

mutations in the *SCN5A* gene that alter α - β 1-subunit interactions also produce an LQT3 variant¹⁵. Our results suggest *SCN5A* along with *SCN1B* as candidates for sodium-channel genes involved in idiopathic seizure disorders.

ACKNOWLEDGEMENTS

This research was supported by the Curtis Hankamer Foundation and American Heart Association G98-193 (H.A.H.), National Institutes of Health NS 29709 and the Blue Bird Foundation for Pediatric Neurology (J.L.N.).

ACCEPTED 21 MAY 1999

1. Fozzard, H. A. & Hanck, D. A. *Physiol. Rev.* 76, 887–926 (1996).

- White, J. A., Alonso, A. & Kay, A. R. *Neuron* 11, 1037–1047 (1993).
- Deisz, R. A. *Neuroscience* 70, 341–51 (1996).
- Hoehn, K., Watson, T. W. & MacVicar, B. A. *Neuron* 10, 543–552 (1993).
- Gellens, M. A. *et al. Proc. Natl. Acad. Sci. USA* 89, 554–558 (1992).
- Yarowsky, P. J., Krueger, B. K., Olson, C. E., Clevinger, E. C. & Koos, R. D. *Proc. Natl. Acad. Sci. USA* 88, 9453–9457 (1991).
- Rogart, R. B., Cribbs, L. L., Muglia, L. K., Kephart, D. D. & Kaiser, M. W. *Proc. Natl. Acad. Sci. USA* 86, 8170–8174 (1989).
- Felts, P. A., Yokoyama, S., Dib-Hajj, S., Black, J. A. & Waxman, S. G. *Brain Res. Mol. Brain Res.* 45, 71–82 (1997).
- Bland, B. H. & Colom, L. V. *Prog. Neurobiol.* 41, 157–208 (1993).
- Wang, Q. *et al. Cell* 80, 805–811 (1995).
- Chen, Q. *et al. Nature* 392, 293–296 (1998).
- Dumaine, R. *et al. Circ. Res.* 78, 916–924 (1996).
- Pacia, S. V., Devinsky, O., Luciano, D. J. & Vazquez, B. *Neurology* 44, 1408–1410 (1994).
- Wallace, R. H. *et al. Nat. Genet.* 19, 366–370 (1998).
- An, R. H. *et al. Circ. Res.* 83, 141–146 (1998).

A new transparent motion aftereffect

Maarten J. van der Smagt^{1,2}, Frans A. J. Verstraten^{1,3} and Wim A. van de Grind¹

¹ Department of Comparative Physiology and Helmholtz Research Institute, Universiteit Utrecht, Padualaan 8, NL-3584 CH Utrecht, The Netherlands

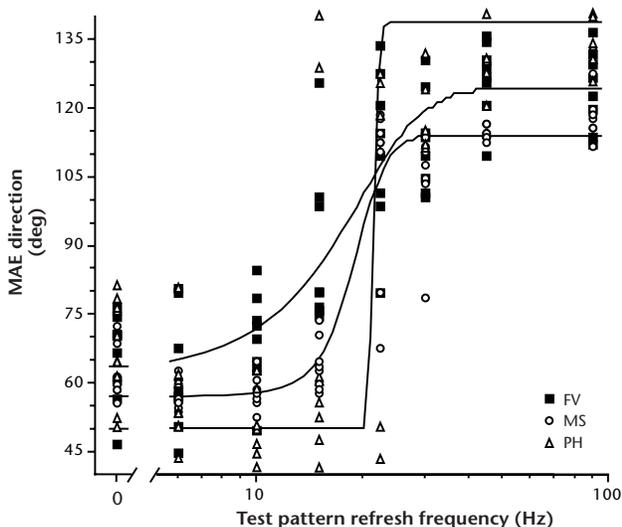
² Present address: The Salk Institute for Biological Studies, La Jolla, California 92037, USA

³ ATR Human Information Processing Labs, Department 5, 2-2 Hikaridai, Kyoto, 619-0288, Japan

Correspondence should be addressed to M.S. (M.J.vanderSmagt@bio.uu.nl)

We report a visual motion aftereffect (MAE) that reveals simultaneous adaptation in independent motion channels coding for 'slow' or for 'fast' velocities. Dynamic random noise test patterns with low refresh frequencies or static test patterns can be used to test for MAEs mediated by slow channel adaptation, whereas MAEs produced by fast channel adaptation may be detected with noise patterns refreshed at high rates. After adaptation to transparent motion containing both a slow and a fast component, test patterns containing both high and low refresh frequencies produce a transparent, two-component MAE, revealing two distinct channels.

When adaptation to a moving stimulus is followed by a scene



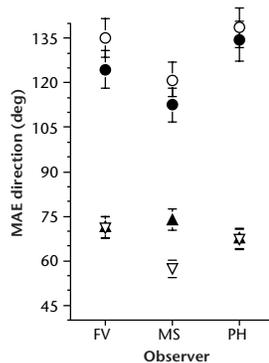
without coherent motion, an illusory motion in the opposite direction is perceived: a phenomenon known as the MAE¹. Two superimposed groups of dots moving in sufficiently different directions and/or speeds are perceived as two segregated, transparent surfaces². The MAE following such a stimulus is not opposite to each of the adaptation vectors (and thus transparent), but has only one direction, opposite that of the (weighted) sum of the adaptation vectors. Challenging the classic explanation of the MAE³, this observation was explained in terms of the relative activity of the entire motion sensor population⁴. MAEs of unidirectional and transparent motion have typically been tested with stationary test patterns and can be elicited for adaptation speeds up to about 25 degrees per second, although humans can perceive much higher speeds.

A much wider range of adaptation speeds was seen for 'dynamic MAEs' tested with dynamic visual noise (resembling a detuned television screen)^{5,6} than for 'static MAEs'. Static MAEs dominate at low speeds, whereas dynamic MAEs prevail after adaptation to higher speeds⁷. Taken with other evidence^{8–10}, one explanation is that these MAEs reveal two separate, speed-tuned motion-sensor populations, which may correspond to distinct channels: sustained (slow and tuned to fine structures) or transient (fast and spatially more coarsely tuned)^{11–14}.

To test this prediction, observers adapted to orthogonally directed transparent motion containing only slow speeds (1.3 and 4 degrees per second, within the range for which the static MAE is stronger than the dynamic MAE), only fast speeds (12 and 36 degrees per second with a dominant dynamic MAE) or mixed speeds (4 and 12 degrees per second) for 45 seconds. The test pattern refresh frequency varied across trials from 0 ('static') to 90 Hz. Observers were instructed to indicate the MAE direction. Irrespective of refresh frequency, they indicated constant MAE direction

Fig. 1. MAE direction as a function of test pattern refresh frequency in the 'mixed' condition (three observers). Each data point shows a single MAE direction judgment. The adaptation stimulus consisted of two orthogonally moving binary random-pixel patterns (pixels, 1.88 min arc squared) viewed through an 8-degree circular window. The test stimulus consisted of a random-pixel pattern of which each pixel was assigned a new value (either dark or bright) every *n*th frame depending on the test frequency (0–90 Hz). Judged MAE direction near the direction opposite the 'slow' adaptation vector (< 90 degrees) can be clearly distinguished from those near the direction opposite the 'fast' adaptation vectors (> 90 degrees). At test pattern frequencies of 15–30 Hz, MAE directions were judged to be approximately opposite either the 'slow' or the 'fast' adaptation vector. Each symbol represents data for one observer; weighted sigmoidal functions fitted to data for each are shown by curves ($r^2 > 0.95$ for each fit).

Fig. 2. MAE directions for the different test patterns in the 'mixed' condition (three observers). Each symbol shows the mean of eight direction judgments. The static MAE (filled triangles) is closer to the direction opposite the 'slow', whereas the dynamic MAE (filled circles) is closer to the direction opposite the 'fast' adaptation component. The two component MAE directions seen with a combined test pattern (open triangles for static; open circles for dynamic) are distinct, each similar to those seen using a single test frequency, yielding a transparent MAE.



for either the slow or the fast condition, for which weighted vector summation of the adapting patterns was apparent. However, in the mixed condition (Fig. 1), the MAE is closer to the direction opposite the fast adaptation component for test frequencies above approximately 20 Hz, whereas it approaches the direction opposite the slow adaptation component for lower test frequencies. No intermediate directions are perceived; thus, MAE direction changes sharply as function of the test refresh frequency. The point of transition at ≈ 20 Hz is comparable with temporal frequency tuning of the transient channel(s) reported by others (for example, peaking at 13 or 20 Hz)^{14,15}. Statistical analysis (Cohen's Kappa > 0.88) revealed that the MAE directions could be divided in two categories, one with refresh frequencies above 20 Hz and MAEs opposite the fast-adaptation component, and the other with lower frequencies with MAEs opposite the slow component.

In the past, MAEs have been tested with either static or dynamic test patterns, exposing only one motion sensor population at a time; hence, it was believed that MAEs reflected integrated activity of all stimulated motion sensors. Because our results suggest two populations, we designed a test pattern that had both static (0 Hz) and dynamic (45 Hz) characteristics, and thus tapped both populations simultaneously. Separate MAEs for each of the two components would be expected only if the two sensor populations were truly

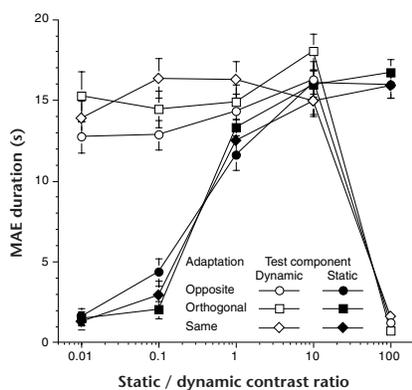
independent. After adaptation under previously used conditions, one of three test patterns was shown: static, dynamic or 'combined' (containing both static and dynamic characteristics). The observers indicated MAE direction of either the static or the dynamic component in the test pattern. As expected, the dynamic MAE was very weak for the slow condition, whereas for the fast condition, static MAEs were virtually absent. In the mixed condition, both MAEs were present, and both components of the combined test pattern elicited an MAE (Fig. 2). The directions of these MAEs are similar to those elicited by the static or dynamic test pattern alone. The combined test pattern is perceived as a transparent, bi-directional MAE, with the 'static component' slowly moving opposite the low-speed-adaptation component and the 'dynamic component' moving rapidly opposite the high-speed-adaptation vector.

This new MAE phenomenon was remarkably robust. Varying contrast ratio (or strength) between the static and dynamic test components had little effect, as long as both were visible (Fig. 3). Moreover, as long as one of the adaptation components was slow and the other fast, a range of adaptation speeds yielded the transparent MAE. One might argue that, because the adaptation stimulus contained two distinct directions, direction tuning rather than speed tuning was the most prominent segregation cue. However, if observers adapted to transparent motion with both slow and fast components moving in the same direction, again a transparent MAE was perceived for the combined test pattern. The effect clearly does not depend on the combination of adaptation directions (Fig. 3).

The notion of two motion sensor populations with distinct temporal characteristics is hard to reconcile with the unidirectional MAE seen with static test stimuli after adaptation to transparent motion of any speed. We suggest that this unidirectionality reflects activation of only one of the populations by stationary test patterns. Our new combined test pattern taps both populations simultaneously, resulting in the perceptual manifestation of both MAEs. This perceptual duality demonstrates independent underlying neural substrates for separate slow and fast channels of motion perception.

Note: a demonstration of the transparent motion illusion is available at http://neurosci.nature.com/supplementary_info/.

Fig. 3. The MAE duration of each of the test components (static or dynamic) pooled across three observers as a function of the contrast ratio between the static and dynamic test components. The adaptation stimulus always had a contrast ratio of one. (Both components had the same contrast during adaptation.) At low contrast ratios (≤ 0.01), there is hardly any static component visible in the test stimulus, whereas the dynamic component is clear and dominant. The reverse is true for high contrast ratios (> 50). The results are similar for each of the adaptation direction combinations. At low contrast ratios, only the dynamic component elicits a clear MAE, whereas at high contrast ratios, the static component shows the only salient MAE. In between, there is a range of contrast ratios for which both components show strong MAEs, resulting in the percept of transparency.



ACKNOWLEDGEMENTS

We thank D. Alais, C. Hofstra and R. van Wezel for their comments. M.S. is supported by the Netherlands Organization for Scientific Research. F.V. is a Research Fellow of the Royal Netherlands Academy of Arts and Sciences.

RECEIVED 5 FEBRUARY; ACCEPTED 5 MAY 1999

1. *The Motion Aftereffect: a Modern Perspective* (eds. Mather, G. Verstraten, F. A. & Anstis, S. M.) (MIT Press, Cambridge, Massachusetts, 1998).
2. Braddick, O. J. *Perception* 26, 995–1010 (1997).
3. Barlow, H. B. & Hill, R. M. *Nature* 200, 1345–1347 (1963).
4. Mather, G. *Perception* 9, 379–392 (1980).
5. Hiris, E. & Blake, R. *Proc. Natl. Acad. Sci. USA* 89, 9025–9028 (1992).
6. Verstraten, F. A., Fredericksen, R. E., van Wezel, R. J., Lankheet, M. J. & van de Grind, W. A. *Vision Res.* 36, 421–424 (1996).
7. Verstraten, F. A., van der Smagt, M. J. & van de Grind, W. A. *Perception* 27, 1055–1066 (1998).
8. Thompson, P. *Vision Res.* 23, 1533–1538 (1983).
9. Georgeson, M. A. in *Models of the Visual Cortex* (eds. Rose, D. & Dobson, V. G.) (Wiley, New York, 1985).
10. Gegenfurtner, K. R. & Hawken, M. J. *Trends Neurosci.* 19, 394–401 (1996).
11. Kulikowski, J. J. & Tolhurst, D. J. *J. Physiol. (Lond.)* 232, 149–162 (1973).
12. Watson, A. B., Thompson, P., Murphy, B. J. & Nachmias, J. *Vision Res.* 20, 341–347 (1980).
13. Murray, I., MacCana, F. & Kulikowski, J. J. *Vision Res.* 23, 151–159 (1983).
14. Anderson, S. J. & Burr, D. C. *Vision Res.* 25, 1147–1154 (1985).
15. Hess, R. F. & Snowden, R. J. *Vision Res.* 32, 47–59 (1992).