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Powerful Motion Illusion Caused by Temporal Asymmetries in ON and OFF Visual Pathways

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Del Viva, Maria Michela, Monica Gori, and David C. Burr. Powerful motion illusion caused by temporal asymmetries in ON and OFF visual pathways. *J Neurophysiol* 95: 3928–3932, 2006; doi:10.1152/jn.01335.2005. Successive presentations of Glass patterns (randomly positioned pairs of dots oriented in a coherent pattern) create a strong sense of global motion along the orientation of the pattern, but ambiguous in direction. Here we report that dynamic “anti-Glass” patterns, created by successive pairs of globally structured pairs of opposite polarity, create an even more powerful motion illusion that is unambiguous in direction: the dark dots always move toward the light. The motion can be cancelled and reversed by introducing a real delay in the presentation of the light dots, suggesting that the effective stimulation of the light is about 3 ms faster than the dark dots. The most plausible explanation for this is that human ON channels are faster than OFF channels, as has been shown in the macaque.

INTRODUCTION

Glass patterns—made up from arrays of randomly positioned but coherently oriented dipoles—carry a powerful sense of global spatial structure (Glass 1969; Glass and Perez 1973). They have long been used in both psychophysical (e.g., Dakin 1997; Kovacs and Julesz 1992; Wilson and Wilkinson 1998) and electrophysiological (Smith et al. 2002) research to investigate processing of spatial form. More recently, they have been used for psychophysical and electrophysiological investigations of interactions between form and motion (Burr 2000; Burr and Ross 2002; Krekelberg et al. 2003, 2005; Ross et al. 2000): successive presentations of Glass patterns create a strong sense of global motion along the orientation of the pattern (see supplementary video 1).¹ Although the sense of motion is most compelling, the direction of motion is ambiguous, sometimes clockwise, sometimes anticlockwise.

It is also possible to generate “anti-Glass” patterns from coherently oriented dipoles of dots of opposite polarity. These create no sense of global structure and are hard to distinguish from quasi-random patterns (Prazdny 1986; see Fig. 1A). Although they themselves create no sense of pattern, adding anti-Glass to Glass patterns destroys the global sense of pattern because their Fourier power spectra are completely complementary (Barlow and Olshausen 2004; Burr and Ross 2006). Here we show that dynamic sequences of anti-Glass patterns also produce a strong sensation of motion. The sensation of

motion follows the orientation of the dots, even though there is no Fourier energy in that direction, nor an impression of spatial structure. Unlike the motion caused by Glass patterns, the motion from anti-Glass patterns is always in a specific direction, from black to white. We argue that this illusory motion results from differential delays in the primate ON and OFF system (Chichilnisky and Kalmar 2002).

METHODS

Figure 1A shows a single frame of the stimulus used in this study. Pairs of opposite polarity (black/white) dots were positioned randomly, with the position of the white dot in each pair rotated about the screen center relative to the black in the same direction throughout a given display (counterclockwise in this example). Dynamic sequences (illustrated in supplementary video 2) were constructed from five frames of uncorrelated images, with the positions of the pairs chosen randomly in all frames (so there is no net motion signal).

Each frame consisted of 70 randomly positioned pairs of opposite-polarity dots of 0.3° diameter, separated by 0.45° (center to center) and orientated tangentially to an imaginary circle centered at screen center (clockwise or counterclockwise). Dynamic presentations constituted five independent anti-Glass patterns, each displayed for six monitor frames (update rate, 33 Hz; total duration, 150 ms). The stimulus diameter subtended 13° at 57 cm, had mean luminance 33 cd/m², and frame rate 200 Hz. At maximum contrast, the white dots were 140 cd/m² and the dark dots near zero cd/m². The screen phosphor (DP104, Clinton Monoray) decayed to <1% in 250 μs (manufacturer specification confirmed by photometric measurements), ruling out the possibility that the effects were generated by physical delays of the oscilloscope.

RESULTS

The primary result can be verified by viewing the supplementary video 2. All observers report a vivid and unambiguous sensation of circular motion, always in the direction of black toward white. This effect has been observed informally by dozens of observers, all of whom saw the effect instantly. We report formal data on three trained psychophysicists, two of whom were naïve to the goals of the study.

To investigate the robustness of the illusory motion, we measured the direction of perceived rotation as a function of contrast and of signal-to-noise ratio. As the contrast decreased, observer responses became less consistent (Fig. 2A). However, even at contrasts as low as 13% contrast, more than 75% of presentations were perceived to rotate toward white, and at 9% (about twice the detection threshold), the bias was still statis-

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¹The Supplementary Material for this article (two videos) is available online at <http://jn.physiology.org/cgi/content/full/01335.2005/DC1>.

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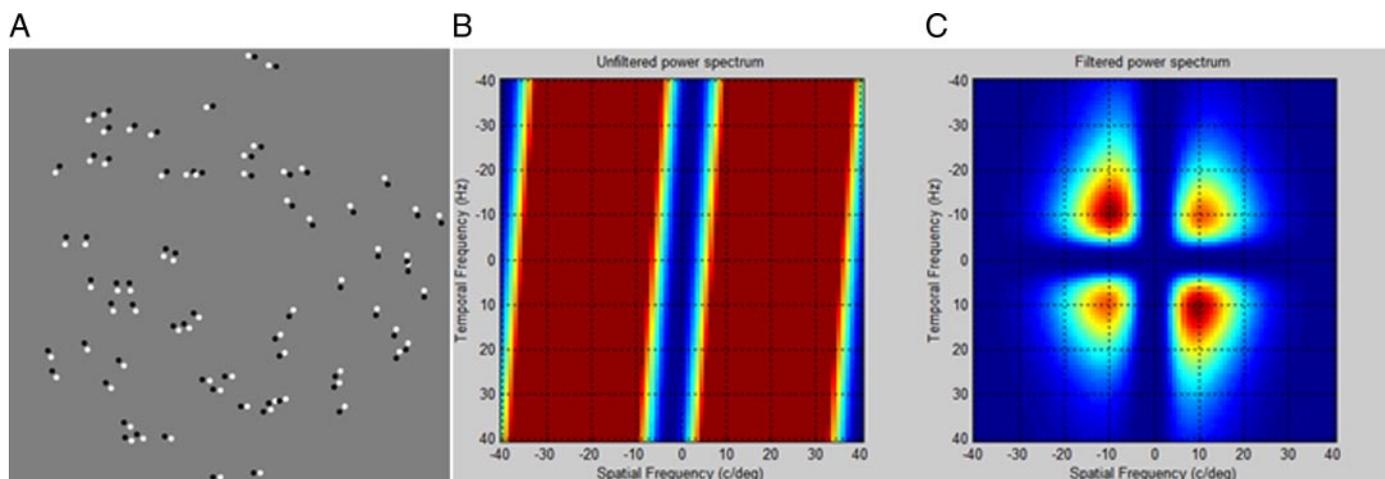


FIG. 1. *A*: example of a single frame of the stimuli used in this study. *B*: spatiotemporal Fourier power spectrum of a single pair of black and white dots with the black dot displayed 10 ms after the white (color code: navy = 0, brown max). Approximating the dots with a delta function, the energy spectrum for the pair E is given by

$$E(u, \eta) = \sin^2 [\delta \cdot v + \tau \cdot \eta] / 2 \quad (1)$$

where v and η are spatial and temporal frequencies, respectively; δ dot separation (0.15°); and τ dot delay (0.01 s). *C*: power spectrum of B multiplied by that of a biologically plausible human motion detector (taken from Anderson and Burr 1985). There is a clear bias in the energy distribution, higher in the negative quadrants, corresponding to a motion signal in the opposite direction of dot presentation: black to white (see also Adelson and Bergen 1985). If neural processing of luminance decrements were delayed relative to increments, this would generate a local motion signal in the direction of black toward white that in turn could produce an impression of global motion. Power spectrum of the spatiotemporal filter F for this particular simulation was given by

$$F(u, \eta) = \exp\{-[\log(v) - \log(u_0)]^2 / (b_s)^2 - [\log(\eta) - \log(\eta_0)]^2 / (b_t)^2\} \quad (2)$$

where u_0 is the peak spatial frequency (4 c/deg), b_s is the spatial bandwidth (0.4 log-units), η_0 is the peak temporal frequency (10 Hz), and b_t is the temporal bandwidth (0.4 log-units).

tically significant ($P = 0.001$). The occurrence of the effect at low contrasts effectively excludes explanations based on nonlinear artifacts in stimulus generation or neural transduction. The open squares of Fig. 2*B* show the robustness of the phenomenon to visual noise. Here contrast was maximal, but only some of the pairs were oriented coherently in the circular direction, the others oriented at random. The response was significantly greater than chance for signal-to-noise ratios >50%. This threshold is high compared with many published studies on flow perception (e.g., Morrone et al. 1995), probably because of the sparse distribution of the dots. However, these coherence thresholds were very similar to those obtained for motion of similar stimuli of the same contrast sign, with real displacement between frames.

The unambiguity and robustness of the perceived motion suggest that it results from an effective temporal offset created by the visual system, and that this offset stimulates human motion mechanisms. To illustrate how this may occur, Fig. 1*B* shows the spatiotemporal Fourier power spectrum of a dot pair in which the black is delayed by 10 ms. In Fig. 1*C* the power spectrum is multiplied by the spatial and temporal filter characteristics of the human visual system (taken from Anderson and Burr 1985), revealing a clear excess of spatiotemporal energy in the *top left* and *bottom right* quadrants. Energy in these quadrants corresponds to motion in the direction opposite to the presentation order, from black to white, like the “reversed phi-motion” of Anstis (1970), which was also explained in these terms by Adelson and Bergen (1985) and Burr et al. (1986). However, if the two dots are displayed simultaneously, then the power spectrum of the stimulus will be symmetrical, and the regions of the filtered energy corresponding to positive

and negative velocity will be equal, the delay being essential for the asymmetry.

To test whether the delay responsible for this motion illusion could result from asymmetries in the neural processing of black and white dots, we measured perceived direction of rotation for stimuli with the black dots advanced or retarded by one or two frames (Fig. 2*C*). Delaying the black dots by 5 ms did not affect the perceived direction, whereas delaying the white dots by the same amount inverted the perceived direction. This suggests that when no physical delay is present in the stimulus, the visual system introduces a delay of the black dots relative to the white. The temporal resolution of our display did not allow for delays <5 ms, but interpolation of the data estimates the neural delay of black dots with respect to white to be about 3 ms for high and medium contrasts and 5 ms for low contrasts. The filled circles of Fig. 2*B* show results for stimuli with the black dots displayed 5 ms before the white, as a function of signal coherence. The delay caused the motion to invert at high coherence levels, falling to chance at similar thresholds to those with no delay (open squares).

Because the effect increased rather than decreased at low contrasts, it is unlikely to result from different effective contrasts. However, to be certain that the effect resulted from polarity rather than effective contrast, we varied separately the contrast of the light and dark dots under two different conditions. In the first (Fig. 3*A*) the contrast of the light and dark dots was varied separately on a gray background. At 100% contrast (of both light and dark dots), the stimulus was identical to the basic stimulus of Fig. 1*A*, always producing motion in the direction of black to white. Lowering the contrast of the black dots (down to 20%), while leaving the white at 100% contrast,

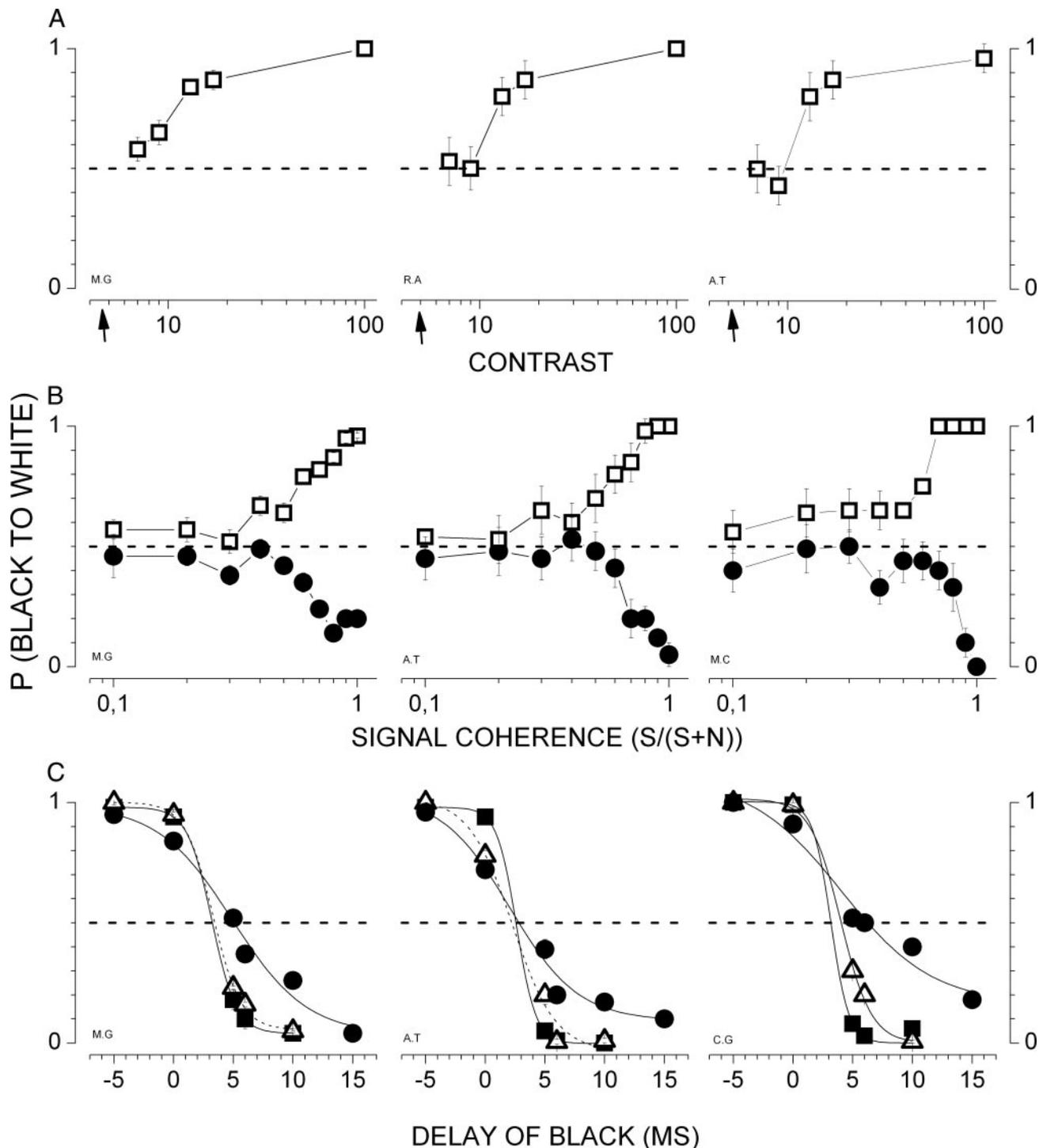


FIG. 2. Probability of seeing motion in the direction black to white for stimuli described in Fig. 1A, as a function of the Michelson contrast of the dots, for 3 observers: one author and 2 naïve to the goals of the study. Orientation of dot pairs was randomly clockwise or counterclockwise on each trial, and responses scored relative to physical orientation. Arrows indicate the detection threshold for these stimuli. Horizontal dashed lines show chance performance (50%). Each point is the average of 50 trials, and error bars show SEs (binomial distribution). *A*: probability of seeing motion in the direction black–white, as a function of signal coherence level (defined as the ratio of signal to total dots). For the open squares the black and white dots were displayed together; for the filled circles the black dots were displayed 5 ms before the white. Delay inverts perceived order, but robustness for noise was very similar. *B*: probability of seeing the motion in the direction black–white, as a function of delay in presentation of the white dots (positive delay means black presented first), for 3 different dot contrasts: 100% (filled squares), 20% (open triangles), and 7% (filled circles). Curves were fitted with a cumulative normal function: the point where this function crosses zero gives an estimate of the relative delay in neural processing of the black dots.

did not affect the result. However, lowering the contrast of the white dots did affect the result, annulling (but not inverting) the illusion. This is consistent with the suggestion that decreasing

contrast also causes delays, and that these delays add to those caused by the sign of the dots: decreasing the contrast of the black dots retards their processing further, enhancing the illu-

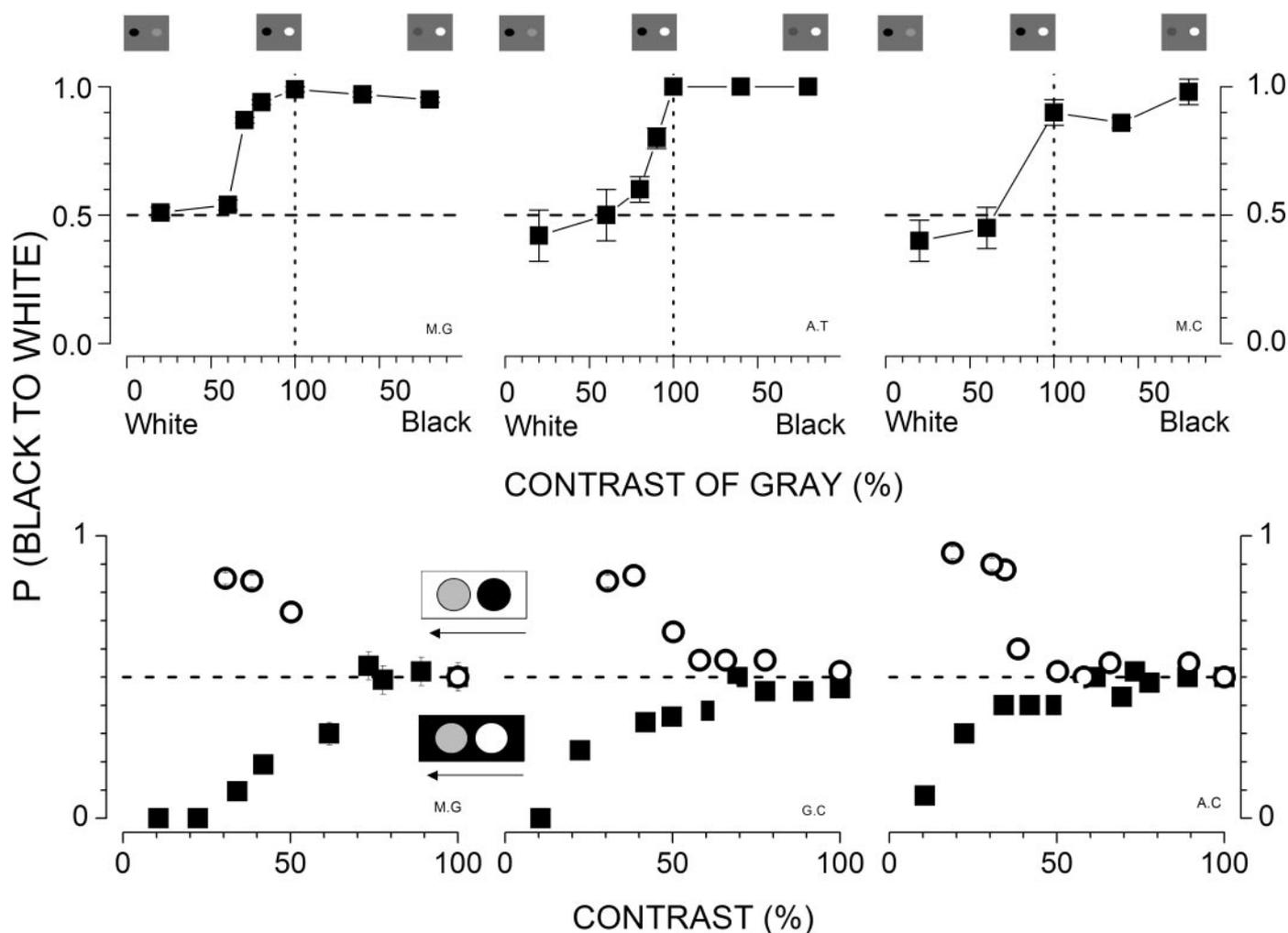


FIG. 3. Effect of varying separately the contrast of light and dark dots. *A*: effect of varying separately the contrast of either the white or black dots, with the others fixed at maximum, on a gray background. With white dots set to full contrast (points at *right* of graph), decreasing the contrast of the black dots ($\leq 20\%$) did not affect the illusion; however, with black dots at full contrast (points at *left*) decreasing the contrast of the white dots canceled the illusion (without inverting it). These results suggest that low contrast also causes delays in neural transmission, and that the effects are additive with those of the luminance sign. *B*: effect of varying separately the contrast of the white and black dots, on a white (open symbols) or black (filled symbols) background. Decreasing the contrast of the gray dot creates illusory motion from high contrast toward low contrast.

sion, whereas decreasing the contrast of the white dots delays their transmission, canceling the delay of the black dots.

That contrast itself can cause delays is shown by a variant of the display in which the background was either white or black, so all dots had the same contrast sign (Fig. 3*B*). Here lowering the contrast of one dot (leaving the other fixed at black or white) created illusory motion, always in the direction of high to low contrast. Note that here no reversed phi motion is to be expected because both dots always had the same contrast sign.

DISCUSSION

This study clearly suggests that black dots are processed more slowly than white dots by the human visual system, by about 3 ms. What may be the neural basis of this delay? In mammals, visual signals are initially processed through the functionally separate ON and OFF channels, which do not interact before converging in the primary visual cortex (Schiller 1982, 1992). Recent measurements of the response dynamics of ganglion cells in primate retina show that ON-center cells

respond more rapidly than OFF-center cells, on average a 5-ms-faster peak response (Chichilnisky and Kalmar 2002). Similar estimates are obtained from primate photopic electroretinogram (Ueno et al. 2004).

A very recent study has suggested that another powerful motion illusion (Kitaoka and Ashida 2003) can be explained by delays in primary visual cortex and in middle temporal (MT) in processing low-contrast stimuli (Conway et al. 2005). However, this cannot explain the current result because the black and white dots were of equal physical contrast in all conditions. Nor is it likely to result from effective differences in contrast because luminance gain control will increase the effective contrast of the black, not the white dots. In any event, the effect actually increased at very low contrasts, when any such nonlinearities would be negligible. Furthermore, when tested directly we showed that decreasing contrast can cause motion illusions under these conditions, and that the effects were additive with those produced by contrast sign. When all dots had the same contrast sign (all brighter or all darker than the background; Fig. 3*B*), motion was always in the direction of

high to low contrast, with no reversed phi motion. However, when dot pairs had different signs (like the main illusion), separately varying the contrast of black and white had an asymmetrical effect, suggesting that the delays produced by contrast sum with those associated with contrast sign. Furthermore, eye movements are unlikely to be involved because the displays were brief (150 ms), and even worked with single presentations. We therefore conclude that the unambiguous motion produced by anti-Glass points to differential delays in ON and OFF pathways.

What causes the differential delays of these pathways? One possibility is that the photoreceptors themselves respond more slowly to decrements than to increments, although this is not supported by data, at least not for low-contrast signals in turtle cones (Baylor et al. 1974). Nor is it likely to result from a faster synaptic transmission from photoreceptors to ON bipolar cells because this transmission requires an inversion of sign by a second-messenger cascade (Nawy and Jahr 1990), which seems to produce slightly longer response latencies (but not peak responses) in ON cells (Chichilnisky and Kalmar 2002). The physiological cause for the difference remains obscure at present.

The current psychophysical results suggest that as in macaques, human ON cells have faster dynamics than that of OFF cells, and that ON and OFF signals combine at the early stages of motion perception. Although the combination of ON and OFF signals in low-level motion detectors runs against some psychological conclusions (e.g., Edwards and Badcock 1994; Wehrhahn and Rapf 1992), it is consistent with motion-perception models that require quadrature-phase filters (e.g., Adelson and Bergen 1985) and with studies of the effects of blocking the ON pathway on cells in primary visual cortex (Schiller 1982).

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