an upcoming pain stimulus. This type of ACC neuron may also contribute to the thermal grill illusion (perception of interlaced cool and warm bars as painful)[13], as PET imaging revealed ACC activation during this illusory pain.

Thus, in the ACC of awake humans, we have identified single cortical neurons modulated by painful somatic thermal and mechanical stimuli. These neurons were nociceptive-specific, with some neurons showing evidence of restricted receptive fields, and some with more complex responses possibly related to higher integrative or cognitive functions. Along with other recent studies, these results provide direct evidence for a role of the ACC in processing of pain experiences.

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1. Sikes, R. W. & Vogt, B. A. *J. Neurophysiol.* 68, 1720–1732 (1992).
2. Koyama, T., Tanaka, Y. Z. & Mikami, A. *Neuroreport* 9, 2663–2667 (1998).
3. Casey, K. L., Minoshima, S., Morrow, T. J. & Koeppe, R. A. *J. Neurophysiol.* 76, 571–581 (1996).
4. Vogt, B. A., Derbyshire, S. & Jones, A. K. *Eur. J. Neurosci.* 8, 1461–1473 (1996).
5. Davis, K. D., Taylor, S. J., Crawley, A. P., Wood, M. L. & Mikulis, D. J. *J. Neurophysiol.* 77, 3370–3380 (1997).
6. Talbot, J. D. *et al. Science* 251, 1355–1358 (1991).
7. Lenz, F. A. *et al. J. Neurophysiol.* 79, 2231–2234 (1998).
8. Lozano, A. M., Hutchison, W. D. & Dostrovsky, J. O. *Acta Neurochir. Suppl. (Wien)* 64, 30–34 (1995).
9. Talairach, J. & Tournoux, P. *Co-Planar Stereotactic Atlas of the Human Brain* (Thieme, New York, 1988).
10. Coghill, R. C. *et al. J. Neurosci.* 14, 4095–4108 (1994).
11. Rainville, P., Duncan, G. H., Price, D. D., Carrier, B. & Bushnell, M. C. *Science* 277, 968–971 (1997).
12. Vogt, B. A., Finch, D. M. & Olson, C. R. *Cereb. Cortex* 2, 435–443 (1992).
13. Craig, A. D., Reiman, E. M., Evans, A. & Bushnell, M. C. *Nature* 384, 258–260 (1996).

Form and motion have independent access to consciousness

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In our conscious perception of the world, form and movement are usually inextricably linked: component contours that bound and fill a moving object seem to share a single trajectory of motion. However, the apparent unity of consciousness for shape and movement is illusory. In some instances, literally invisible contours contribute to the perceived direction of motion, implying that shape and movement have independent access to our awareness of the visual scene.

Viewed through a circular aperture, a moving surface covered with parallel stripes is generally seen as drifting in a direction orthogonal to the grating's orientation, whatever the actual direction of surface movement. If other contours are added to the surface, however, the ambiguity is resolved, and the entire pattern appears to move in a single direction corresponding to the shared movement vector of the component contours. The simplest demonstration of such 'pattern' motion is provided by the superposition of two orthogonal, drifting gratings, forming a 'plaid'. Whereas each grating presented alone seems to move in its own 'component' direction, orthogonal to the contours, the plaid as a whole seems to fuse and drift along an axis midway between the two components. Thus, both gratings contribute to the perceived direction of motion.

We wondered whether the system responsible for awareness of movement can integrate component motion signals delivered separately to the two eyes. If two static gratings of different orientation are presented to corresponding spots on the two retinae, they usually undergo binocular rivalry[2]. At each point in space, one grating completely dominates perception, and the other is simply erased from consciousness. Over extended periods of such dichoptic presentation, perception alternates between the two gratings every few seconds. We presented moving gratings of different orientation to the two eyes and studied whether the perceptually suppressed grating could nevertheless influence the awareness of movement.

We used orthogonal grating patches that were so small (0.8° diameter) and presented for such a short time (1.5 s) that, on most trials, one orientation dominated completely over the entire area and for the whole period of exposure[3]. Occasionally, the two gratings appeared fused for a very brief interval at the onset[4] or a perceptual switch occurred during presentation; these trials were always aborted. Hence, all data came from presentations resulting in conscious perception of only one grating. At the end of each trial, the subject chose the perceived direction of grating motion from eight directions spaced at intervals of 45°. The two gratings were always of oblique orientation and each could move in one of the two possible component directions. Orientations and directions were randomized from trial to trial, producing four possible combinations (Fig. 1a). We expected to see the grating that dominated perception move in its component direction (that is, orthogonal to its contours), just as it would in the absence of the other, perceptually suppressed pattern.

Randomly alternated with these conflicting presentations were non-rivalrous, control stimuli: grating patches identical in orientation and direction of drift shown to both eyes. With such small patches and brief presentations, subjects were usually unaware of whether the stimulus was binocularly fused or rivalrous. They simply had the impression of a single, drifting grating.

For non-rivalrous stimuli, as expected, both subjects saw the grating moving in the appropriate component direction on 90% or more of trials (Fig. 1b); only occasionally did the grating seem to move along a neighboring cardinal direction (vertically or horizontally). For rivalrous stimuli, the grating that dominated consciousness seemed to move orthogonally to its orientation (the expected component direction) on about 50% of trials. However, for fully half of the presentations, the perceived grating seemed to drift in the direction of pattern motion predicted from the combination of movements in the two eyes (Fig. 1b), just as if the two gratings were actually superimposed.

This influence of an unseen grating on perceived movement is compatible with findings that suggest parallel processing of several attributes of a stimulus in the visual system[5,6]. More interestingly, it shows that form and motion can access consciousness separately. Previous reports also suggest that, when stimuli of different color are presented to the two eyes, chromatic rivalry occurs independently of binocular interaction for shape or movement[7,8]. Thus, color might have a 'private line' to conscious awareness as well.

It is not obvious why interocular pattern motion was perceived

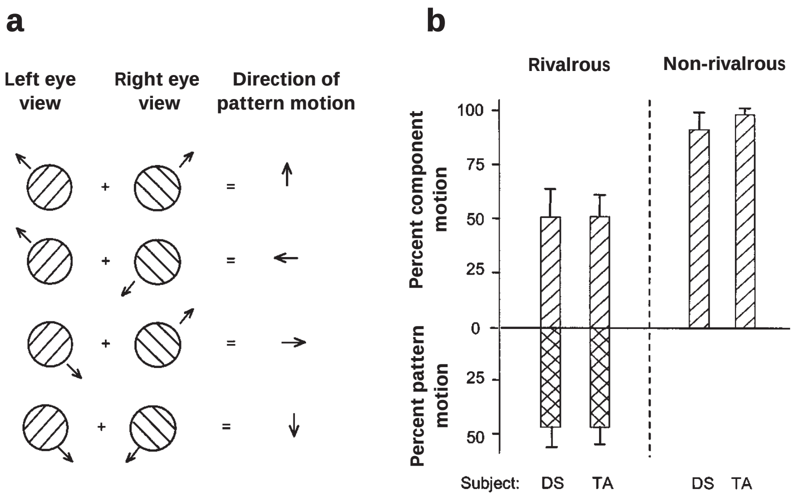

Fig. 1. Direction of pattern motion. Stimuli were drifting, circular patches of grating with sinusoidal luminance profile (spatial frequency, 4 cycles/degree; mean luminance, 25 cd/m^2; contrast, 0.3; temporal frequency of drift, 1 cycle/s, equivalent to 0.25°/s) generated by a VSG graphics card (CRS, Rochester, England) linked to a high-resolution color monitor (Vision Master 17, Ilyama) at a frame rate of 110 Hz. Stimuli were viewed from an adjustable chin rest and forehead bar at a distance of 0.57 m through Ferro-Electric Shutter Goggles (CRS, Rochester, England), which alternately occluded the two eyes at 110 Hz. With both eyes, the subject fixated a dark square, 0.12° across, in the center of the display. Both subjects had normal or corrected-to-normal vision and good stereopsis. For each trial, the subject initiated stimulus presentation with a key press. On pattern disappearance, the subject pressed a button to indicate apparent direction of grating drift. Non-rivalrous, control stimuli consisted of presentation to both eyes of identical, oblique gratings drifting in the same direction. At this high frame rate, they appeared fused, with no flicker. Orientation/direction combination was varied randomly. For rivalrous patterns, the display alternated between two orthogonal gratings on successive frames, each seen by only one eye; the four stimulus combinations are schematically represented in **(a)**. Arrows next to each grating indicate direction of component motion. If each pair of gratings were simply superimposed, the resulting plaid would be expected to drift in the indicated direction of pattern motion. During each of 10 test sessions, the 4 rivalrous stimuli were each presented 5 times, randomly alternated with 20 presentations of non-rivalrous stimuli. Rivalrous trials on which both gratings were perceived, either fused or successively, were immediately aborted. **(b)** Histograms show proportion of trials on which apparent grating drift matched component motion direction (upper ordinate, hatched blocks; bars, s.d.). For non-rivalrous stimuli (right), this was the case for 90% or more of trials; on remaining presentations, the grating appeared to move horizontally or vertically along one of the neighboring cardinal axes. In approximately 50% of the rivalrous trials, the perceived grating also seemed to move in its component direction (as if the other stimulus were not present). However, in almost half the rivalrous trials (mean ± s.d., DS, 46.5 ± 12.7%; TA, 48.0 ± 10.3%), gratings appeared to drift in the pattern-motion direction appropriate to a combination of visible and invisible contours (lower ordinate, cross-hatched blocks). For 1–2% of dichoptic presentations, perceived direction corresponded neither to the expected component motion nor to the pattern motion expected for binocularly superimposed gratings.

on only about half the trials. One interpretation is that, under the experimental conditions, the form system consistently underwent binocular rivalry, whereas the motion system was equally likely to summate or to undergo rivalry, perhaps reflecting a difference in the degree of suppression.

Motion information may also be processed despite perceptual suppression[9]. For instance, apparent motion can occur even when one of the static elements essential for motion detection is itself invisible because of rivalry[10], and movement suppressed during rivalry can lead to motion aftereffects[11].

Where do the underlying neural processes take place? Neurophysiological studies have suggested that analyses of form and motion are closely linked. Most neurons in the primary visual cortex (V1) of monkeys respond selectively to bars and gratings at particular orientations, and some of them also prefer one direction of movement[12]. However, in anesthetized monkeys, these direction-selective neurons in V1 respond to component motion[13]. In response to plaids moving in various directions, they fire only when one of the component gratings has an orientation close to the optimum for the receptive field, as if they are 'blind' to the other grating. Clearly, activity of such neurons cannot account for pattern motion perception.

V1 sends information directly and indirectly to the extrastriate area MT (V5), where the vast majority of neurons are direction selective[13,14]. Moreover, a sizeable fraction of MT cells are selective for pattern motion: preferred direction for drifting plaids is the same as for single gratings[13]. Such cells, which presumably combine component motion signals from earlier stages of analysis, seem to encode perceived direction of pattern motion.

The phenomenon reported here implies that orientations of stimuli whose component motion signals are integrated by the pattern motion system do not necessarily enter consciousness. It has been argued that that we are unaware of neuronal activity in V1 (ref. 15); indeed, it is possible that both form and motion signals are made perceptually 'explicit' in activity of neurons much higher in the visual cortical processing hierarchy [5]. However, the spatial scale of contour rivalry matches the topographic magnification in V1 (ref. 3). It is therefore conceivable that the neural representation underlying contour perception occurs in cells of V1 that are not direction selective. Perceptual encoding of movement seems to be mediated by neurons that derive pattern motion by combining signals from cells whose activities do not directly contribute to consciousness of either movement or orientation.

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1. Adelson, E. H. & Movshon, J. A. *Nature* 300, 523–525 (1982).
2. Blake, R. *Psychol. Rev.* 96, 145–167 (1989).
3. Blake, R., O'Shea, R. P. & Mueller, T. J. *Vis. Neurosci.* 8, 469–478 (1992).
4. Wolfe, J. M. *Perception* 15, 413–417 (1986).
5. Felleman, D. J. & Van Essen, D. C. *Cereb. Cortex* 1, 1–47 (1991).
6. Bartels, A. & Zeki, S. *Proc. R. Soc. Lond. B Biol. Sci.* 265, 2327–2332 (1998).
7. Creed, R. S. *J. Physiol. (Lond.)* 84, 381–392 (1935).
8. Carney, T., Shadlen, M. & Switkes, E. *Nature* 328, 647–649 (1987).
9. de Weert, C. M. & Wade, N. J. *Vision Res.* 24, 883–887 (1984).
10. Weisenfelder, H & Blake, R. *Vision Res.* 31, 1589–1599 (1991).
11. Lehmkuhle, S. W. & Fox, R. *Vision Res.* 15, 855–859 (1975).
12. Hubel, D. H. & Wiesel, T. N. *J. Physiol. (Lond.)* 195, 215–243 (1968).
13. Movshon, J. A., Adelson, E. H., Gizzi, M. S. & Newsome, W. T. in *Pattern Recognition Mechanisms* (eds. Chagas, C. R., Gattass, C. & Gross, C.) 117–151 (Springer, New York, 1985).
14. Dubner, R. & Zeki, S. *Brain Res.* 35, 528–532 (1971).
15. Crick, F. & Koch, C. *Nature* 375, 121–123 (1995).