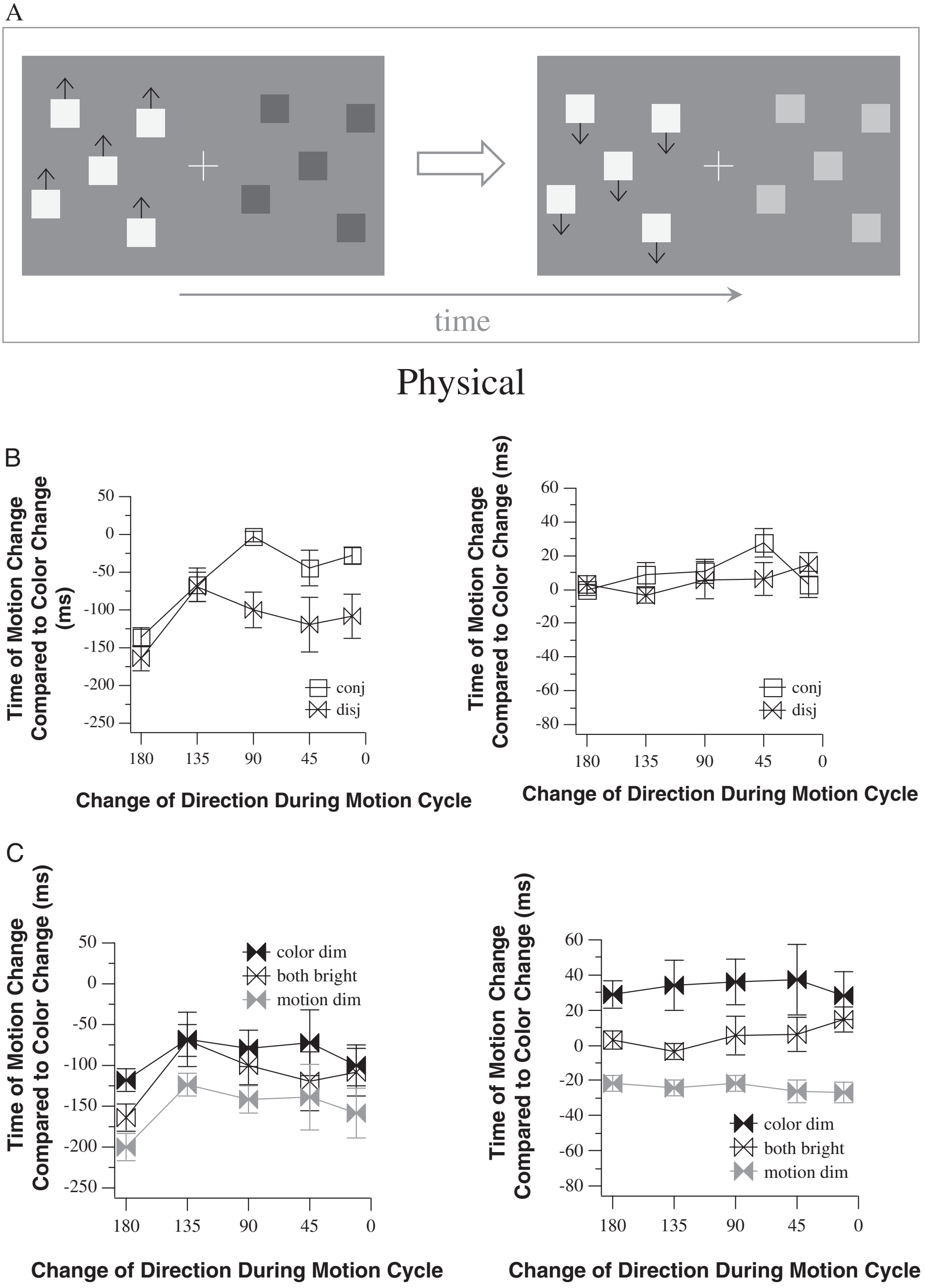


Figure 14.2
(*A*) A field of moving dots that synchronously changes color from red to green and direction of motion from up to down is perceived to change in color during both upward and downward motion. This stimulus, in which each dot undergoes both a color and direction-of-motion change, is referred to as the *conjunctive* stimulus in the text. Red and green colors are indicated by relatively darker and lighter shades of gray in the figure, but in our experiments both stimulus colors were adjusted to be equally above the detection threshold. (*B*) The temporal asynchrony between the change in color and the change in direction of motion that is required for perceptual synchrony between color and motion depends on the observers' task. Depending on the magnitude of the direction change, the direction of dot motion has to change between 50 and 150 ms before dot color in order for observers to perceive the motion and color of the dots to correspond temporally (left panel). Regardless of the magnitude of the direction change, the direction of dot motion and dot color have to change at approximately the same time for observers to perceive both changes to occur simultaneously (right panel). Data are the averages of four (left) or three (right) observers, for three velocities of dot motion (Bedell et al., 2003). The temporal period of each cycle of color and motion change was 706 ms.

We replicated this finding, using a single, composite stimulus like that used by Moutoussis and Zeki (1997a) for a range of motion-direction changes between 45 and 180 deg (see figure 14.2B). In one condition, the color and direction of motion of the stimulus changed just once during each trial. In another condition, the color and direction of motion changed repetitively, but the observers waited until the final half cycle of color and motion change, signaled by an auditory cue, to make the temporal order judgment. In neither of these conditions did the perceived temporal asynchrony between the change in color and direction of motion differ significantly from zero, regardless of the magnitude of the direction change. In contrast, the same observers judged the color and direction of motion of the repetitively changing stimulus to correspond when the change in direction of motion occurred 30 to 140 ms earlier (depending on the magnitude of the direction change) than the change in stimulus color. Clifford et al. (2003) reported a similar task-dependent outcome for stimuli that changed in color and orientation.

On the basis of the influence of target luminance on the FLE, we expected that changing the detectability of a stimulus that alternated in color and direction of motion should systematically influence the magnitude of the apparent temporal asynchronies in the color correspondence and temporal order tasks. To test this hypothesis, we modified our stimulus, so that the luminance of the color and motion components could be manipulated separately. The stimulus that we adopted was similar to the one described above for the temporal order experiment of Nishida and Johnston (2002) and, previously, by Moutoussis and Zeki (1997b). As depicted in figure 14.3A, a field of stationary 1.1 deg squares on the right side of fixation changed periodically (1.42 Hz) from red to green, and a field of yellow squares on the left side of fixation changed periodically between upward and downward motion at 30 deg/s. At the observers' viewing distance of 21 cm, each stimulus field subtended 11.3 × 11.3 deg, and the edge-to-edge separation between the right and left fields was 1.4 deg. In agreement with the results of Moutoussis and Zeki (1997b), the motion in the left field had to reverse in direction substantially earlier than the change in color in the right half field, in order for the observers to judge the color and motion of the stimuli to be in correspondence (see figure 14.3B). For other magnitudes of motion-direction change, this "disjunctive" stimulus yielded results that were similar, although not identical, to those obtained on the color–motion correspondence task using the original "conjunctive" color–motion stimulus (see figure 14.3B). As with our original, conjunctive stimulus, temporal order judgments made with the disjunctive stimulus showed no significant color–motion asynchrony.

In the experiment described above, each of the stimuli in the color–motion display were approximately 4.4 log units above the observers' detection threshold. Decreasing the luminance of the targets on either the right or the left side of the display produced the expected changes in timing in both the color–motion correspondence


A
time
Physical
B
Time of Motion Change Compared to Color Change (ms)
50
0
-50
-100
-150
-200
-250
180
135
90
45
0
conj
disj
Change of Direction During Motion Cycle
Time of Motion Change Compared to Color Change (ms)
60
40
20
0
-20
-40
-60
-80
180
135
90
45
0
conj
disj
Change of Direction During Motion Cycle
C
Time of Motion Change Compared to Color Change (ms)
50
0
-50
-100
-150
-200
-250
color dim
both bright
motion dim
180
135
90
45
0
Change of Direction During Motion Cycle
Time of Motion Change Compared to Color Change (ms)
60
40
20
0
-20
-40
-60
-80
color dim
both bright
motion dim
180
135
90
45
0
Change of Direction During Motion Cycle

task and the temporal order task (see figure 14.3C). Specifically, when the luminance of the right-hand (changing-color) side of the display was reduced by 2 log units, the apparent temporal asynchrony in the color–motion correspondence task decreased by approximately 25 ms, for all tested directions of motion change. When the luminance of the left-hand (changing-direction-of-motion) side of the display was reduced by 2 log units, the apparent temporal asynchrony between color and motion increased by approximately 40 ms. Across all directions of motion change, the absolute magnitude of the luminance-induced changes in apparent asynchrony does not depend on which side of the display was made dimmer, $t(4) = 0.93$, $p = .40$. Very similar changes, of approximately ±30 ms, were obtained for the temporal order judgments when the luminance of the color or the motion stimulus was decreased by 2 log units.

14.3 A Qualitative Model for Perceived Temporal Asynchronies

Figure 14.4 shows a qualitative model to account for the findings of experiments on the flash-lag and color–motion asynchrony, which are summarized in the sections above. Consistent with previous physiological and psychophysical data, we envision that the cortical processing of visual information is modular, with separate specialized brain areas devoted to the processing of visual motion, color, static position, and so forth (Livingstone & Hubel, 1988; van Essen et al., 1992; Tootell et al., 1996). The model in figure 14.4 incorporates separate delays between the retina and each brain module, in order to represent the possibility that each of these retinocortical delays may not be the same. Rather, the delay for retinal information to reach each cortical module is likely to depend on the processing stream that is involved, the amount of preprocessing that is required before the information reaches each module (e.g., in early stages of V1), and on the characteristics of the stimulus (see below).

Figure 14.3
(*A*) The *disjunctive* stimulus consists of two fields of dots that straddle a central fixation target. The right-hand field of dots changes color and the left-hand field of dots changes direction of motion, both with a period of 706 ms. (*B*) Temporal asynchronies between the change in color and the change in direction of motion to achieve perceived temporal correspondence between color and motion vary similarly with the direction of motion change for the conjunctive (conj) and disjunctive (disj) stimulus (left panel). However, the direction of dot motion and dot color have to change at approximately the same time for observers to perceive both changes simultaneously, for both the conjunctive (conj) and disjunctive (disj) stimulus (right panel). Plotted data are the average of two observers, for a speed of dot motion of 30* deg/s. (*C*) A 2 log-unit decrease in the luminance of the dots that change in color or direction of motion produces a systematic shift in the temporal asynchrony that is required to achieve perceived temporal correspondence (left panel) or perceived simultaneity (right panel) between color and motion. Note that the *y*-axes are scaled differently in the left and right panels. The plotted data are the averages of the same two observers shown figure 14.3B, using the "disjunctive" stimulus and dot motion of 30 deg/s.

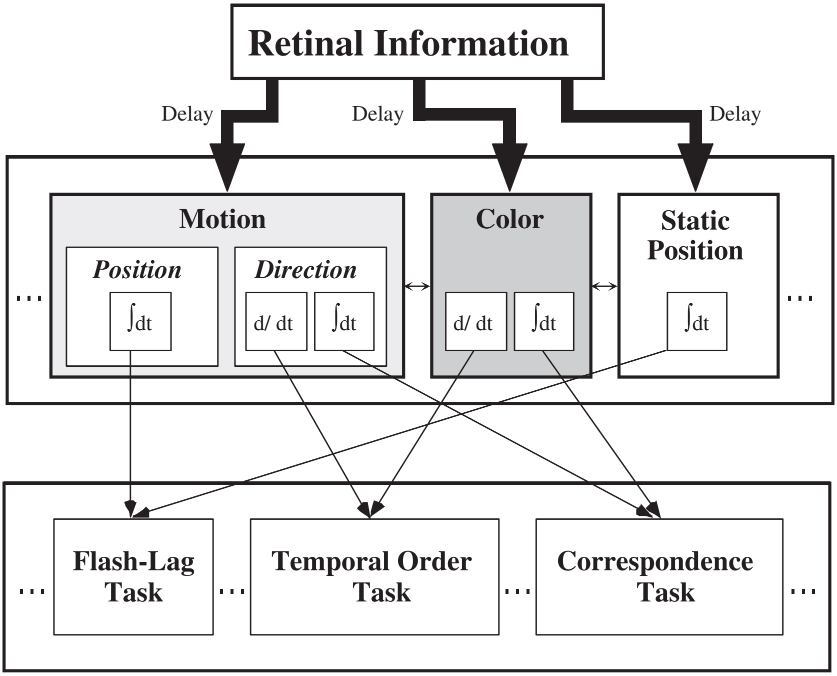


Figure 14.4
A qualitative model to account for the perceived temporal asynchronies between various stimulus attributes, for different perceptual tasks. The components of the model and their temporal properties are described in the text.

The color processing module in the center of the figure is subdivided functionally according to the temporal characteristics of the information processing that occurs. This module can provide sustained information about stimulus color, based on a relatively slow process that includes an obligatory stage of temporal integration. In addition, we propose that a different subdivision of the same color module can provide more rapid information about *changes* in color, based on operations that respond selectively to transients or variation in the chromatic content of the stimulus.[2] In our scheme, the rapid information about color change is not necessarily informative about the actual color that is present, which becomes available only after integration of the stimulus-related input in the slower, sustained subdivision of this module.

The motion processing module at the left of the figure is shown to include more than one functional component. One of these provides integrated, sustained information about the direction of motion, as well as more rapid information that specifies the occurrence of a change in the direction of motion. A second, presumably parallel component uses motion information to determine the position of a moving target. A separate module shown at the right of the figure provides sustained output about the position of nonmoving targets.[3]

Like the color module and the direction component of the motion module, other modules not shown in the figure (such as modules for processing orientation and depth) are envisioned to have a similar architecture, with the ability to provide separate information about sustained and transient features of various visual stimuli. Although the general characteristics of sustained and transient signal processing are presumed to be similar within each module, we do not believe that each module's temporal properties are identical (cf. the discussion of the FLE, below).

The final layer that is shown in the model represents a highly flexible level of processing that compares the information from relevant modules or module subdivisions, in order to meet the requirements of the observer's specific task. Based on the topics that we discussed in this chapter, the figure shows the proposed comparisons between visual information for just three types of tasks: (1) the perceived positions of a moving and a nonmoving target that give rise to the FLE, (2) target color and the direction of stimulus motion as in the color–motion correspondence task described originally by Moutoussis and Zeki (1997a, 1997b), and (3) *changes* in the color and the direction of motion of one or more stimuli as in the temporal order judgments reported by Nishida and Johnston (2002) and others. In the remainder of the chapter we will consider how the model in figure 14.4 accounts for the principal results that are reported for these three tasks. However, the model permits a much larger number of stimulus comparisons to be made, especially if one considers additional visual (and nonvisual) processing modules and divisions that are not currently represented explicitly in the figure.[4]

The main findings that the model can account for are:

1. The flash-lag paradigm requires observers to compare the temporally integrated position signals from the motion and static-position modules. We assume that this comparison occurs at the instant the flash becomes visible, as specified by a transient signal of target brightness or contrast that is not depicted explicitly in this representation of the model (see Öğmen et al., 2004b). Presumably, the FLE occurs because retinal information is delayed less in reaching the motion module compared to the static-position module and/or because, for a continuously moving stimulus, the processing of motion into a signal of target position occurs more quickly than the generation of a static-position signal. Systematic variations in the magnitude and direction of the FLE for targets of different luminance are attributable primarily to luminance-dependent changes in the delays that retinal information undergoes before it reaches the cortical modules that analyze motion and static position. In contrast, the reported modulation of the FLE according to the predictability of the flashed target (Khurana et al., 2000; Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000b; Baldo et al., 2002; Namba & Baldo, 2004) could reflect an unequal

facilitation of position processing by attentional mechanisms within the motion and static-position modules.

2. In the model, judgments of color–motion correspondence require a comparison between the temporally integrated information from the color–processing module and the subdivision of the motion-processing module that determines the direction of target motion (Bedell et al., 2003). As indicated above, the apparent temporal asynchrony between color and motion is appreciably longer when the motion stimulus reverses its direction, compared to when the change in the direction of motion is smaller than 180 deg (Arnold & Clifford, 2002; Bedell et al., 2003). To interpret this result, we note a moving stimulus that reverses in direction will sequentially stimulate a pair of opponent motion channels, whereas a stimulus that changes direction by an appreciably smaller angle (e.g., 135 deg or less) will not. When opponent motion channels are activated one after the other, the response to the first direction of motion may have to be terminated before a response to the opposite direction of motion can begin. Consequently, the generation of an integrated signal to indicate the direction of motion would be expected to include a longer delay within the motion-processing module when a pair of opponent motion channels are activated than when opponent channels are not involved (i.e., for direction changes that are less than 180 deg). A similar added delay could accrue when opponent *color* channels are stimulated in succession, but the results of color–motion correspondence experiments suggest that this delay must be relatively small. Possibly, motion information is integrated over a longer period of time than color, in order to generate a reliable steady-state signal for the direction of motion. Clifford et al. (2003) offered a similar interpretation of their data on the apparent perceptual asynchronies between color and orientation changes, namely, that differences in the integration properties for different dimensions of the stimulus would be expected to produce an effective phase shift in perceived temporal correspondence.

3. In contrast to judgments of color–motion correspondence, temporal order judgments do *not* require integrated information about either the current stimulus color or its direction of motion. Consequently, these judgments can be based on the detection of transients that occur in association with a change in stimulus color or direction of motion. In the model, information about changes in the color and direction of motion of the stimulus are available from the transient subdivisions of each processing module. Because the transient signals for color and direction change do not require temporal integration (and, specifically, do not involve the relatively slow integration of information within opponent motion channels), each module can provide these signals quickly and with very little *relative* delay.

Nishida and Johnston (2002) reported that the apparent temporal asynchrony between color and motion varies systematically with the temporal frequency of the color and motion changes. Specifically, when the color and the direction of motion of their stimuli alternated at 2 Hz, observers judged these changes to occur in phase if the direction of motion changed physically about 100 ms earlier than the change in color. In contrast, when the color and direction of motion of their stimuli changed at 0.25 Hz, the observers' judgments about relative phase were close to veridical. Our interpretation of these data is that their observers used information from the transient subdivisions of the color and motion modules to make temporal order judgments when the temporal frequency of color and direction changes was low. When the temporal frequency of color and direction changes increased, it may have been difficult for the observers to compare the resulting transients accurately for the same half cycle. If so, then the observers would have been forced to rely on the temporally integrated information about color and direction of motion to make a comparison, thereby switching to a color–motion correspondence judgment.

4. Reducing the luminance of either the color or the motion component of the stimulus introduces comparable changes in timing, both for judgments of color–motion correspondence and of temporal order. Analogous to our discussion of the influence of target luminance on the FLE, above, the most parsimonious interpretation of these results is that a decrease in the luminance of one component of the stimulus increases the neural delay before information about that component reaches the cortical module that analyzes color or motion.[5] This analogy between the effects of target luminance in the color–motion asynchrony and the FLE paradigms can also be examined quantitatively. As shown in figure 14.3, a decrease in the luminance of the color or the motion target from approximately 4.4 to 2.4 log units above its luminance detection threshold produced approximately a 30-ms change in timing. In agreement with this result, we reported recently that the FLE also increases by approximately 30 ms when the luminance of the flashed target decreases from 4 to 2 log units above its detection threshold (Öğmen et al., 2004b). The correspondence between these values is striking, as the luminance-dependent changes in delay that occur in these different experiments involve different cortical modules as illustrated in the model in figure 14.4.

14.4 Summary and Conclusions

The principal points in this chapter may be summarized as follows:

1. The relative timing of perceived visual events is influenced by the characteristics of the neural channels and mechanisms that respond to specific stimulus characteristics. For example, the FLE suggests that the processing of position for a moving stimulus occurs more quickly than the processing of position for a flashed stimulus.

2. The relative timing of perceived visual events varies also with stimulus parameters that influence the delay involved in low-level visual processing, such as luminance and retinal eccentricity.

3. The observers' task also influences the relative timing of perceived events, based on the type of information and information processing (e.g., temporally averaged vs. transient) that is required to perform the task.

Acknowledgments

Preparation of this chapter and the studies that are reported in it were supported by Research Grants R01 EY05068 (to Harold E. Bedell), R01 MH49892 (to Haluk Öğmen), and R01 EY12810 (to Susana T. L. Chung) from the National Institutes of Health. We thank our collaborators, Gopathy Purushothaman and Kaan Camuz, who were instrumental in collecting some of the data that we describe.

Notes

1. Viviani and Aymoz (2001) reported a nonzero temporal asynchrony between a change in color and a change in motion using a temporal order task. However, in their experiment the changes in color and motion occurred at different retinal eccentricities, which may have introduced an additional timing difference (see Bedell et al., 2003).

2. However, even the transient subdivision includes a finite period of integration, which places an upper limit on the temporal frequency of visual changes to which it can respond.

3. Although not represented in the figure, the static position module and the position component of the motion module could include transient as well as sustained functional subdivisions.

4. Our representation of the model is *not* meant to suggest that separate sites are required for each possible comparison between stimuli. Although it remains unclear how and where such comparisons occur, the model stipulates only that the comparison site(s) must be able to observe simultaneously the outputs of the relevant processing modules.

5. The smallest change in the direction of motion that we presented in our experiments was 11.3 deg (the right-most data points in each panel of figure 14.3B and 14.3C). This value is only about four times the threshold for discriminating a change in the direction of motion for this stimulus. Based on the difficulty of discriminating such a small change in the direction of motion, one might expect that the apparent temporal lag between motion and color would increase, compared to conditions in which the change in the direction of motion is larger. This expectation is supported by findings that reaction times are prolonged substantially when observers are asked to respond to small compared to larger changes in the direction of stimulus motion (Mateeff et al., 1999; Genova et al., 2000). Nevertheless, our results indicate that the apparent temporal lag in the color–motion correspondence task is similar for changes in the direction of motion from 11.3 deg to 135 deg, and that the perceived temporal order between color and motion is similar for changes in the direction of motion from 11.3 deg to 180 deg. Our explanation for these results, which may be applied also to other reported dissociations between judgments of temporal order and reaction times (e.g., Williams & Lit, 1983), is that an additional delay can be introduced for stimuli of low discriminability *after* the stimuli are processed by the cortical color and motion modules, at the level where the module outputs are compared. Clearly, this additional delay is task specific and therefore presumably represents an operation, such as thresholding (e.g., Sternberg & Knoll, 1973), that is implemented differently in the reaction time and temporal order tasks.