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The line-motion illusion can be reversed by motion signals after the line disappears

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Abstract. In the line-motion illusion, a briefly flashed line appears to propagate from the locus of attention, despite being physically presented on the screen all at once. It has been proposed that the illusion reflects low-level visual information processing that occurs faster at the locus of attention (Hikosaka et al 1993 *Vision Research* **33** 1219 – 1240; *Perception* **22** 517 – 526). Such an explanation implicitly embeds the assumption that speeding or slowing of neural signals will map directly onto perceptual timing. This 'online' hypothesis presupposes that signals which arrive first are perceived first. However, other evidence suggests that events in a window of time after the disappearance of a visual stimulus can influence the brain's interpretation of that stimulus (Eagleman and Sejnowski 2000 *Science* **287** 2036 – 2038; **289** 1107a; **290** 1051a; 2002 *Trends in Neuroscience* **25** 293). If the online hypothesis were true, we should expect that events occurring after the flashing of the line would not change the illusion. Consistent with our hypothesis that awareness is an a posteriori reconstruction, we demonstrate that the perceived direction of illusory line-motion can be reversed by manipulating stimuli *after* the line has disappeared.

1 Introduction

Despite mounting evidence for physiological effects of attention throughout visual cortex (Motter 1998), it is unclear how these physiological responses relate to visual perception. Attention is often conceived as a filter on incoming sensory information, enhancing processing at the locus of attention (and suppressing processing at other locations) (Broadbent 1958). This tacitly assumes that visual awareness (what the observer reports) is an online phenomenon that comes about as soon as the leading edge of the represented stimulus reaches a 'perceptual end-point'. However, recent studies suggest instead that awareness is 'postdictive', meaning that perceptions are retrospectively attributed after the brain has integrated information from an additional window of time after the event in question (Eagleman and Sejnowski 2000a). In contrast to the online hypothesis, the postdiction hypothesis implies that the outcome of certain experiments might be changed by manipulating events after the experiment would have traditionally ended.

We tested this hypothesis with the line-motion illusion, in which a line that is physically presented all at once is perceived to propagate away from a cued location. The illusion has been interpreted as arising from an attentional gradient (Hikosaka et al 1993b), with the supposition that "the facilitatory effect of attention is exerted at relatively early stages of visual information processing where visual signals are to be fed into the motion detecting mechanism" (Hikosaka et al 1993a, page 1219). Others have proposed, instead, that the illusion can be accounted for by apparent motion mechanisms (Kawahara et al 1996; Downing and Treisman 1997): the illusion is usually generated by the appearance of a dot followed by the nearby presentation of a line, and the visual system may interpret the dot and the line as corresponding pieces of a single object (albeit one that changes form as it moves). Shimojo et al (1997) have argued against that possibility by demonstrating a cross-modal line-motion illusion, in which a line appears to move to the right if a beep (or tactile vibration) is presented on the left side of the observer, demonstrating the effect is not specific to vision.

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We propose a different framework that makes a new prediction. Given the postdictive nature of visual awareness, we hypothesize that a wholly different percept might be generated in the line-motion illusion by manipulating events after the disappearance of the line. To assess this, we recruit a second illusion, path-guided apparent motion (Shepard and Zare 1983), in which a line flashed between the appearances of two dots enhances the percept of apparent motion, and gives the illusion that the dot moved along the trajectory of the line. The visual system apparently interprets the flashed line as a blurred streak of motion in between the two dots; real motion stimulates a trail of sensory receptors as an object passes, and the flashed line putatively stimulates a swath of such receptors. This mirrors the hypothesis that motion streaks provide a code for direction by activating detectors for oriented lines (Geisler 1999).

2 Experiment 1: Apparent motion following the line-motion illusion

What will be perceived when the line is not simply a test probe for the line-motion illusion, but instead comes to have another meaning based on later events? Can the line be retrospectively interpreted as a motion streak moving *toward* the attentional locus? In the experiment illustrated in figure 1, observers fixated a central point; on the right and left were two open boxes, one of which had a dot inside. Attention was

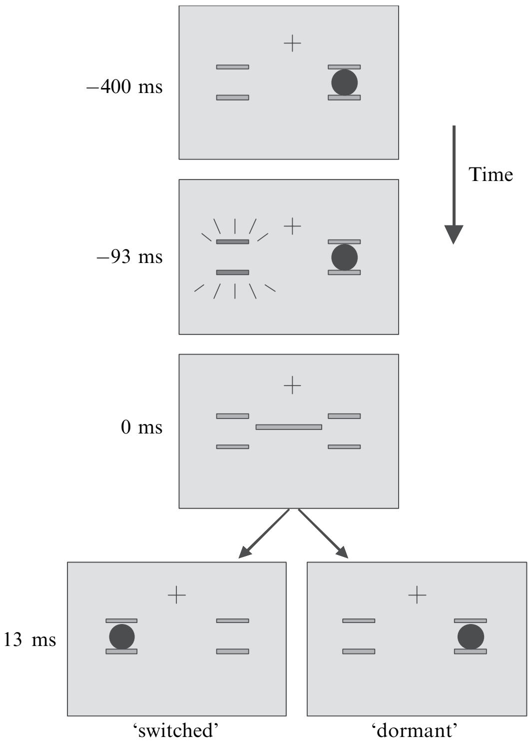

Figure 1. Example of the experimental paradigm. One of the two boxes elicits a shift of attention by making an abrupt color and luminance change 93 ms prior to the appearance of a dim-gray line. The line is flashed for 13 ms; after its disappearance, the dot that was in one of the boxes either remains there ('dormant') or is redrawn in the other box ('switched'). Observers indicate with a keypress whether the line appeared to move to the right or left, with no time constraints. For simplicity, the figure illustrates only two conditions—in the remaining two conditions, the dot begins on the cued side. The four conditions are randomly interleaved, and the display is left/right mirrored on half the trials. After each presentation, the screen is blank for at least 1 s before the next trial begins. Observers are instructed to fixate on the central cross; eye fixation was not monitored, as the random interleaving should obviate any predictive effects. Stimuli were programmed in C on a Silicon Graphics workstation, with a monitor refresh rate of 72 Hz.

drawn to one side by an abrupt change in color and luminance of one of the boxes ('cued' box). Shortly afterward, a dim gray line was flashed on the screen for 13 ms. Then, in the video frame *following* the flashed line, the dot either remained in place ('dormant') or was redrawn in the other box ('switched'). Since the dot could appear on the cued or uncued side, and could be either dormant or switched, this generated four conditions, which were randomly interleaved. Three of the four conditions were controls, in which the line-motion illusion should be seen normally, ie the line should appear to propagate away from the cued box. However, we wondered whether in the fourth case, wherein the dot began in the non-cued box, and then switched to the cued box after the disappearance of the line ('counter-movement' condition), the line would be interpreted as a motion steak in the apparent motion of the dot. In this case, the streak should appear to propagate *toward* the cued box, not away from it. This condition pits the attentional cueing that engenders the line-motion illusion against apparent motion in the opposite direction—and which is completed after the line is gone.

In trials when the dot was dormant, the normal line-motion illusion was seen as expected, ie the line appeared to propagate away from the cued box (figure 2a, $86.4\% \pm 5.3\%$ probability when dot was inside the cued box, $84.09\% \pm 10.8\%$ when dot was in the non-cued box, $n = 4$). In condition 3, wherein the dots began in the cued box and then switched, the line-motion illusion was enhanced (100% probability of reporting line motion away from the cue). By contrast, in the counter-movement condition (the dot began in the uncued box and ended in the cued box), observers reported illusory line-motion *toward* the cue $73.9\% \pm 14.9\%$ of the time. Thus, in the three control conditions, the line is generally perceived to have propagated *away* from the attentional cue, but when the dot moves in the counter-direction, the better interpretation seems to be that the flashed line was a motion streak *toward* the cue.

This striking result appears incompatible with the online hypothesis, in which attention speeds or slows signals in their race to a perceptual finish line. Note that the apparent motion of the dot occurs *after* the line has disappeared, ie after the line information has entered the visual system and presumably been filtered by attention. Instead, this result supports the hypothesis that visual awareness is delayed to take into account information *after* the disappearance of the line and to settle on a best interpretation of the scene (Eagleman and Sejnowski 2000a, 2000b, 2000c; Eagleman 2001).

3 Experiment 2: Eliminating apparent motion

An alternative possibility might be that a 'moving spotlight' of attention (especially one that moves sluggishly) explains our results—eg in the 'counter-movement' condition the spotlight moves toward the flashed line, then reverses direction when the dot appears in the cued box, and the perceived motion direction is a function of the spotlight's final direction. To rule out this hypothesis, we expanded the distance of the boxes (and the dot within) to 6 deg of arc, which is past the proximity required for a percept of apparent motion: at this larger distance, when a dot disappears from one side and is redrawn at the other, observers report no sensation of movement. With this separation, we find that the line is generally viewed as moving away from the cued box, as expected by the line-motion illusion, under all four conditions (figure 2b, conditions 1 through 4: $94.2\% \pm 5.2\%$, $84.1\% \pm 15.1\%$, $94.8\% \pm 6.8\%$, $72.7\% \pm 21.1\%$, respectively). As with other studies, it seems the cueing depends only on the side to which attention is drawn (Shimojo et al 1997), and not, in this case, on the eccentricity.

Thus, the 'counter-movement' condition seems to reverse the line-motion illusion only when the flashed line can be interpreted as a motion streak. We suggest more generally that the traditional line-motion illusion is also best understood in terms of motion streaks. That is, the visual system may interpret a flashed line as a 'motion streak to nowhere' that begins at the cued box. Versions of this idea have been suggested in

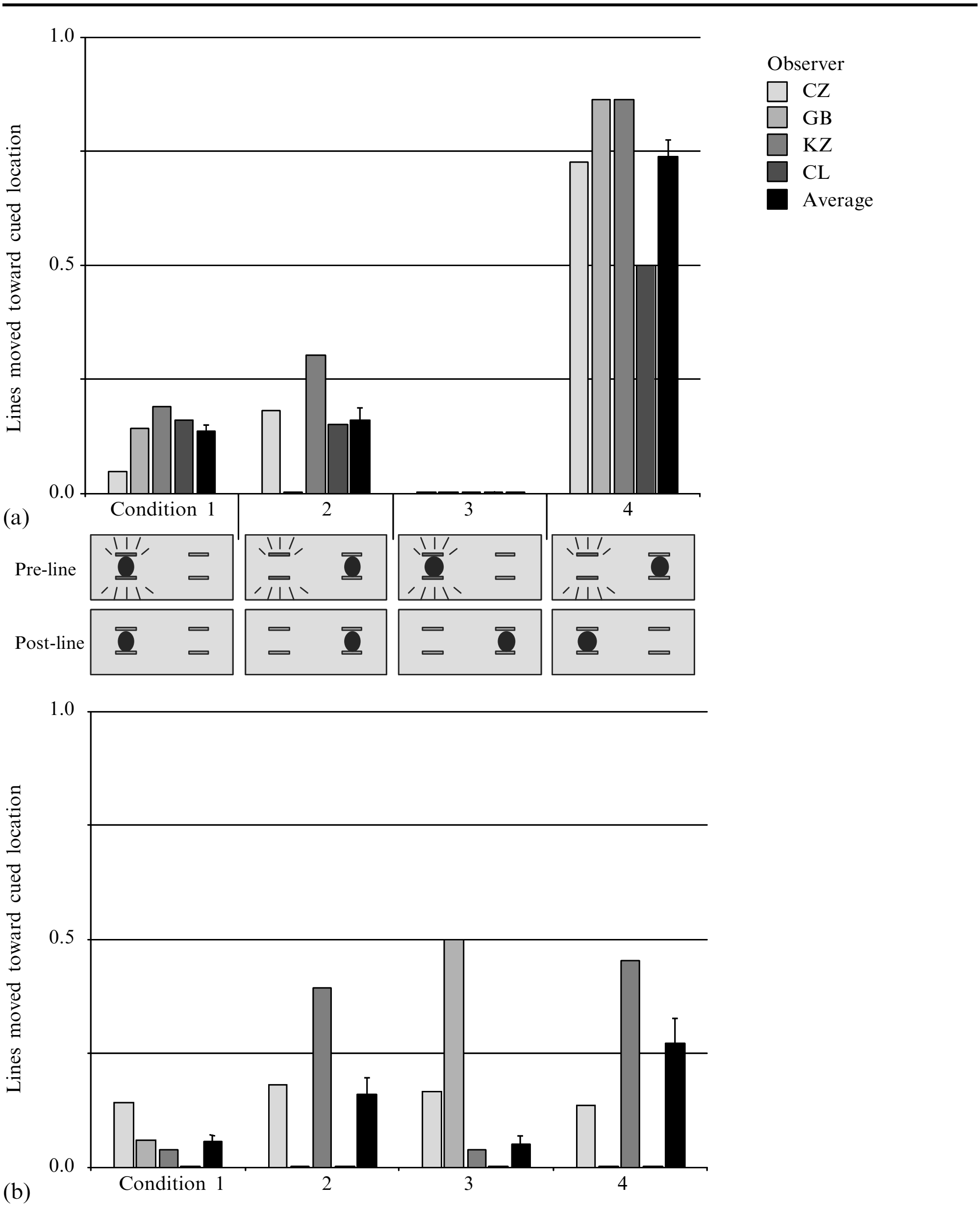

Figure 2. The direction of illusory line-motion can be reversed by apparent motion following the disappearance of the line. (a) Observers reported whether they perceived line motion to the right or left (2AFC). Bars represent the proportion of trails in which an observer reported line motion toward the cued location (100 trials/observer). In post-experiment interviews, observers reported that the line clearly appeared to propagate in one direction or the other, indicating that the forced-choice nature of the task was not problematic. Boxes were separated by 2 deg of arc. (b) When the distance between the boxes (and dots) is increased to 6 deg of arc, the switching of the dot does not yield a percept of apparent motion. Therefore, as predicted, observers generally report that the line propagates away from the cued side, as expected with the traditional line-motion illusion.

the past (Kawahara et al 1996; Downing and Treisman 1997), although no attempt was made to account for events that occur after the line disappears. The fact that the line-motion illusion can be cued non-visually (Shimojo et al 1997) does not rule out the motion-steak interpretation, since there is no reason why the visual machinery interpreting motion streaks should not consult other modalities—after all, something that makes noise on your left side is more likely to be an object moving from left to right than in the other direction.

4 General discussion

Although it is advantageous for an organism to operate as close to the present as possible, information from a window of time after an event seems to influence perceptions. This is consistent with a range of experiments including backward masking (Bachmann 1994), the color-phi phenomenon (Kolers and von Grünau 1976), the perception of phosphenes (Pascual-Leone and Walsh 2001), and the flash-lag effect (Eagleman and Sejnowski 2000b), all of which suggest that what an observer perceives to be happening at a moment in time depends on information integrated from a window of time after that event. While it has long been appreciated that the visual system performs spatiotemporal filtering, it is almost always assumed that the filtered time window extends from the event in question into the past. Instead, we have suggested that information after the event is included in the analysis—and this is, of course, only possible when perception is delayed (Rao et al 2001). While many neural models in the literature assume that a well-defined input is neatly mapped onto a particular output as soon as the leading edge of the information reaches some end point, the present studies support the hypothesis that neural dynamics are influenced through time by the ongoing input of sensory information.

These results call into question the notion that attention acts as a filter on feedforward information; however, they do not rule it out. An alternative hypothesis consistent with our data is that attentional filtering generates an initial motion signal, which is temporally integrated with the effects of the later dot displacement, and the resulting winning motion signal is later applied to the line itself. If the observers' motion reports are the result of integrating motion information over the whole trial time, the effects of attention could, in theory, act at any point within that time.

The attentional filtering concept has been encouraged by a number of cortical physiology experiments, which suggest that information near the focal point of attention is enhanced, while surrounding information, even within the same receptive field, is suppressed (Motter 1998). However, it is unclear how we should interpret the spike trains of individual cortical neurons: it may not be that an increase or decrease in firing rate is isomorphic with passing on more or less information to 'higher' areas. The massive anatomical feedback typical of all cortical areas may mediate top–down influences of attention on visual cortical responses. The visual cortex may be more than a feedforward gain controller, and feedforward information may not be perceived until there is sufficient feedback from other brain areas. Whereas a filter in a feedforward system must jettison information on its race to an interpretation, an integrative system is more prudent: never knowing what might happen next, it retains current sensory information in case events in the near future render it useful.

Demonstrations of the stimuli are available on the *Perception* website at http://www.perceptionweb.com/misc/p3314/.

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