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Research Focus

The wagon-wheel illusion in continuous light

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The fact that a perceptual experience akin to the familiar wagon-wheel illusion in movies and on TV can occur in the absence of stroboscopic presentation is intriguing because of its relevance to visuo-temporal parsing. The wagon-wheel effect in continuous light has also been the source of considerable misunderstanding and dispute, as is apparent in a series of recent papers. Here we review this potentially confusing evidence and suggest how it should be interpreted.

Some years ago we wrote a paper that described and analyzed an intriguing perceptual phenomenon, pointing out its possible implications [1]: when the spokes of a wheel or other stimuli with elements that move continuously in one direction are observed in sunlight, the elements are sometimes seen to be moving in the opposite direction. Because of the general similarity to the backwards motion of wagon wheels in movies, TV or other forms of stroboscopic presentation, we called this phenomenon the 'wagon-wheel illusion in continuous light' (see Box 1) and suggested on this basis that the visual system can segregate visual information into meaningful episodes from which perception is then constructed. Although this idea had been raised from time to time [2,3], a general assumption is that the visual scene is monitored continuously.

Over the next few years, the wagon-wheel illusion in continuous light attracted the attention of researchers interested in temporal parsing [4–6]. However, no further experimental work on this issue was carried out until the past year or two, when several new papers appeared that variously: (i) Denied the effect altogether [7]; (ii) Confirmed the effect, but provided new evidence taken to refute its relevance to visuo-temporal parsing [8]; and (iii) Confirmed the effect and provided new evidence taken to validate visuo-temporal parsing, specifying its parameters more exactly [9,10]. Given these conflicting observations and conclusions, we thought it useful to consider the new results together in an effort to make some sense of this important but potentially confusing subject. The basic phenomenology of the wagon-wheel illusion in both stroboscopic and continuous light is outlined in Box 1.

Evidence taken to refute visuo-temporal parsing

The recent paper by Kline *et al.* [8] carefully confirms that the vast majority of subjects tested see the wagon-wheel effect in continuous light, but presents additional observations that the authors interpret as arguing against the idea of visuo-temporal parsing.

The first of these observations is that the durations of the epochs of perceived reversal follow a gamma distribution, a statistical pattern characteristic of rivalrous percepts [11]. Based on this evidence, they argue that prolonged exposure to the stimulus elements causes the neurons that normally signal movement in that direction to adapt. Neurons sensitive to the opposite direction of motion and activated by temporal 'aliasing' (under-sampling) would then become dominant, leading to brief periods of apparent reversed motion. Thus, the continuous light effect would signify rivalry between neural sensors selective for opposite directions of motion, rather than visuo-temporal parsing. Their second observation is that the perceived reversals of two different objects rotating identically can, and usually do, occur independently, a finding that is inconsistent with 'visual snapshots' of the entire scene being acquired and parsed by a 'strobe in the head'.

Interpreting these observations

The experiments reported by Kline *et al.* [8] are well conceived and the observations not in doubt. However, concluding that visuo-temporal parsing does not occur seems unwarranted.

Categorizing the effect as rivalrous is not inconsistent with visuo-temporal parsing. Rivalry demands two stimuli capable of competing perceptually, and for this type of moving stimulus the spatio-temporal energy has a single direction. Thus, the competing stimulus, if there is one, must be created by the visual system. The motion-processing mechanism proposed by Kline and colleagues provides one way of creating an internal competitor based on direction-selective neurons that receive input from receptors at different spatial locations [12]. The crucial feature of such neurons is that the input from one receptor is delayed with respect to the other, which causes a given neuron to be sensitive to motion in a particular direction (Figure 1). A periodic stimulus moving at a particular rate in the non-preferred direction of a detector could therefore elicit a competing motion signal. However, two recent papers have shown that the illusion depends on the temporal frequency of presentation rather than the velocity of the stimulus, with the greatest effect at a frequency of 10–15 Hz [9,10]. Because Reichardt motion detectors are tuned to velocity rather than temporal frequency, they cannot provide a complete explanation of

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Box 1. The wagon-wheel phenomenon in stroboscopic and continuous light

When a moving wheel or similar stimulus is presented as a sequence of discrete images over time, as occurs in illumination with a strobe light, in the sequential frames of a movie or with any form of mains-driven AC light (which alternates between light and dark), the perceived elements can be seen as moving forward, backward, or standing still. The reason for these various percepts is that the sequential position of the stimulus elements can, with respect to the initial position of a spoke or other feature, progress, regress or remain in the same position (Figure I; [1]). Thus depending on the angular velocity of the rotating wheel and the rate at which the sequential images are captured, the physical presentation of the stimulus elements can cause them to be seen as moving 'backwards' despite the actual direction of rotation.

Remarkably, reversed motion of the stimulus elements can also be seen in continuous light (i.e. in sunlight or DC-generated light), as three of the new studies have confirmed [8–10]. In fact, J.F. Schouten [14], much better known for his classical work in audition, noted this effect nearly 30 years ago, and many non-scientists have wondered about it over the years. The reason why the existence of this illusion has been disputed [7] is presumably that the authors were not fully aware of the differences between the stroboscopic and the continuous light illusion.

The differences are: (1) Static patterns are never seen in continuous light; the appearance of orthograde and reversed rotation simply alternate, with a strong preference for the direction of real motion; (2) The illusion in continuous light does not always appear immediately, but can take many seconds, or even a few minutes, to develop [8], whereas the stroboscopic effect is immediate; (3) Supernumerary elements – additional spokes or other elements – appear by addition in continuous light, whereas they multiply in stroboscopic presentation; and (4) The effect in continuous light is only seen at rates of element presentation between ~2 and 20 Hz; the strobe effect is not limited in this same way.

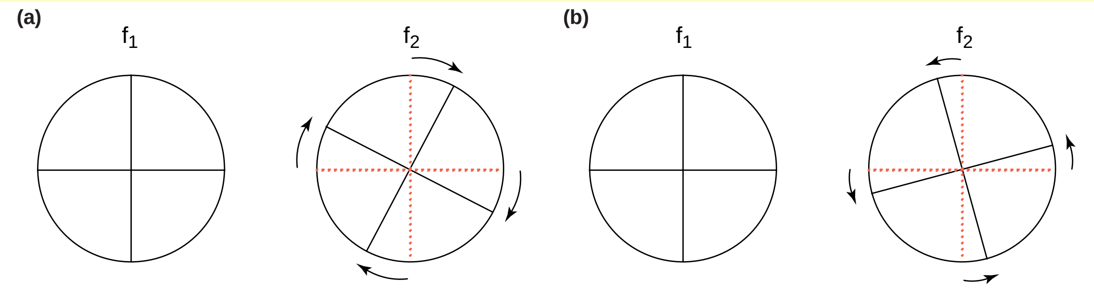

Figure I. When rapidly moving objects are presented on TV or in movies, the frame rate is too slow to represent the physical movement accurately. A well-known consequence is the wagon-wheel illusion, in which wheels appear to be turning backwards. **(a)** If the spokes of the wheel rotate a small distance between frames (f), then the visual system can match each spoke in f_1 with the same spoke in f_2. **(b)** If, however, the spokes move a greater distance between frames, spokes in f_1 are matched with different spokes in f_2, which, depending on the particulars, produces a sense of reversed motion or an illusory sense of forward motion. Note further that if the wheel rotates 90° between frames, it will appear to be standing still.

this illusion. The demonstrated temporal selectivity is more consistent with a temporal parsing process.

Nor does the observation by Kline *et al.* that two identically rotating objects in continuous light do not reverse together argue against visuo-temporal parsing. As these authors mention, the independent reversal of two image streams is compatible with temporal parsing if different motions in a scene are tracked independently. Consistent with this interpretation, the recent study by VanRullen and colleagues [10] shows that the incidence of illusory motion is diminished when attention is diverted away from the moving stimulus. Such temporal segmentation would be analogous to the way scenes are spatially segmented for the biological advantages that accrue from seeing and tracking specific objects. Indeed, because the objects in a scene commonly move at different speeds and in different directions, independent tracking is quite plausible.

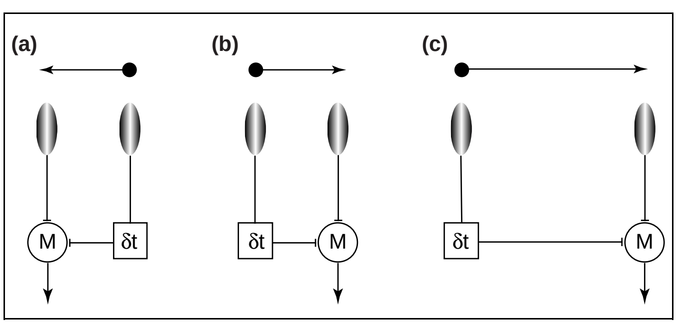

Figure 1. A standard model for neurons that detect leftward **(a)** or rightward **(b)** motion. A crucial feature of this type of motion detector (M) is that it compares the output from two stimulus locations in space at two different times. To detect different velocities of motion, different detectors are taken to be tuned to different fixed delays (δt) and/or different fixed locations in space **(c)**.

A prudent conclusion

What implications, then, does this illusion have for how the brain routinely processes visual information? First, it is important to recognize that, quite apart from this odd effect, temporal parsing of visual information is clearly part and parcel of visual processing. This strong statement is based on the obvious demands of normal saccadic eye movements, which entail the replacement of one retinal stimulus by another every 300 ms or so [13]. Thus, at a minimum, temporal parsing must occur at this rate. The question, then, is not whether temporal parsing of visual information occurs – it clearly does in various ways – but how, more specifically, this parsing is carried out by the visual system, and how the various experimental observations described here are related in a process that is fundamental to vision. The recent flurry of interest and new observations on the wagon-wheel effect should stimulate other attempts to understand this basic aspect of vision, which is equally pertinent to neural processing in other sensory modalities.

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