transmission almost irrelevant (but we should not forget our roots, and new chemical transmitters keep appearing). All neurons may express machinery for chemical transmission, but many of them also transmit electrically. Identification of connexins, the family of gap junction proteins, should be nearing completion for mammals. The sequence information permits identification by in situ hybridization and northern analysis as well as RT-PCR from single cells. Antibodies to connexinspecific peptides are being used at the light and electron microscope levels. A major breakthrough for mammalian electrical synapses is the cloning of Cx36, a (nearly) neuron-specific connexin^{5,6}. In situ hybridization and immunocytochemistry show much broader distribution of this connexin than was previously appreciated for electrical synapses (J.E. Rash, T. Yasumura, W.A. Staines, D. Patel & J.I. Nagy, Mol. Biol. Cell. 10, 404a, 1999). Cx36 appears abundant not only in areas where many electrical synapses are known (retina, inferior olive, olfactory bulb, striatum and now neocortex) but also in areas where electrical coupling or gap junctions are less clearly demonstrated.

Where have all these putative gap junctions been hiding? Very likely some of them have been seen, but adequate fixation of the mammalian CNS for electron microscopy is difficult. Visualization of the diagnostic seven layers of a gap junction in cross section requires optimum preparations, and junction diameter must be large enough to extend through the entire section. The literature contains, appropri-

ately, phrases such as "gap junction-like". The freeze-fracture technique displays large areas of membrane surface and can reveal junctions smaller in diameter than the usual ~70 nm of thin sections, and these junctions would be difficult to detect by that technique. In freeze fracture, cell type may be hard to identify, and because there are many CNS gap junctions between glia, neuronal localization of a gap junction must be demonstrated. The situation can be improved by a new and laborious approach, where there is the interest and manpower to apply it15. Slices of CNS tissue are frozen, fractured and shadowed, and the remaining tissue and replica are mounted, replica down, on an EM grid. After confocal microscopy to identify cells at specific sites, the tissue is dissolved away and the replica examined with knowledge of what cells were at the fracture surface. This approach has demonstrated a high incidence of morphologically mixed synapses, that is, with both gap junctions and transmitter release sites, in the rat spinal cord.

Clearly, tissue slices and IR microscopy coupled with whole-cell patch clamping make feasible the characterization of the microcircuitry of neighboring neurons. Cells can be visualized, activated directly or synaptically, and filled with tracer for Golgi-like analysis. Immunocytochemistry of physiologically characterized neurons is in the offing. Neurons can express specific connexins, and it is clearer than before that electrical transmission is likely to be found wherever it is 'useful'. At many sites, the selective advantage can be ascribed to reciprocity and transmission of subthreshold potentials that facilitate synchronization. This general physiological outcome may be achievable in other ways, but electrical transmission is definitely in the common neuronal repertoire.

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Targeting visual motion

Jochen Braun

A new stimulus display reveals that humans summate the motion energies of all components consistent with a single velocity, rather than optimizing sensitivity by ignoring noise.

In vision research, decisive advances are often the result of cleverly targeted stimulus displays. Two classic examples are Bela Julesz' demonstrations that the visual system can process both binocular disparity¹ and differences in visual textures² at a surprisingly early level. The aim of

Jochen Braun is at the Institute of Neuroinformatics, Uni/ETH Zürich, Winterthurerstr. 190, 8057 Zürich, Switzerland. e-mail: achim@ini.unizh.ch targeted displays is to remove all but one type of visual information, so that the stimulus activates only a very restricted class of perceptual mechanisms. This allows the mechanisms in question to be studied in quasi-isolation, and in many cases it can lead to the identification of the underlying neural substrates of perception within the visual cortex. On page 64 of this issue, Schrater *et al.*³ present a new type of motion stimulus that promises to provide important insights into how the brain analyzes the motion of complex visual patterns.

An early step in understanding motion processing was the 'moving plaid' stimulus⁴, which is a superposition of two sinusoidal gratings moving in different directions. Depending on the details of the stimulus, this display can be perceived either as two sets of gratings sliding past each other, or as a single coherent 'plaid' pattern moving in a third direction (Fig. 1a). Where in the brain do these perceptions arise? In visual cortical area V1, which represents an early stage in visual processing, motion-sensitive neurons respond merely to the separate 'component' motions of the two gratings5. This is because neurons at this level are sensitive only to contours at a particular visual location and orientation, and can only signal the motion component that is orthogonal

to their preferred orientation (the so-called 'aperture problem'). The perception of coherent motion, which requires the separate motion components to be combined, seems to arise in MT, a higher area that is known to be involved in motion perception, and where a proportion of neurons responds to the coherent 'pattern' motion that is actually perceived^{6,7}. The moving plaid is of course a highly simplified stimulus, and real-world objects are typically defined by outlines composed of contours with many different orientations. The various component motions from these contours are expected to be represented in area V1, but underlying motion of the object as a whole is thought to be recovered only in area MT (Fig. 1b). A major open issue is how this recovery is accomplished; that is, how do neurons in area MT integrate and combine the information they receive through projections from neurons in area V1?

When moving plaid displays were first introduced, there were high hopes that they would reveal how component motions are combined into pattern motion. Unfortunately, these hopes have not been fulfilled. The problem is that the moving plaid display is not sufficiently 'targeted', in that it still contains several kinds of motion information. Specifically, the intersections between the two gratings create moving discontinuities, or 'nodes', and these nodes (rather than the component gratings) can govern the perception of coherent motion^{7,8}. For this reason, moving plaids may tell us more about visual sensitivity to moving nodes than about the integration of component motions. Schrater et al. now introduce a new type of visual display that finally overcomes this limitation³ (Fig. 1c). To generate this display, the authors filter dynamic random noise in a way that concentrates motion energy in several distinct subregions of spatio-temporal frequency space, each corresponding to one component motion (Fig. 2). The stimulus is perceived as an amorphous pattern that appears to drift in one or more directions, but which (unlike the moving plaid display) lacks any persistent features that could serve as the basis for a feature-tracking mechanism of motion detection. Crucially, the energy distribution within each subregion matches the sensitivity of V1 neurons, being concentrated at one particular combination of spatial and temporal frequencies, ω_{x}, ω_{y} and $\omega_{t}^{5,9}$.

To understand this, recall that V1 neurons are tuned not only for orientation but also for particular spatial and temporal frequencies. A typical real-world pattern contains information at many different spatial scales. Because velocity equals temporal frequency divided by spatial frequency, a multiscale pattern that is moving with a given velocity contains motion energy at many different combinations of spatial and temporal frequencies. Moreover, because of the aperture problem, the amount of energy at a particular combination of spatial and temporal frequency depends also on the orientation preference of the detector. For this reason, motion components along the *x* and *y* axes must be considered separately.

Movement in a given velocity thus creates motion energy over a range of temporal frequencies and spatial frequencies along the *x* and *y* axes. The set of all combinations that are consistent with a particular velocity (speed and direction of movement) lie on a tilted plane; specifically, the tilt angle (angle between the plane and the ω_t -axis) reflects the speed, and the direction of the tilt (the angle in the ω_x , ω_y -plane) reflects the direction of the velocity vector.

Figure 2 illustrates the energy distribution for each of the five variants of the display used by Schrater and colleagues. The simplest variant is the 'component' display, which contains only one component motion and targets one population of area V1 neurons. A slightly more complex variant is equivalent to a 'plaid display', in which two component motions target two separate populations of area V1 neurons (see also Fig. 1c).

The displays of Schrater and colleagues³ differ not only from moving plaids, but also from translating patterns of random dots10, which have also been popular for studying motion. Whereas Schrater et al. can target particular populations of V1 neurons, random dot displays give rise to motion energy that is distributed over the entire velocity plane. Random dot displays thus suffer from an important but rarely recognized limitation: they make it difficult to study interactions between the respective neural representations of distinct but consistent component motions, because they do not stimulate these representations differentially. In other words, random dot displays turn out to be a poor choice for studying the integration of component motions.

Armed with their new displays, Schrater et al. revisit the question of how component motions are integrated to recover pattern motion. To this end, they combine one or more component motions and, by varying the contrast in their stimuli, measure how readily an observer can detect the presence of motion in each case. Statistical decision theory predicts how an 'ideal' observer would perform in this situation: the contrast necessary to detect motion of n components decreases in proportion to $1/\sqrt{n}$. By definition, an ideal observer summates motion energy from all relevant parts of $\omega_x, \omega_y, \omega_t$ space (that is, parts stimulated by a component motion) and ignores motion energy from all irrelevant parts.

The authors show that human observers generally do not conform to this prediction, which implies that they are unable to mon-



Fig. 1. Computation of motion from its components. (a) Real-world objects contain contour segments of many orientations. Object motion causes each contour segment to move orthogonally to its orientation. These 'component motions' must be pooled to recover the 'pattern motion' of the object as a whole. (b) Moving plaid stimulus, consisting of two gratings drifting, respectively, toward the upper right and the lower right of the *x*–*y* plane. The pattern as a whole is perceived as moving directly rightward. The top and side surfaces show how the pattern changes over time (*x*–*t* plane and *y*–*t* plane. (c) Stimulus of the type used by Schrater *et al.* This stimulus is equivalent to the moving plaid in (b), in that it contains motion energy in the same two directions and is perceived as moving directly rightward. Note, however, the lack of specific features that can be tracked over longer times (compare top surfaces in **b** and **c**).

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Fig. 2. Stimuli used by Schrater *et al.*, depicted in three-dimensional spatiotemporal frequency space. The graphs can be understood as representing the motion energy at each point in the space. Any given velocity is defined by a single plane. The filters used by the authors concentrate the energy at certain locations in space, and the shape of each filter is indicated by a surface representing 65% of the peak response. (a) A single component is ambiguous and does not define an unique plane. (b) Two components form a plaid and define a plane corresponding to the perceived pattern motion. (c) A series of coplanar filters allow all possible motion signals that are compatible with a particular motion velocity. (d) A third component is added in the same plane as the previous two. (e) A third component is added that is out of plane, and thus incompatible with a single motion velocity.

itor arbitrary subsets of $\omega_x, \omega_y, \omega_t$ space. The only situation in which human observers approach 'ideal' performance is when the displays contain 10 consistent component motions, in which the energy is distributed over (almost) an entire velocity plane ('planar' display, **Fig. 2c**). In this case, the factor by which human thresholds differ from the one-component display is indeed approximately $1/\sqrt{10}$.

This outcome suggests that human observers summate motion energy over the entire planar subspace corresponding to any particular velocity, rather than over arbitrary subspaces (as an ideal observer would do). To corroborate this suspicion, the authors performed an additional experiment in which they examined the effect of adding a third component motion to a display already containing two component motions. In one case, the third component was consistent with the velocity of the first two components ('in-plane' display, Fig. 2d), whereas in the other case the third component was inconsistent with this velocity ('off-plane' display, Fig. 2e). If observers do indeed summate motion energy over planar subspaces, the addition

of a third motion component on the velocity plane should reduce thresholds by 2/3, whereas a third component that is off the velocity plane should leave thresholds almost unaffected. Both predictions are borne out by the results from human observers, further strengthening the already compelling case for planar summation.

Naturally, not all questions about the integration of component motions can be answered by a single study. In particular, the planar summation revealed by the psychophysical results of Schrater et al. is only partially consistent with the responses of neurons in area MT. Planar summation is consistent with the sensitivity of some MT neurons to pattern velocity, which can be explained by assuming that they sum excitatory inputs from V1 neurons that are tuned to points lying in the preferred velocity plane in $\omega_x, \omega_v, \omega_t$ space¹¹. However, other properties of MT neurons suggest that they may also receive inhibitory input from V1 neurons tuned to points that lie far away from the preferred velocity plane. In particular, many MT neurons show a phenomenon called 'motion opponency', that is, a reduced response to their preferred

velocity when inconsistent motion components are present^{12,13}. Given the evidence for motion opponency in area MT neurons, it is puzzling that there seem to be no psychophysical counterpart in the results of Schrater and colleagues³. Perhaps the reason is that opponent motions interact only in close spatial proximity¹², which these spatially unstructured displays do not provide.

Another unresolved issue is how the spatial organization of a visual display influences integration over component motions. In many situations, motion integration depends critically on whether component motions are aligned to form edges, corners and so on^{14,15}. The importance of the 'nodes' in moving plaid displays5,7 provides one example. The display of Schrater et al., which purposefully avoids any lasting spatial structures, cannot be expected to address this important issue. Thus it remains to be determined whether the planar summation rule holds true also under more natural stimulus conditions, which typically involve the dynamic transformation of lasting spatial structures. Whatever the answer to this question, these innovative displays, with their ability to target specific populations of area V1 neurons, will surely prove to be a great boon to research on the perception of visual motion.

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