sulin to *Xenopus laevis* oocytes. We found previously that EE was a very weak agonist compared to progesterone, and an antagonist of progesterone when the two steroids were used together, implying a competition for possible "steroid sites" on the oocyte membrane (1). When insulin was substituted for progesterone, no antagonistic effect of EE was observed (Table 1). Rather, we observed that EE potentiated the effects of insulin in a dose-dependent manner. The efficacy of insulin was comparable to that of progesterone and the lag before the first GVBD was similar to that observed with progesterone. If EE interacts with the steroid sites (1) and insulin interacts with a typical insulin receptor, and both are in the oocyte membrane, then there might be some interaction between these two loci or some cooperation between effects initiated at two separate places.

It has been suggested that in "metabolic" target cells, calcium may play the role of second messenger in insulin action (16) and that cyclic AMP concentrations decrease in response to insulin (17). These two possibilities are interesting to consider, because Ca^{2+} (2-4) and cyclic AMP (5) have both been found to interfere with the effect of progesterone on meiosis. The amphibian oocyte may thus serve (unexpectedly) as a model system for the study of the poorly understood mechanism of insulin action.

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Mutual Repulsion Between Moving Visual Targets

Abstract. *When two spatially intermingled sets of random dots move in different directions, the direction of each set may be misperceived. Observers report that each set of dots appears to move in a direction displaced by as much as 20° from the direction of its companion set. Probably the result of inhibitory interactions, this mutual repulsion occurs at a central site in the visual system and may normally enhance discrimination of direction.*

Inhibition is a nearly universal component of sensory systems (1), permitting coarsely tuned neural elements to support discriminations more acute than would otherwise be possible (2). A byproduct of inhibition's role in discrimination is a large set of perceptual distortions in which differences between two simultaneous stimuli are exaggerated perceptually. Such distortions include Mach bands (3) and illusory expansions of acute angles (4). Here we report an analogous newly discovered and powerful distortion in the domain of motion: an exaggeration of the angular difference between visual targets that move in different directions relative to one another.

Our targets consisted of two sets of random dots presented under computer control on a cathode-ray tube (CRT). Each set contained 200 bright dots that moved continuously as a unit in a characteristic direction. Within a set, all dots maintained a fixed spatial arrangement as they moved along parallel paths (5). In preliminary research, observers described the direction of each set of dots with reference to an imaginary clock face. When the two sets of dots moved in different but similar directions, the angular differences in direction were markedly exaggerated; this misperception, which was reliably reported by all six observers, involved an apparent expansion, or broadening, of the angle in a manner that suggests some form of mutual repulsion from the actual directions of motion. With certain angular differences, the misperception exceeded 20° for each set of dots. We then set about to make systematic quantitative measurements of the mutual repulsion, simplifying the task so that observers would be required to report the direction of only one of the two moving patterns.

Dots were presented behind an aperture of 9.2° diameter for 1 second. Seen against a uniform veiling background of 3 cd/m^2, the dots had a contrast approximately 50 times their own threshold. One set of dots always moved horizontally from left to right across the CRT (the ends of the CRT were functionally connected in a wrap-around fashion); the second set moved in a direction θ, for which increasing θ indicates directions more counterclockwise relative to the rightward-moving dots. Regardless of direction, all dots moved at 4° per second.

In the first experiment, observers viewed the CRT binocularly, holding their gaze steady on a fixation point in its center. After a 1-second exposure, the dots were extinguished, and the observer used a protractor scale ringing the CRT to estimate the direction of just the dots that had moved in direction θ. The actual value of θ varied randomly from trial to trial. The same three observers served in all experiments. Two were paid volunteers, naïve as to the purpose of the research; the third was W.M. Our main findings were verified by the informal reports of several other observers as well.

Almost always, dots that actually moved in direction θ were judged to move in a direction more counterclockwise than θ. This error in perceived direction increased rapidly with θ, peaked in the vicinity of 22.5° and gradually declined thereafter [$F (1, 2) = 33.87$, $P < .05$] (Fig. 1). The maximum misperception of direction, about 20°, is nearly an order of magnitude greater
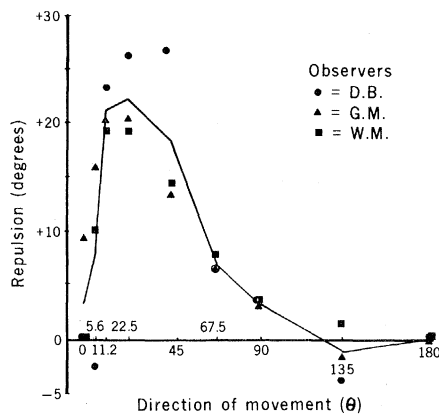
Fig. 1. Mean error in perceived direction as a function of the angular difference between the judged direction and rightward motion. Positive values on the ordinate indicate that perceived direction was shifted counterclockwise away from the actual direction. For each observer, a data point is based on 16 responses; the solid line connects the group mean.

than the mean error in judgments of direction made when a single set of dots was presented alone (6).

In order to clarify the neural origin of the direction shift, we compared the shift under two new conditions: (i) with both sets of dots presented to the same eye (monocular condition) and (ii) with the two sets presented to different eyes (dichoptic condition). To accommodate these conditions, we modified the display, replacing the single large aperture with two smaller, adjacent apertures each 4.6° in diameter. Prisms were placed in front of each eye so that the two apertures, separated by a baffle, could be easily fused. On monocular trials, we randomized which eye would receive the pair of moving patterns; on dichoptic trials, we randomized which eye would receive the pattern moving in direction θ. These randomizations equalized possible effects of eye dominance.

Dichoptic viewing significantly attenuated, but did not eliminate, the repulsion effect [F (1, 8) = 234.89, $P < .01$] (Fig. 2). That any direction shift was still present under dichoptic viewing conditions indicates that at least part of the effect arises in the nervous system at or beyond a point at which information from the two eyes is integrated (7). Because the shifts were smaller under dichoptic conditions than those observed monocularly, however, we cannot rule out the possibility that, though primarily central in origin, the effect may also have a smaller, peripheral component (8).

The dichoptic viewing conditions yielded another noteworthy result: Observers reported that they experienced no binocular rivalry. During rivalry, one

eye's view is suppressed by that of the other, often in alternation over time (9). It is well known that rivalry can result from a variety of different inputs to the two eyes, including gratings of different orientation or homogeneous fields of different color. The absence of binocular rivalry with moving dots reinforces the functional separation between visual mechanisms that support the perception of moving targets and those that support the perception of nonmoving targets (10).

Stationary intersecting lines can produce effects that superficially resemble the direction shifts we have described. Two intersecting lines repel each other, causing each one's orientation to be misperceived. This effect, attributed to lateral inhibitory interactions between orientation-sensitive visual elements (4), differs from the direction shifts in two important ways. (i) Direction shifts can be obtained with directions differing by as much as 90°, but orientation shifts are obtained only with small acute angles between the lines. (ii) Direction shifts are tens of degrees in magnitude but orientation shifts are only 3° to 4° on the average. Larger orientation shifts can be obtained when the lines are briefly flashed rather than presented for prolonged periods (11).

We considered several possible explanations for the direction repulsion effect. First, we wondered whether the direction repulsion was simply a manifestation of the well-known phenomenon of induced motion. In its most common form, induced motion is seen when a stationary dot is surrounded by a slowly moving frame (12). The frame's movement causes the dot to appear to move in the opposite direction. Alternatively, if the dot is moving slowly in one direction and the surround is moving in another direction, the induced direction of the dot approximates the resultant of the two direction vectors (13). We believe, however, that the direction shift reported here is not a form of induced motion. Very large differences between the directions of the dot and the surround lead to strong induced motion, yet we observed no repulsions when the directions differed by more than 90°. In addition, preliminary observations indicate the direction repulsion is tuned to velocity in such a way that the observed shift is greatest when the two sets of dots move at the same speed; fourfold mismatches in speed attenuate the shift by more than 50 percent. This sort of velocity tuning, which has been observed in several other motion phenomena (14), is difficult to
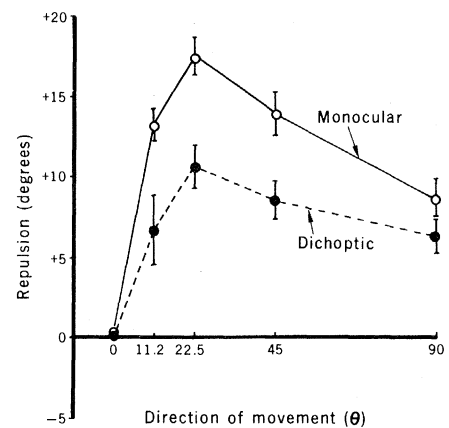

Fig. 2. Mean error in perceived direction as a function of the difference between the judged direction and rightward motion, for dichoptic and monocular viewing. Each point is the mean of 54 observations.

account for in terms of induced motion.

We also wondered whether pursuit eye movements, either along the horizontal or following the pattern moving in direction θ, could account for the shifts in direction (15). To test this possibility, one of our observers used a powerful strobe light to create a well-defined central afterimage of a narrow, vertical line. Then, while viewing the CRT display in the actual conditions used in our experiment, he monitored the afterimage for any departure from its projection onto the fixation point. Since the afterimage was locked on the center of the retina, movements of the eye would cause the afterimage to shift relative to the fixation point (16). The experienced observer found that steady fixation could be maintained easily, and, although he noticed no drift of the afterimage, he obtained direction shifts of normal magnitudes.

There is one other reason for believing eye movements did not play a role in our results: substantial repulsions could be obtained with exposures so brief (125 msec) that pursuit eye movements could not have been initiated.

Several lines of psychophysical evidence indicate that human motion perception involves the product of activity in an array of mechanisms, each sensitive to different but partially overlapping ranges of directions (17). Probably these collections of directionally selective cells are like those recorded neurophysiologically (18). In this framework, direction shifts could result from mutual inhibition among elements sensitive to each of the two directions of motion present. Indeed, physiological data have shown that a cell in the visual cortex, maximally sensitive to objects moving in one direc-

tion, can be inhibited by the presentation of other directions of motion. Using CRT displays of moving dots very much like our own, Movshon (*19*) has demonstrated such inhibition in the visual cortex of cats.

If only one direction of motion were present in the field, inhibition within the array would attenuate the responses of mechanisms tuned to other, similar directions. This attenuation would sharpen the distribution of responses within the array, rendering the directional information present in that distribution more unequivocal (*20*). If two directions of motion were present, as in our experiments, inhibition would distort perception of direction, exaggerating the differences between the two (*21*).

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Human Language Cortex: Localization of Memory, Syntax, and Sequential Motor–Phoneme Identification Systems

Abstract. *Subdivisions of the human peri-Sylvian language cortex were derived from stimulation mapping during craniotomies under local anesthesia. Naming, reading, short-term verbal memory, single and sequential orofacial movements, and phoneme identification were tested. Sequential orofacial movements and phoneme identification were altered from the same brain sites and thus identified a common system for language production and understanding. This system surrounded a final motor pathway for speech and was surrounded by a separate short-term verbal-memory system. Between the sequential motor–phoneme identification and memory systems were sites where only naming or reading were altered, including sites related exclusively to syntax.*

Human language is usually localized in the peri-Sylvian cortex of the dominant hemisphere, with an inferior frontal subdivision for the production of speech and a parietal-temporal subdivision for the understanding of language (*1*). Recent studies, however, suggest that the distinction into disorders of language production or understanding is rarely if ever absolute (*2*). Rather, both expressive and receptive deficits are present in all aphasic patients, though one or the other may predominate. In addition, aphasic patients of all types often show disorders in sequential control of movement and short-term verbal memory, which suggests other subdivision of the language cortex (*3*). We have identified some of these subdivisions by the location of changes in naming, reading, short-term verbal memory, single and sequential orofacial motor movements, and phoneme identification with stimulation mapping during craniotomies of the dominant hemisphere under local anesthesia in patients with medically intractable epilepsy.

This study is based on four adult patients (mean age 21.5 years, range 17 to 32) undergoing left anterior temporal lobectomy (*4*). Before the operation, intracarotid amobarbital testing revealed that all patients were left-brain dominant for language (*5*). During craniotomy, before any brain resection, the effects of bipolar electrical stimulation on tests of naming, reading, and short-term verbal memory were observed at 10 to 15 sites in the peri-Sylvian cortex of each patient. At half of these sites, stimulation effects on tests of orofacial movement and phoneme identification were also measured (*6*). The cortex was mapped with 4- to 8-second trains of 60-Hz, $2^{1}/_{2}$-msec, biphasic square-wave pulses from a constant current stimulator delivered through electrodes 5 mm apart at the largest current that did not evoke afterdischarges for the sampled cortex. Sites of stimulation were identified by a sterile number

ticket, and the location was photographed and reconstructed by the relation to the cortical veins on venous phase angiograms. Figure 1 is traced from the angiogram for each patient.

The test of naming, reading, and short-term memory consisted of 25 consecutive trials. Each trial contained three achromatic slides: (i) A naming slide, shown for 4 seconds, was a picture of a common object with a phrase such as "This is a" above it. The patient read the phrase and named the object aloud. (ii) A reading slide, shown for 8 seconds, had a sentence eight to nine words long with a portion near the end omitted. The patient read the sentence aloud and generated specific syntactic forms to complete it correctly. (iii) A slide with the word "recall" on it appeared for 4 seconds. This cued the patient to say aloud the name of the object pictured on the naming slide. This represented the retrieval portion of a single-item measure of short-term verbal memory, with the object name as input and reading as distractor during which the object name must be stored. Stimulation was applied for the entire duration of one of the slides on some trials interspersed with control trials without stimulation, the sequence predetermined pseudorandomly. The same site was not stimulated consecutively, and three samples of stimulation at each site were obtained during each test condition. Responses and stimulation markers were recorded on magnetic tape.

Orofacial movements were measured by having the patient mimic postures representing terminal positions of simple movements, such as lip protrusion, pictured on a slide. One series of slides showed the same position repeated three times; the other a sequence of three different positions. Stimulation occurred during a randomly selected half of the slides of each type with three samples of stimulation at each site during each test condition, without consecutive stimulation of the same site. The patient's facial