

[Holcombe, A.O. \(2009\)](#) Seeing slow and seeing fast: Two limits on perception. *Trends in Cognitive Science*, 13(5):216-21.

[doi:10.1016/j.tics.2009.02.005](https://doi.org/10.1016/j.tics.2009.02.005)

THIS IS A POST-PRINT. THERE MAY BE SMALL DIFFERENCES WITH THE PUBLISHER'S VERSION

## Seeing slow and seeing fast: Two limits on perception

### Abstract

*Video cameras have a single temporal limit set by the frame rate. The human visual system has multiple temporal limits set by its various constituent mechanisms. These limits appear to form two groups. A fast group comprises specialized mechanisms for extracting perceptual qualities such as motion direction, depth, and edges. The second group, with coarse temporal resolution, includes judgments of the pairing of color and motion, the joint identification of arbitrary spatially separated features, the recognition of words, and high-level motion. These temporally coarse percepts may all be mediated by high-level processes. Working at very different timescales, the two groups of mechanisms collaborate to create our unified visual experience.*

### Spatial versus temporal scales

Our visual system has a spatial grain, making small details completely invisible, such as the individual molecules forming the surface you are currently viewing. Less appreciated is that our processing of time is also confined to coarse scales. Events confined to thousands of a second, and sometimes even hundredths of a second or longer, are not perceived. For example, until brief-exposure photography was invented in the 1870s, it was not known whether a galloping horse lifts all four hooves off the ground at any one time [1].

Just as the microscope probed small spatial scales long before stroboscopic photography investigated small temporal scales, so vision scientists have traditionally concentrated on vision's spatial resolution rather than its temporal resolution. But recent years have seen an upsurge in interest in temporal processing. Much of this growth has been in areas of temporal illusions, such as distortions in time perception [2], asynchronies in binding the features of an object [3], and possible interactions between object motion and the time an object is perceived [4]. Recent reviews of these topics are available [5-7], but missing from the literature is a modern synopsis of the temporal limits of vision—the timescales on which the machinery of perception operates. These temporal limits set the foundation necessary to understand temporal illusions, and in bringing together the diverse psychophysical literature on temporal limits, a broad generalization emerges regarding the functional organization of the visual system.

## Understanding multiple temporal scales

Let's begin with a naïve question—does your visual experience display the world at five, twenty, or one hundred frames per second? In the case of the cinema, we know there is a frame rate, a temporal grain of twenty-four per second. But our visual system does not operate like movie equipment. Visual processing is more continuous [8]—although see [9] for the suggestion of a discrete component. In continuous processing, although there is no frame rate because discrete snapshots are not taken, the system still can be said to have a temporal grain. The grain, or temporal interval over which the system blurs information together, is known as *temporal resolution*. A movie camera has one temporal resolution, reflecting its frame rate. But the visual system has multiple temporal resolutions.

The high temporal resolution of some of our perceptual mechanisms presents a problem for the cinematographer working with a film shot, as most are, at twenty-four pictures per second. If films were projected at 24 frames per second, the flicker would be obvious and annoying, because our flicker perception mechanism is fast enough to detect 24-Hz flicker. To thwart both flicker perception and some motion artifacts that our fast motion mechanisms are sensitive to, cinema projectors flick each frame on and off twice before moving on to the next frame. The resulting 48 per second (48 Hz) flicker rate is almost invisible to us.

Although the technique eliminates the flicker perception problem, one might expect other problems to remain. As each object is shown twice in the same location before moving on, a cinematic car chase might appear as a stuttering procession rather than as the familiar fluid and seamless experience. Fortunately for the cinematographer, our visual perception fails to register the stuttering—a consequence of the coarse temporal scale at which most perceptual mechanisms process the scene. As will be described below, the 24 pictures per second rate is already too fast for many of our visual mechanisms. Our perception comprises some mechanisms, like flicker and motion, that inform us of rapid changes, while others are restricted to much slower changes and thus fooled by a 24 Hz simulacrum of reality.

Two of the temporal limits underpinning experience can be demonstrated with a simple animation. In Movie 1, adjacent striped patches alternate between leftward-tilted and rightward-tilted. When the alternation rate is only a few per second (top row), it is easy to perceive whether the two patches are always opposite in orientation (top left) or are always oriented in the same way (top right). If the patches are alternated at a faster rate, say between 8 and 12 frames per second (second row), it becomes difficult or impossible to judge whether the patches have the same orientation or opposite orientations [10]. Interestingly, although too fast for the temporal relationship of the two features to be perceived, this rate is nevertheless slow enough to identify the two orientations [11] and to detect the flicker. Not until the rate is increased much further would the movie appear completely fused (bottom row), with neither the relationship of the two

patches, their individual patterns, nor their flicker perceived.

Each speed limit likely corresponds to the narrowest temporal scale at which a perceptual mechanism operates. Consider the perception of fluorescent lights, which illuminate the workdays of most office workers. Fluorescent lights flicker—120 times per second (120 Hz) in the US and 100 Hz in many other places. We do not perceive this flicker because our underlying visual detectors average their inputs over a longer interval. Indeed, our visual mechanisms average over 20 milliseconds or more, blurring together an entire 10-ms cycle of 100 Hz flicker and therefore obliterating the changes in luminance in the fluorescent lights and in the 48-Hz flicker of the double-projected cinema.

At first, one might think this integration interval could be revealed by presenting a stimulus a single time rather than in a cycle, and determining the shortest duration for which it can still be perceived. But a 5-ms stimulus flash, if sufficiently high contrast, can be analyzed even by a mechanism that operates at a slow 100-ms scale, because averaging over 100 ms will not eliminate the stimulus information. This point has been key to a debate in the literature on the timescale of visual grouping [12]. The alternating displays referred to in the present article are specifically designed to provide no information when a mechanism integrates over the cycle of alternation. Restricting ourselves to such displays will lead us to ignore for now (but see Box 1) the interesting literature on the effect of varying presentation duration of a single stimulus.

Although many studies have probed the temporal limits of visual judgments using the alternating stimulus technique, because these studies have used very different stimuli and tasks, the results usually cannot be compared with quantitative precision. However, in some cases the speed limits found differ so much that the differences are unlikely to be caused by experiment details. Figure 1 shows some of these limits. The limits fall into two clusters, slow and fast, separated by a large gap.

### **Fast limits on visual percepts**

The fast cluster includes flicker perception. The “flicker fusion” limit, like others, depends on mean luminance, luminance contrast, and other factors, but is usually at least 50 Hz on ordinary computer screens. Only six other types of visual judgments have been found to be of comparable speed:

- **first-order motion**: A moving sinusoidal grating with bright peaks and dark troughs is seen through a window. Even when its velocity is so high that 30 of its bright peaks pass each location per second (30 Hz), observers still perceive its direction of motion [13]. If the input to motion detectors was blurred or jumbled over this timescale, determining the motion direction would be impossible. Flicker is a degenerate case of motion and the same bank of fast detectors could be responsible for both the motion and flicker limits.
- **depth from binocular disparity**: Two identical gratings, one in each eye, are

viewed through identical windows. One is spatially shifted relative to the other, introducing a binocular disparity that is perceived as depth. Even when they move at a 30-Hz rate, the depth is still perceived [14]. If the input to depth mechanisms were blurred at a  $>30$  ms timescale, detecting the depth would be impossible at this rate.

- **edges and texture boundaries:** Against a gray background, a field of white dots is adjacent to a field of black dots. Both fields are set in rapid alternation between white and black, but out of phase—when one is white, the other is black. The conspicuous boundary between them is perceived even at fast rates of 30 Hz [15, 16], while at faster rates the black and white are averaged by the brain into the same color as the background. Texture boundaries defined by orientation differences can also be seen at fast rates [11].
- **binding of color and orientation sharing a spatial location:** If a red, right-tilted patch is alternated with a green, left-tilted patch, it is easy to distinguish from the complementary pairing of red left alternating with green right, even at fast 20 Hz rates [17] (demo at [www.psych.usyd.edu.au/staff/alexh/research/binding/](http://www.psych.usyd.edu.au/staff/alexh/research/binding/) )
- **color and orientation as individual features:** Fast binding of color and orientation could not occur without fast processing of the individual color and orientation features. Indeed, the features might be perceived at rates even faster than is their pairing [18] although this remains unsettled as the slower limit for the pairing could instead be caused by an asynchrony in processing of the features.
- **binding of local orientation elements into a global form:** The visual system can efficiently integrate hundreds of local oriented elements distributed across the visual field into an overall shape, and do so even when rapid alternation requires the computation to occur over less than 30 ms [19] (demo at <http://www.psych.usyd.edu.au/staff/colinc/HTML/dynamics.htm> ) Symmetry judgments of such patterns might be similarly rapid [20].

### **Slow limits on visual percepts**

Measurements of other visual judgments all appear to have yielded much slower temporal limits. The pairing of two orientations was one such limit (Movie 1). For a variety of features, such pairing or binding judgments are confined to rates less than 4 Hz. A stunning example occurs with a field of dots moving back and forth behind a window. When the dots change direction, they also change color, between black and white (Movie 2). The color-motion pairing (leftward with white or with black) is easy to perceive at slow alternation rates, as can be seen in the version at top of Movie 2. However, at a faster rate of about 5 alternations per second (bottom of Movie 2) it is difficult to perceive the pairing between color and motion [21, 22] (even after compensation for a possible asynchrony in feature processing [22]), although this rate is far slower than the flicker fusion rate. Many observers report that, despite an inability to determine the pairing, the constituent

colors and motions are still easily perceived. As in Movie 1, apparently the process of pairing visual features takes more time than identifying them.

Other percepts are confined to similarly slow rates. It is possible that each is extracted by a separate process with the similar speed limits only a coincidence. A more interesting possibility is that a common, late visual processing stage limits the whole lot. This slow-limit group includes:

- **binding of form and color across space**: Alternating color-shape pairings can only be reported at rates below about 3 Hz [17] (demo at [www.psych.usyd.edu.au/staff/alexh/research/binding/](http://www.psych.usyd.edu.au/staff/alexh/research/binding/)).
- **binding of global form with color**: Two specially-constructed dot patterns that form distinct shapes alternate, with all the dots of one red and all the dots of the other green. At alternation rates faster than several a second it is very difficult to determine the shape-color pairing even though the shapes and colors themselves are easily identified [19].
- **direction change and acceleration perception**: A moving stimulus alternates between two speeds (acceleration) or two directions. When the alternation occurs faster than several per second, these changes are unperceivable [23]
- **attention-mediated motion and other forms of higher-order motion**: Conventional Reichardt-like motion detectors can only detect a common subset of moving stimuli. Other stimuli are thought to reveal a high-level motion mechanism possibly controlled by attention [24] with a low temporal limit [25, 26]. Its 8-10 Hz limit makes it the fastest of this list.
- **word perception**: certain pairs of words (such as "jump" and "pink"), when alternated in the same location, cannot be distinguished from another matched pair ("junk" and "pimp"; demo at [www.psych.usyd.edu.au/staff/alexh/research/words](http://www.psych.usyd.edu.au/staff/alexh/research/words)) at rapid rates as one perceives only the sum, which is the same for both pairs. They can be distinguished only at rates slower than several items per second [27]

### Explaining the gap

What could account for the gulf (Figure 1) separating the temporal limits of these two sets of visual judgments? Possibly this is simply selective reporting (see **Box 1**), but there is reason to believe instead that the fast limits reflect specialized mechanisms, with the slow limits imposed when a visual representation must be constructed by central, possibly attentive processing. This notion of fast peripheral processing and slower central processing is an old one [28, 29]. However, over the last decade or so the number of established **slow limits** (Figure 1) has doubled. Words, on the low-resolution list, are not recognized until inferotemporal cortex [30], and attention-mediated motion and binding of arbitrary features are apparently mediated by parietal cortex [31, 32]. Furthermore, some of the limits are set by long-range, object-based summation [33] rather than retinally local alternation rate or short-range stimulus trajectory [34]. Because

visual signals probably are not compared with auditory signals until late in the sensory processing streams, the finding that audio-visual binding is limited to 4 Hz [35] is yet another indication that central stages are limited to low frequencies. If central stages of processing including visual experience are indeed slow in general, then one might wonder how any conscious visual judgment could show a fast rate limit. Fortunately, when visual cognition cannot extract information because it is confined to rapid rates, fast lower-level mechanisms can create labels so that later stages can know what is going on at short timescales. These labels are subsequently temporally combined before reaching visual experience. This yields a temporally extended object such as a single moving surface [13] or, in the case of alternating colored gratings, a transparent display of two seemingly simultaneous surfaces ([36], demo at <http://www.psych.usyd.edu.au/staff/alexh/research/transparency/Home.html>). But with visual cognition thus dependent on specialized mechanisms to inform it of high frequency information, much is lost.

### **Understanding high-level visual processing**

The temporal limits of the early stages of vision are typically explained with the linear systems concept of temporal blurring used to explain the flicker limit earlier in this article [37, 38]. It is uncertain whether the slow limits of high-level visual processing can be explained in the same way. The temporal filtering or blurring explanation assumes that all information ascending the hierarchy eventually makes it to perception. Coarse temporal resolution would cause a stimulus to be inappropriately combined with the stimuli that precede and follow it, obliterating rapid changes, but nothing is actually discarded. Theories of visual cognition propose instead that only some visual representations are transferred to cognition, with the rest ignored [39, 40].

These twin frameworks, temporal resolution theory and attentional selection, rarely coincide in the literature, with the first applied only to low-level temporal limits and the second only to higher limits at visual cognition. A rare exception has arisen with motion perception, which is present in both our fast *and* slow list. That the form of motion perception mediated by attention [24, 25] appears to have a much slower temporal limit, and greater attentional involvement, provides evidence for the present theory of a large temporal divide, and some support for the use of twin frameworks to explain the high-level limits.

The discounting of information by attention before cognition is reached is commonly experienced when viewing a rapid-cut music video. You might feel you have seen and heard many things in the video, but that most went, you might say, in one ear and out the other. "Attentional blink" experiments document one of the temporal limits involved. In these experiments, participants are asked to process two stimuli at different times, much like the attempt to follow the succession of brief scenes in the music video. Processing of the second stimulus is severely impaired if the first stimulus appeared shortly before. The culprit is thought to be a time-consuming stage required to process the first stimulus, such

as short-term memory consolidation [40], or one required to switch to processing the second stimulus, such as re-setting of attentional control [41].

Could the slow process involved in the attentional blink be the same as that which causes the resolution limit to be low for binding widely-separated features and for perceiving acceleration? Both limits are probably caused by limits at high-level processing stages. However the attentional blink requires a first task as a trigger, possibly to consume high-level resources, whereas the perceptual limits reviewed in this article occur despite the benefit of full resources. The attentional blink is substantially more time-consuming than even the slowest visual percept reviewed here and might be imposed by a bottleneck or switching limit at a more cognitive stage.

Experiments designed to target specific perceptual processes sometime miss and instead reflect low-resolution, high-level processes. Flash-lag experiments, designed to measure position perception, have observers report the position of a moving object at the time of a sudden flash. The moving object is perceived farther along its trajectory than it actually was at the time of the flash, as if the visual system actively shifted it. However, the task requires binding the time of the flash with the simultaneous position of the moving object, and binding separated elements usually has low temporal resolution. Consistent with this, the positions reported vary across trials, occupying a 60-70 ms swath of the moving object's trajectory [42]. Indeed, at higher velocities this distribution fills a larger spatial area, such that the temporal imprecision remains constant (Linares, White & Holcombe, 2008 unpublished manuscript). This limit on task performance is therefore a process with coarse temporal resolution. Could the coarse binding limitation be related to the shift in the direction of motion? Possibly yes (as suggested by [7]), since other work on binding motion with a static feature also yields a temporal bias—the static feature is perceived as co-occurring with a later phase of the motion [3, 43]. Also consistent with a causal role for high-level binding is that the flash-lag shift is not evident at mid-level visual mechanisms [44].

## Summary

The title of this article referred to the phenomenon of “seeing fast”, which may seem ungrammatical in isolation. But the meaning here is not to see quickly or rapidly, but rather to see things that occupy fast timescales. After hitting the retina, visual signals rocket towards cortex, and on the way only changes on the order of a few milliseconds are lost [45], perhaps due to membrane fluctuations and temporal summation of signals at geniculate and geniculo-cortical synapses. Shortly after reaching cortex, specialized motion detectors and edge detectors cross-correlate the incoming signals, outputting representations of certain events at narrow timescales. These specialized, high temporal resolution motion detectors and edge detectors are replicated across the visual field. But with a high cost in cortical territory to be paid for having these special-purpose mechanisms, evolution has provided for only a select set. Visual signals continue

past the secondary visual cortices and move towards visual cognition, but then hit slow going. Visual cognition can make nearly any judgment about its inputs, but these computations are so slow that information at narrow timescales cannot be accessed if not already explicitly represented by the low-level specialized detectors. Making matters worse is that cognition is also limited in resources and only able to process one or a few objects at a time. Not all incoming signals can then be processed, just as for Lucille Ball in her famous encounter with a fast assembly line (<http://youtube.com/watch?v=4wp3m1vg06Q>). Hapless Lucy was told she must box every chocolate on the line; fortunately cognition can afford to let many signals just pass it by, with only a few needing its special treatment. Attentional selection is usually able to choose a few for further processing and discard the rest. But with certain repetitive trains of stimuli, such as in the demonstrations of slow limits described in this article, attention is unable to select one stimulus and isolate it from succeeding visual representations. In color-motion binding (Movie 2) for example, the second color and second motion are fed into visual cognition at a time when it has only just begun to bind the first pair, and our percept remains unbound.

Vision science has a strong foundation in psychophysics, which can functionally identify the early visual stages and their simple filtering properties. But higher stages bear little resemblance to simple filters. Up in the clouds of visual cognition, as processing becomes more general and flexible, conventional psychophysics loses its power. To understand this realm, research should focus on the hallmarks of higher-level processes: low capacity managed by a selection process, attentional resource demands, and as argued here, limited temporal resolution.

### **Box 1. A true dichotomy?**

The limits discussed in the main text, and schematized in Figure 1, appear to form two distinct groups, slow and fast. This review is intended to be comprehensive in reviewing the high-resolution limits, but due to space and relevance considerations some limits in the slow group have been omitted, and others are yet to be measured. These considerations, and others discussed below, leave open the possibility that the suggested dichotomy is not truly dichotomous.

The fast group of limits are not homogeneous, as underscored by the existence of the different flicker limits. Flicker between two colors of the same luminance (equiluminant flicker) is commonly invisible above about 25 Hz, much slower than the 50 Hz typically observed with flicker of white and black. This puts it on the slow end of the fast limits reviewed, and the large difference from the luminance flicker limit could undermine the idea of the dichotomy between slow and fast limits. But when the stimuli are set to similar signal strength by equating cone contrast, the flicker limits are not nearly as different [46]. Thus a large difference in temporal limit can stem from an unfair comparison rather than a difference in the temporal resolution of the underlying mechanisms. This issue must still be



addressed for many comparisons of temporal limits.

The divide between slow and fast limits can be partially bridged by distance between stimulus elements. Some of the fast temporal limits require identification and binding of two simultaneous stimuli. As the visual cortices are retinotopically organized, if the binding is to take place within visual cortex then far-flung neurons must interact when the stimulus elements are far apart. If signals diffuse gradually across cortex, then noise can accumulate and interactions across greater distances will be temporally imprecise. Behaviorally, the temporal limit for some judgments does decrease with stimulus separation [16]. As signals ascend the processing hierarchy, receptive field sizes increase until there is little spatial selectivity and the neural connectivity distance is less dependent on the spatial stimulus separation. Nevertheless one judgment classified here as high-level, the same-different judgments of orientation described in the introduction and shown in Movie 1, is affected by distance (Motoyoshi 2004). When the oriented elements are abutting, whether they are the same orientation or different can be perceived at rates as high as 8 Hz, whereas once they are a few degrees apart as in the movie, the judgment is impossible above 4-5 Hz. Perhaps the relevant computation is mediated at an intermediate level of the visual system. Distance dependence of the other putatively high-level judgments is an underexplored yet important issue.

An important omission from this article's list of temporal limits is an aspect of percepts that is not thought to be high level, but nonetheless has coarse temporal resolution. The perceived brightness of a patch is influenced by the surrounding spatial context, as in the simultaneous contrast illusion, where a grey patch on a dark background appears much lighter than the same grey on a bright background. If the background is alternated between bright and dark, the grey alternates in appearance at the same rate, but only up to a background alternation rate of about five times per second [47]. This is consistent with other evidence that surface appearance involves signals that spread slowly across the visual cortex [48-50], and is consistent with the distance effects described in the previous paragraph.

## **Box 2. Temporal masking and temporal resolution**

The stimulus presentation method of the visual temporal masking literature bears a strong resemblance to that of the experiments reviewed in this article. In both, two stimuli follow in rapid succession. But instead of alternating between two stimuli to be identified as in Movie 1, masking displays usually consist of a non-repetitive display, with a single target stimulus followed (or preceded) by a neutral high-contrast pattern which impairs the visibility of the target. The discussion in the "Understanding multiple temporal scales" section of this article explains why such experiments do not necessarily reveal temporal resolution. Poor temporal resolution may nevertheless be the reason for the invisibility, resulting in the target integrating with the mask.

Studies of visual masking currently focus on the more complicated possibility that

a mask presented at certain times disrupts selected components of target processing, such as edge vs. surface processing or feedback vs. feedforward mechanisms [51]. Masks could also, rather than integrating (blurring) with the target as suggested by the temporal resolution concept, simply terminate target processing [52]. The implications for the understanding of the temporal limits reviewed here is not understood. Detailed computational models of masking have proliferated and are successful in explaining the data from traditional masking paradigms [53], but they do not seem capable of explaining the temporal limits reviewed here. The critical exposure duration for visibility in most masking studies is shorter than that for the temporal resolution studies in the slow category here, yet longer than that for the temporal resolution studies in the fast category. In principle this difference could be due to the presence of low temporal frequency information in the non-repetitive masking displays, but this is unlikely to explain the differences in every case. The challenge is to create models of visual processing that can bridge both paradigms.

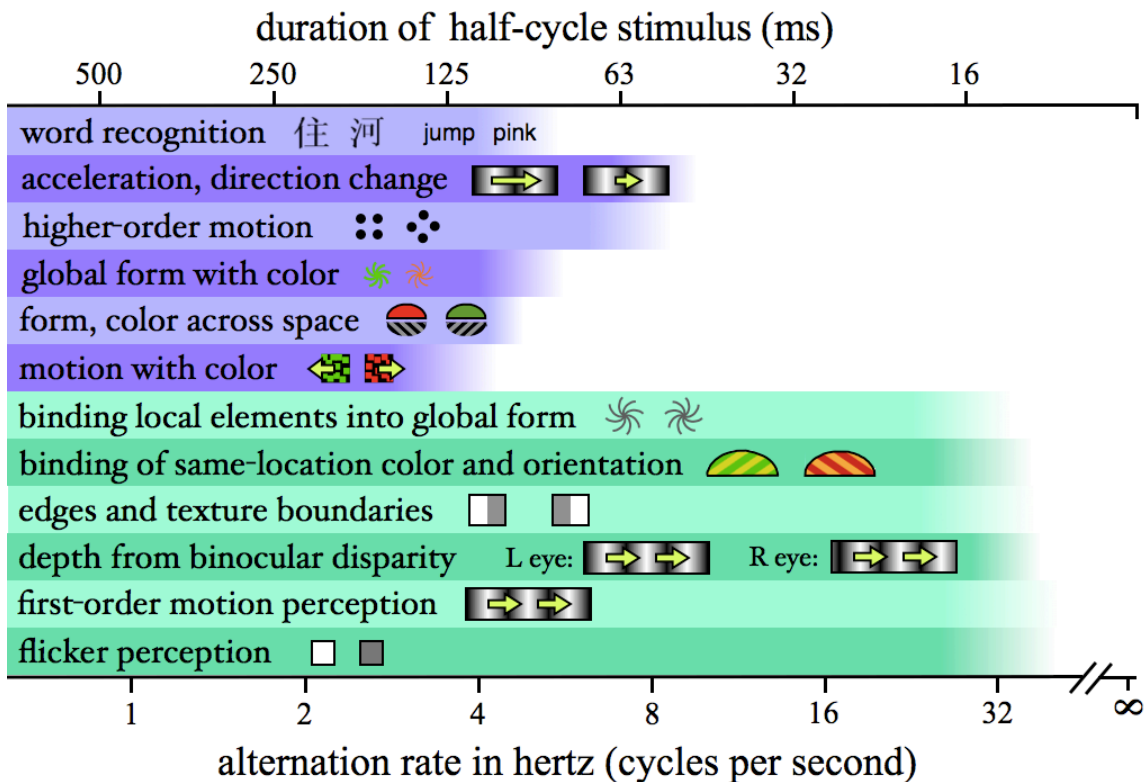
### **Box 3. Future Questions**

If high-level visual processing has poor temporal resolution, what about inter-sensory processing? Intensive work has only recently begun on this question, with Fujisaki and Nishida [35, 54, 55] leading the way.

Why are low temporal resolution processes low temporal resolution? It is not understood what aspect of the underlying neural processing is so time-consuming.

Low-level luminance mechanisms adapt their integration time somewhat to fit the current input [56]. Do higher mechanisms also do so? Or could they rely on fixed component mechanisms working simultaneously on different timescales [57] so each is available if needed?

How do visual mechanisms collaborate so harmoniously that most people never realize their visual experience comprises disparate rate limits? How do visual processing mechanisms with different processing times keep perceptual qualities in temporal register? (see [7])



## Figure and Movie Captions

Figure 1. Temporal limits on visual judgments. Each colored strip represents the results of an experiment in which the rate of change of a display was varied to determine the maximum rate at which something could be perceived. In a flicker perception experiment, the stimulus alternates between two luminance values. Flicker is perceived from slow rates up to speeds exceeding 50 Hz, indicated by the fading of the strip around that rate.

Movie 1. Each stripe alternates between leftward-tilted and rightward-tilted. The orientation of those in the left pair always differs, and the orientation of those in the right pair is always the same. This should be easy to perceive at the rate of the top display, but in the middle display if the stripes alternate as fast as intended, whether the orientations are the same or different should be difficult to perceive as the speed limit for this judgment has been exceeded. The bottom display illustrates the percept when the alternation is speeded until it exceeds even the limit for flicker perception. This bottom display was created by averaging the two frames together, as the visual system does at high alternation rates.

Movie 2. A field of dots moves back and forth and changes between black and white with each direction change. At the speed of the top display, it should be easy to perceive that when moving leftward, the dots are white. The middle display should show the dots alternating at a rate fast enough (greater than 5 frames per second) that the pairing of motion and color cannot be determined.

The bottom display illustrates the outcome when the alternation rate exceeds the flicker limit so that only the average of the two dot colors—which is the same as the background luminance—is perceived. It was created by averaging the two frames together, as the visual system does at high alternation rates.

## Acknowledgments

Over a decade ago, Patrick Cavanagh introduced me to some core ideas of this article and since then has continued to collaborate on related projects and provide sage advice. Alex L. White, Paul Dux, Daniel Linares, and two anonymous reviewers provided many helpful comments.

Supplementary material associated with this article can be found at [doi:10.1016/j.tics.2009.02.005](https://doi.org/10.1016/j.tics.2009.02.005).

## References

1. Coe B (1992) *Muybridge and the Chronophotographers* (MOMI/British Film Institute, London).
2. Johnston A, Arnold DH, Nishida S (2006) Spatially localized distortions of event time. *Curr Biol* 16:472–479.
3. Moutoussis K, Zeki S (1997) A direct demonstration of perceptual asynchrony in vision. *Proc R Soc Lond B* 264:393–399.
4. Whitney D, Murakami I (1998) Latency difference, not spatial extrapolation. *Nat Neurosci* 1:656–67.
5. Eagleman DM (2008) Human time perception and its illusions. *Curr Opin Neurobiol* 18:131–136.
6. Whitney D (2002) The influence of visual motion on perceived position. *Trends Cogn Sci* 6:211–216.
7. Nishida S, Johnston A (in press) in *Problems of Space and Time in Perception and Action*, eds Nijhawan R, Khurana B (Cambridge University Press,
8. Kline K, Holcombe AO, Eagleman DM (2004) Illusory motion reversal is caused by rivalry, not by perceptual snapshots of the visual field. *Vision Res* 44:2653–2658.
9. VanRullen R, Koch C (2003) Is perception discrete or continuous? *Trends Cogn Sci* 7:207–213.
10. Motoyoshi I (2004) The role of spatial interactions in perceptual synchrony. *J Vis* 4:352–361.
11. Motoyoshi I, Nishida S (2001) Temporal resolution of orientation-based texture segregation. *Vision Research* 41:2089–2105.

12. Farid H (2002) Temporal synchrony in perceptual grouping: a critique. *Trends Cogn Sci* 6:284–288.
13. Burr DC, Ross J (1982) Contrast sensitivity at high velocities. *Vision Research* 22:479–484.
14. Morgan MJ, Castet E (1995) Stereoscopic depth perception at high velocities. *Nature* 378:380–383.
15. Ramachandran VS, Rogers-Ramachandran DC (1991) Phantom contours: A new class of visual patterns that selectively activates the magnocellular pathway in man. *Bulletin of the Psychonomic Society* 29:391–394.
16. Forte J, Hogben JH, Ross J (1999) Spatial limitations of temporal segmentation. *Vision Research* 39:4052–4061.
17. Holcombe AO, Cavanagh P (2001) Early binding of feature pairs for visual perception. *Nature Neuroscience* 4:127–128.
18. Bodelon C, Fallah M, Reynolds JH (2007) Temporal resolution for the perception of features and conjunctions. *J Neurosci* 27:725–730.
19. Clifford CWG, Holcombe AO, Pearson J (2004) Rapid global form binding with loss of associated colors. *Journal of Vision* 4:1090–1101.
20. Tyler CW, Hardage L, Miller RT (1995) Multiple mechanisms for the detection of mirror symmetry. *Spat Vis* 9:79–100.
21. Moradi F, Shimojo S (2004) Perceptual-binding and persistent surface segregation. *Vision Res* 44:2885–2899.
22. Arnold DH (2005) Perceptual pairing of colour and motion. *Vision Res* 45:3015–3026.
23. Werkhoven P, Snippe HP, Toet A (1992) Visual processing of optic acceleration. *Vision Research* 32:2313–2329.
24. Cavanagh P (1992) Attention-based motion perception. *Science* 257:1563–1565.
25. Lu ZL, Sperling G (2001) Three-systems theory of human visual motion perception: review and update. *J Opt Soc Am A Opt Image Sci Vis* 18:2331–2370.
26. Verstraten FAJ, Cavanagh P, Labianca A (2000) Limits of attentive tracking reveal temporal properties of attention. *Vision Research* 40:3651–3664.
27. Holcombe AO, Judson J (2007) Visual binding of English and Chinese word parts is limited to low temporal frequencies. *Perception* 36:49–74.
28. He S, Cavanagh P, Intriligator J (1997) Attentional resolution. *Trends In Cognitive Science* 1:115–121.

29. Van de Grind WA, Grusser OJ, Lunkenheimer HU (1973) in *Handbook of Sensory Physiology(VII/3)*, pp 462–464.
30. Vinckier F, Dehaene S, Jobert A, Dubus JP, Sigman M, Cohen L (2007) Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. *Neuron* 55:143–156.
31. Battelli L, Cavanagh P, Intriligator J, Tramo MJ, Henaff MA, Michel F, Barton JJ (2001) Unilateral right parietal damage leads to bilateral deficit for high- level motion. *Neuron* 32:985–95.
32. Friedman-Hill SR, Robertson LC, Treisman A (1995) Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. *Science* 269:853–856.
33. Cavanagh P, Holcombe AO, Chou W (2008) Mobile computation: spatiotemporal integration of the properties of objects in motion. *J Vis* 8:1.1–123.
34. Nishida S, Watanabe J, Kuriki I, Tokimoto T (2007) Human visual system integrates color signals along a motion trajectory. *Curr Biol* 17:366–372.
35. Fujisaki W, Nishida S (2005) Temporal frequency characteristics of synchrony- asynchrony discrimination of audio-visual signals. *Exp Brain Res* 166:455–464.
36. Holcombe AO (2001) A purely temporal transparency mechanism in the visual system. *Perception* 30:1311–1320.
37. Kelly DH (1979) Motion and vision. II. Stabilized spatiotemporal threshold surface. *Journal of the Optical Society of America* 69:1340–1349.
38. Burr DC, Morrone MC (1993) Impulse-response functions for chromatic and achromatic stimuli. *Journal of the Optical Society of America A* 1706–1713.
39. Broadbent DE (1958) *Perception and communication* (Pergamon Press, London).
40. Chun MM, Potter MC (1995) A two-stage model for multiple target detection in rapid serial visual presentation. *Journal of experimental psychology: Human perception and performance* 21:109–127.
41. Di Lollo V, Kawahara J, Shahab Ghorashi SM, Enns JT (2005) The attentional blink: resource depletion or temporary loss of control? *Psychol Res* 69:191–200.
42. Murakami I (2001) The flash-lag effect as a spatiotemporal correlation structure. *J Vis* 1:126–136.
43. Holcombe AO (2009) Temporal binding favours the early phase of colour changes, but not of motion changes, yielding the colour-motion asynchrony illusion. *Visual Cognition* 17:232–253.

44. Linares D, Lopez-Moliner J (2007) Absence of flash-lag when judging global shape from local positions. *Vision Res* 47:357–362.
45. Gegenfurtner KR, Kiper DC, Levitt JB (1997) Functional properties of neurons in macaque area V3. *J Neurophysiol* 77:1906–1923.
46. Metha AB, Mullen KT (1996) Temporal mechanisms underlying flicker detection and identification for red-green and achromatic stimuli. *J Opt Soc Am A Opt Image Sci Vis* 13:1969–1980.
47. De Valois RL, Webster MA, De Valois KK (1986) Temporal properties of brightness and color induction. *Vision Research* 26:887–897.
48. Paradiso MA, Nakayama K (1991) Brightness perception and filling-in. *Vision Research* 31:1221–1236.
49. Caputo G (1998) Texture brightness filling-in. *Vision Res* 38:841–851.
50. Ringach DL, Shapley R (1996) Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Research* 36:3037–3050.
51. Breitmeyer B (2007) Visual masking: Past accomplishments, present status, future developments. 3:9–20.
52. Reeves A (2007) An analysis of visual masking, with a defense of 'Stopped Processing'. *Advances in Cognitive Psychology* 3:57–65.
53. Francis G (2007) What should a quantitative model of masking look like and why would we want it? *Advances in Cognitive Psychology* 3
54. Fujisaki W, Nishida S (2008) Top-down feature-based selection of matching features for audio-visual synchrony discrimination. *Neurosci Lett* 433:225–230.
55. Fujisaki W, Nishida S (2007) Feature-based processing of audio-visual synchrony perception revealed by random pulse trains. *Vision Res* 47:1075–1093.
56. Stromeyer CF, Martini P (2003) Human temporal impulse response speeds up with increased stimulus contrast. *Vision Research* 43:285–298.
57. Koenderink JJ (1988) Scale-Time. *Biological Cybernetics* 58:159–162.