

patterns as well as luminance gratings. Now, Mareschal and Baker¹ have characterized the orientation selectivity of area 18 neurons, and find that their preferred orientations for a luminance grating and for a second-order envelope are almost exactly the same. This finding indicates that these neurons show cue-invariance, and raises the possibility (yet to be tested) that they may signal the presence of occluding boundaries.

The authors went on to examine the response to envelope stimuli in more detail. As shown in the figure, the orientation of the envelope and the carrier can vary independently. In the upper panel they are parallel, so each boundary has the same contrast along its entire length, but the contrast varies between different bars. In the lower panel, however, the envelope is at 90 degrees to the carrier, so that the contrast between the bars of the carrier grating is modulated along their length. The authors' second result is that envelope-responsive neurons have an orientation preference not only for the envelope but also for the carrier. (The carrier itself evokes no response, because it is too fine-grained to be detected by the large receptive fields of these neurons; it is only the envelope response that allows the sensitivity to carrier orientation to be measured.) Moreover, the orientation preference for the fine carrier grating bears no relationship to the preference for the envelope (or for a luminance grating of similar spatial scale).

These findings suggest several important conclusions regarding the organization of the early visual cortical areas. First, they are relevant to the ongoing debate about the origin of orientation tuning, which remains controversial despite many years of study^{8,9}. The classical view, proposed by Hubel and Wiesel more than 35 years ago¹⁰, is that orientation selectivity arises from the convergence of (non-oriented) inputs from the lateral geniculate nucleus (LGN) of the thalamus to the primary visual cortex. On this view, the activity of orientation-responsive cortical neurons represents the linear sum of their thalamic inputs, and their orientation selectivity reflects the geometry of thalamocortical connectivity¹¹. Other experimental and theoretical studies, however, suggest that cortico-cortical interactions play a predominant role in sharp orientation tuning¹²⁻¹⁴. The new findings about orientation tuning for envelope stimuli are difficult to explain in terms of the classical view. To account for cue invariance, one must postulate that these neurons receive two separate parallel inputs, one channel to generate the response to bright and dark bars of a luminance grating in the

usual way, and a second, highly non-linear pathway to generate the response to the envelope stimulus. (A non-linear pathway is required to explain the temporal pattern of these neurons' response to drifting envelope stimuli^{1,7}.) How the non-linear pathway's response can be tuned for envelope orientation, and how the preference for envelope stimuli can be the same as for simple luminance gratings, remains unexplained; these questions represent challenges for future theoretical and experimental work.

What the results make clear, however, is that the response to the envelope must arise in the cortex itself, and that the non-linear pathway must be cortical. The envelope-responsive neurons have clear orientation preferences for the carrier grating that are often different from the preferred orientation of the envelope itself; because the precortical stages of the visual pathway (the retina and the LGN) are not orientation selective, the non-linear channel that provides input to envelope neurons must itself be cortical. Moreover, because the orientation preference for the envelope is the same as for luminance stimuli, it seems likely that they both have a common origin within the cortical network.

Thus, it is becoming apparent that the notion that neurons in the early visual areas are passive, stimulus-locked filters is now inadequate. Clearly, understanding early

visual processing is going to be more difficult, but also more interesting, than we might have anticipated a few years ago. In unraveling the detailed circuitry of these early visual cortical areas, we are learning more about the sophistication of the cerebral cortex as a whole.

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Visual psychophysics: synchrony in motion

Karl Gegenfurtner

Studies with ambiguous visual stimuli are claimed to indicate that synchronous neuronal oscillations can mediate perceptual binding. But the authors' interpretation will be controversial.

Human vision is commonly divided into low level and high level processes. At the lower level, feature analysis occurs to extract information about edges, colors or depths at a particular location in the visual field. At a higher level, the visual system must recognize the objects that are built up from these low level features. But there is also an

intermediate stage, which presents a major challenge to any theory of vision; how does the visual system know which features belong to which object? When several contours occur in different locations in the visual field, we have to determine whether they represent different parts of the same object, or whether they belong to separate objects. In order to link features into objects, signals from different parts of the retina, mapped onto different parts of the retinotopic cortical areas, must be bound together. This is a very difficult

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problem, particularly because in the real world objects are often partially occluded, so elements that are not topographically connected must nevertheless be linked perceptually.

On page 160 of this issue, Alais *et al.*¹ for the first time present psychophysical evidence that temporally synchronous contrast changes provide a powerful cue for linking individual features of moving objects to give the percept of a single moving object. They used multi-stable displays such as the one in Fig. 1, in which the motion of four separate components can either be seen as a single coherent diamond shape moving upward behind an imaginary aperture, or as four separate, non-coherent components². The situation shown in Fig. 1 illustrates the problem faced by the visual system. Since the elementary motion detectors in primary visual cortex have small receptive fields, they might only see the motion of a single (one-dimensional) edge of a two-dimensional object. The direction of motion is ambiguous, since only the component of motion that is perpendicular to the edge can be detected through each of the apertures or receptive fields³. The local motion cues are compatible with both physical causes—a single diamond shaped object moving upwards (a), or four separate, smaller objects moving in four different directions (b). How can the visual system solve this “aperture problem”, as it is commonly called?

It is known that the similarity of the components' features is an important factor for the degree of coherence observed in such displays³. This makes sense; since objects tend to be relatively uniform in their color or texture, the hypothesis of a single moving object is unlikely if the components differ in respect to these elementary surface properties. But moving objects also introduce temporal cues. If a single object moves under the apertures, its local features will vary synchronously over time. The question is then, whether synchrony by itself can provide a cue for motion linking. Alais *et al.*¹ came up with a clever experimental manipulation that allowed them to separate the similarity and synchrony cues. Their stimuli consisted of moving sine wave gratings seen through an aperture as in Fig. 1. The contrast of each grating was changed randomly in a rhythmic manner (at frequencies ranging from 12.5 Hz to 75 Hz). This allowed

the authors to manipulate similarity (the contrast difference between the individual patches) and synchrony independently, while maintaining the same average contrast over time in all conditions. In one condition, the contrasts of the different gratings at each instance were different, but were modulated in synchrony. In another, the contrasts of the four gratings were also different, but were modulated out of synchrony. The authors found that when modulations occurred out of synchrony the gratings were perceived as independent, but when they were in synchrony, the gratings were more likely to be perceived as belonging to a single moving object.

Earlier experiments investigating the role of temporal synchrony in perception have looked at texture segregation tasks^{4,5}. The results were ambiguous and pointed towards small or no effects. The results presented by Alais *et al.*¹ show that the influence of temporal synchrony is large enough to tip the fine balance between local and global motion cues in viewing ambiguous motion displays. The authors argue that their finding might relate to the hypothesis that synchronous activity of neurons at different locations in the brain may underlie the binding of the features they encode^{6,7}. If the oscillating stimuli produce oscillatory neuronal responses, the effect of the experimental manipulations would be to drive the brain oscillations in or out of synchrony, thereby affecting perception. Such behavioral evidence would provide critical evidence in support of a temporal code as the solution for feature binding^{6,7}, one of the most controversial topics in contemporary visual science.

It has been argued by some researchers that oscillatory brain activity is the crucial link between features and objects—between low level

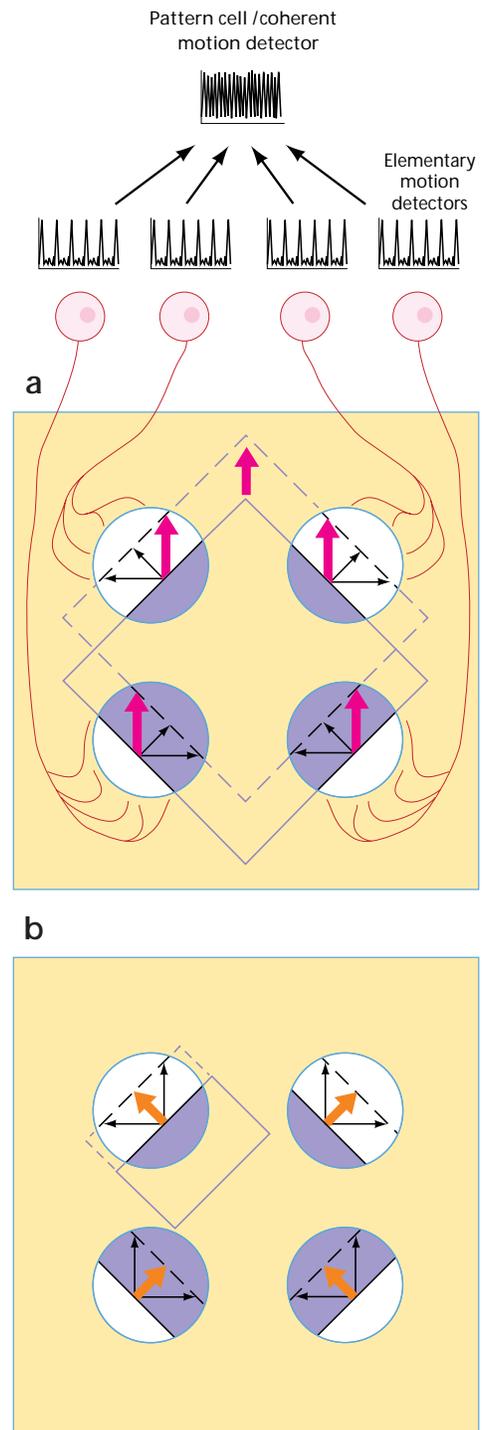


Fig. 1. The motion linking problem. Elementary motion detectors (EMDs) with small receptive fields can only determine motion perpendicular to one-dimensional edges. (a) The motion of the diamond needs to be extracted by combining the output of many EMDs in higher-level 'pattern' cells³. (b) If the signals from the EMDs are not combined, the individual motion components appear to arise from independent moving objects (of which only one is shown here for clarity). Alais *et al.* showed that synchronous changes in contrast increase the coherence observed in such displays, i.e. the upper perceptual interpretation is favored.

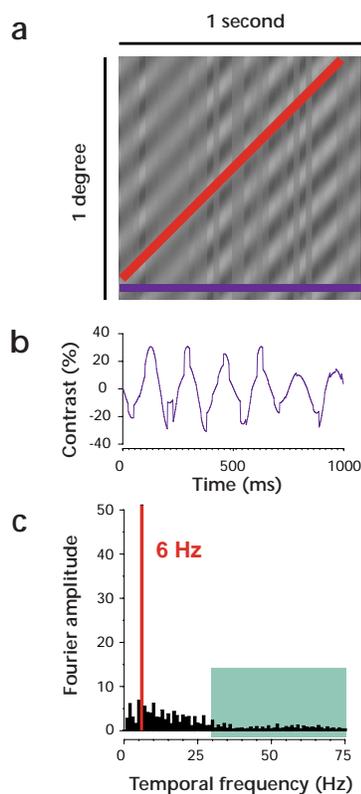


Fig. 2. Illustration of the spatio-temporal structure of one of the stimuli used by Alais *et al.*¹, a 5.5 cycle/degree sinewave grating whose contrast is modulated with a rate of 38.5 Hz, moving at a temporal rate of 6 Hz. **(a)** The space-time distribution of the stimulus. The red line indicates the fundamental frequency of movement. **(b)** Instantaneous contrast at a fixed location of the display, as indicated by the blue line in **(a)**. **(c)** Fourier transform of the contrast signal from **(b)**. The red bar indicates the energy at the fundamental frequency. The shaded region shows the range of frequencies where oscillatory brain activity has been observed in physiological experiments.

and high level vision^{6,7}. Neurons activated by the same object would produce a unique code, defined by a synchronous oscillatory firing pattern, that would allow subsequent processing stages to disambiguate between different groups of neurons signalling different objects. In physiology, the discovery of oscillatory activity of neurons in the cat visual cortex seemed to support such a temporal binding mechanism⁸. However, other researchers regard oscillatory activity more sceptically, as an epiphenomenon⁹. One good reason for scepticism is that synchronized oscilla-

tions have been observed mostly in the multi-unit responses of cats looking at a single moving bar^{7,8}, not a situation that poses a great challenge for perceptual organization. And, most importantly, conclusive behavioral evidence was missing for an important role of oscillations in feature binding.

The most interesting interpretation of the new findings, which the authors favor, is that they reflect the importance of synchronized neuronal oscillations for perceptual grouping. But have the authors proved their case? The range of oscillation frequencies observed in the above mentioned physiology experiments^{7,8} range from 30 - 80 Hz, the very same frequencies that seemed to be effective in establishing perceptual coherence. However, the spatio-temporal structure of these stimuli is more complex than it appears. Figure 2 shows a space-time diagram of one of the stimuli used by Alais *et al.*¹, a sinewave grating randomly modulated in contrast at a rate of 38.5 Hz. The figure also shows the contrast variations that might be seen by an individual motion sensor at one particular location (Fig. 2b), together with the Fourier transformation of the very same signal (Fig. 2c). Naturally, since the stimulus is a sinewave grating drifting at a temporal rate of 6 Hz, most of the energy is concentrated at 6 Hz. But interestingly, there is almost no Fourier energy at 38.5 Hz, and very little above 30 Hz. Since the stimuli do not contain such temporal frequencies, they would also fail to produce neuronal responses at such frequencies. Therefore, while the data themselves seem clear, the authors' attempt to draw a link between their psychophysical observations and the synchronous oscillations hypothesis should, in my view, be treated with considerable skepticism.

If synchronized oscillations are not the cause for the improved perceptual coherence, how might it be explained? I suggest the answer lies in Fig. 2c. Even though there is no motion energy at high frequencies, there is quite a spread of activity at the low temporal frequencies near the fundamental frequency of 6 Hz. This spread, which also causes the motion in these displays to appear jerky, causes the stimuli to be detected by a larger group of motion detectors. Their joint activity is then interpreted as a larger signal for perceptual coherence. When the contrast modulations are uncorrelated, the low frequency spread

will be different for each grating patch at each instance. Thus, different groups of detectors might get activated at each location at each instance. In the worst case, the pattern of local motions might not even be compatible with a single, coherently moving object (if the arrows in Fig. 1 are all of different length). Therefore, a decrease of perceptual coherence is not unexpected under these conditions.

Alais *et al.*¹ results are important for understanding motion coherence, but they do not in my view provide the missing link to give oscillations and synchrony the primary role in all forms of perceptual organization, as proposed by Singer and his colleagues⁷. It is also interesting to see that all the evidence gathered so far in favor of a role for synchrony in perceptual binding comes from experiments with moving stimuli^{7,8,10}. But motion perception is—in the end—nothing but the determination of the spatiotemporal correlational structure of the stimulus¹¹. It should therefore not come as a major surprise that synchronized contrast changes have a major effect on such correlations. True, synchrony, whether it be in contrast or in speed, provides an important cue for motion linking. But the question of whether synchrony is simply another feature, or whether it provides the elusive glue that binds features together in all perceptual situations, awaits confirmation.

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