## Visual perception

## Predicting the present

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ichard Gregory has said that vision allows us to live a little bit in the future - to react to things before they happen. But in one sense, he is quite wrong. There is a delay of about 50 msec between the arrival of photons at the retina and the response of higher visual areas. During this time a moving object has continued on its way, so the higher visual areas will be analysing the past history of the object, not its current location. On page 66 of this issue, Nijhawan1 brightens our outlook by showing that in some cases we can regain at least the present: we can see things not as they were, but as they probably are. This kind of predictive perception, compensating for neural delays, can only happen for objects that are undergoing smooth change (in location, brightness or size, for example), and visual motion is the basis of this particular example.

Suppose the brain does extrapolate the perceived location of a smoothly moving bar ahead of its actual position, potentially compensating for neural delays2. What should happen then, if a thin target line is flashed briefly, exactly on top of the moving bar? The flashed line will be perceived at its actual location but, according to Nijhawan, the position at which the moving bar is seen will be extrapolated to a location ahead of the target line (Fig. 1). Moreover, if the moving bar has one colour and the flashed target has a different colour, the stimulus on the retina will have the sum of the two colours. Yet when they are disentangled, the bar and the target line are sorted out into their original colours — the bar is green, and the flashed target is red. So although the stimulus is yel-

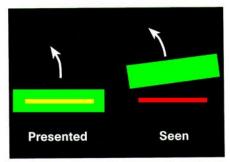


Figure 1 Neural delays that occur between the arrival of photons at the retina and the responses of higher visual areas mean that we live forever slightly in the past. But Nijhawan' has used a simple technique to show that the brain can, under certain circumstances, compensate for the neural delay. The red target line is flashed briefly at the centre of the smoothly moving green bar. Nevertheless, the green bar is seen ahead of the line at the moment the flash is perceived. The location of the moving bar has been extrapolated along the direction of motion, and the appropriate colour of the flashed line (red) has been recovered from the sum present in the physical stimulus on the retina (yellow).

low (the sum of the two), the observer sees a red flash trailing a green bar. How has this decomposition occurred?

Much of our understanding of the analysis of colour in the visual system emerged from observing the consequences of mixing coloured lights — discovering how, for example, red and green combine to provoke the experience of yellow. In reversing this process, the new study shows that the green

colour of the bar can be subtracted from the yellow to yield the original red of the target. There are other instances where one colour can be discounted, revealing another. For example, viewing a multi-coloured Mondrian-like pattern in, say, a reddish light leads to correction for the illumination. So patches whose spectra would be seen as yellow if viewed in isolation, seem close to the green that would be seen under white light. Nijhawan's example may involve a similar mechanism of discounting or subtraction but, unusually in his case, the two colour components are also seen as being spatially separated.

The use of yellow as the combination colour is probably of no special importance — a red herring so to speak. Certainly, other colour pairs ought to be equally well decomposed, for example, yellow and blue, or white and green. But what about black? Imagine that the target is a dark line, briefly presented as an area of decreased brightness centred in the moving green bar. When the target is seen trailing the green bar, it ought to seem blacker than black; a darker area in a background that is already black. Or if the moving bar is textured and the target is briefly presented as a filled, untextured region, subtraction would predict that, when it is seen alone, the target line will appear as the complementary texture to the moving bar.

The second component of Nijhawan's effect, extrapolation, is both more striking and more controversial than subtraction. Neural delays between the arrival of photons at the retina and the responses of higher visual areas mean that it is the past history of an object that is analysed, not its current state. The author claims that this lag is corrected the location at which the object is perceived is extrapolated ahead, along its path, to compensate for the delay. But why bother? Neural delays affect all of our sensations: our perception of auditory events must lag behind the arrival of sound at the ear; and our awareness of our moving arms and legs will lag behind the proprioceptive and visual cues of their position. The benefit of using extrapolation - predictive perception - in all of these modalities is not immediately obvious. Moreover, the cost is that signals undergoing change which will permit extrapolation should be mislocalized relative to signals which have abrupt onsets or offsets. For example, when two objects are moving towards each other at a constant velocity, the sound of their collision should seem to lag behind the visual perception of the collision. (Observers, however, are not very sensitive to small asynchronies between modalities such as hearing and seeing<sup>3</sup>.)

How would extrapolation occur? A sensed location needs to be assigned to individual neurons, or groups of neurons, and that location is linked in some way<sup>4</sup> to the areas of the retina that activate the neurons.

In the case of a motion-sensitive unit, Nijhawan's results indicate that the location is simply assigned to a region that is shifted away from the receptive-field centre of the neuron, in the direction of the preferred motion.

There is an alternative to extrapolation which could also explain the striking results persistence. A stimulus remains visible for a brief moment after it has physically been turned off, and this persistence is shorter for a moving stimulus than it is for a flashed stimulus<sup>5</sup>. This difference acts as a 'motion deblurring' mechanism, to remove the smeared traces which should otherwise trail moving objects. A short while after the moving bar has passed the flashed target line, no trace of the bar remains there, whereas the flashed target lives on longer (persists), to be seen as physically separate from the moving bar. Nijhawan has addressed this possibility in his last experiment, but two other considerations argue that persistence is not the sole cause of the phenomenon.

First, the motion-specific suppression would also have to be colour-specific; it must extinguish only the green bar, and not the red line which falls at the same location. But colour-specific motion mechanisms<sup>6</sup> seem to act sluggishly 7-9, and it is unlikely that they would be fast enough to support deblurring. Second, the trailing suppression can speed the disappearance of the moving bar's trace, but it should not affect the bar's perceived time of arrival at the location of the target. As the arrival of the moving bar and the onset of the flashed line physically occur at the same time, the bar and the line should seem, at least initially, to overlap. The longer persistence of the flashed line may then give the impression that it remains on after the moving bar has passed over, but persistence cannot explain how the bar and line can initially appear with no overlap at all.

Overall, Nijhawan's observation presents two visual mechanisms that are more capable than we might have imagined: a subtraction process which can disentangle the combined colours of superimposed stimuli and reassign them to different locations in space; and an extrapolation process which allows us to live, if not a little bit in the future, at least in the present.

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