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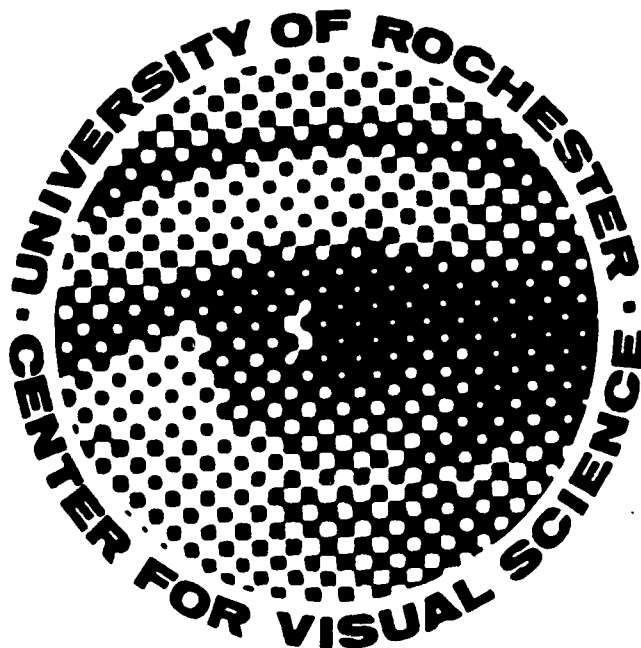
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13. ABSTRACT (Maximum 200 words) This meeting was motivated by recent progress in our understanding of how visual information specifying the spatial relations of objects and the layout of the environment controls an observer's perceptual judgments and motor performance. This meeting was intended to spread knowledge of these new advances and to foster their discussion and refinement. Eighteen leaders in this field who are also excellent expositors presented 45-minute addresses at a meeting lasting two and a half days. Presentations were organized into sessions on (1) retinotopic calibration, (2) perceptual stability, (3) the metrics of 3-D space, (4) perceptual adaptation, and (5) eye-hand coordination. Each session was followed by a 30-minute discussion of the presentations led by a moderator/discussant selected to challenge the speakers and to foster productive interaction with the audience.					
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NEURAL MECHANISMS FOR COORDINATE TRANSFORMATIONS

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Area 7a of the posterior parietal cortex of the primate brain is concerned with representing head-centered space by combining information about the retinal location of a visual stimulus and the position of the eyes in the orbits. We previously trained a neural network model of area 7a to perform this coordinate transformation task using the back-propagation training procedure. The hidden units of this network developed properties very similar to those of area 7a neurons presumed to code for spatial location.

Here we describe two neural networks with architecture similar to that of our previous model and trained them to perform the same coordinate transformation task. However, the networks were trained with a version of the "associative reward penalty" (Ar-p) algorithm that we modified to work on a multi-layered network. This learning procedure was devised by Barto and colleagues, and is more biologically plausible than back-propagation. Our networks learn to perform the task successfully to any accuracy and almost as quickly as the original model, and the hidden units develop response properties very similar to those of area 7a neurons. We found that the synaptic strengths computed by the (Ar-p) algorithm are equivalent to and interchangeable with those computed by back-propagation. Our networks also acquire interesting generalization properties, that is, they learn to perform the correct transformation on pairs of eye and retinal positions never encountered before. All these results are unaffected by the interposition of an extra layer of units between the hidden and output layers.

These results show that the response properties of the hidden units of a layered network trained to perform coordinate transformations, and their similarity with those of area 7a neurons, are not a specific result of back-propagation training. They seem rather to derive from the parallel architecture of the model network and from the principles involved in learning by examples. The fact that they can be obtained by a more biologically plausible learning paradigm corroborates the validity of this type of neural network structure as a plausible model of how area 7a may compute coordinate transformations.

ANIMATE VISION

DANA BALLARD
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Animate vision systems have gaze control mechanisms than can actively position the camera coordinate system in response to physical stimuli. Compared to passive systems, animate systems show that visual computation can be vastly less expensive when considered in the larger context of behavior.

The most important visual behavior is the ability to control the direction of gaze. This allows the use of very low resolution imaging that has a high virtual resolution. Using such a system in a controlled way provides additional constraints that dramatically simplify the computations of early vision. Another important behavior is the way the environment "behaves." Animate systems under real-time constraints can further reduce their computational burden by using environmental cues that are perspicuous in the local context. A third source of economy is introduced when behaviors are learned. Because errors are rarely fatal, learning algorithms can amortize computational cost over extended periods. Further economies can be achieved if the learning system uses indexical reference, which is a form of dynamic variable binding. Animate vision is a natural way of implementing this dynamic binding.

OPTIC FLOW AND THE PERCEPTION OF SELF MOTION AND RELATIVE DEPTH

MARTIN S. BANKS
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Performance varies dramatically with retinal eccentricity in a variety of visual tasks. In the first part of the presentation, I will discuss eccentricity-dependent variations in contrast sensitivity, spatial summation, and grating and vernier acuity. Then, using an ideal observer analysis, I will describe the extent to which optics, photoreceptor properties, and receptor pooling at various eccentricities limit such capabilities. In the second part of the presentation, I will discuss eccentricity-dependent variations in observers' abilities to make heading judgments from optic flow displays. Performance in this task varies much less with eccentricity than in the tasks considered in the first part of the presentation. Finally, I will describe a simple, biologically plausible model of how heading information can be extracted from optic flow displays.

CONSTRAINTS ON LEARNING MAPPINGS BETWEEN SPATIAL DIMENSIONS

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University of Arizona

The coordination of spatial maps from different modalities is essential for the experience of a coherent world and the production of appropriate behavior. Little is known, however, about how the different dimensions are put together. Two new variants of the classic prism-adaptation paradigm were used to investigate the rules and constraints on learning new mappings between visual and proprioceptive dimensions. First, rather than distort a large continuous region of space, only a few isolated locations were altered. The form of generalization to untrained regions was then inspected to determine the hidden rules the system brings to bear. Second, rather than a simple lateral displacement, more complicated new mappings were imposed such as a many-to-one mapping, to determine behavior in a variety of situations. A new technique was used that enabled individual regions to be isolated and manipulated separately. The experiments find a preference for linear relations and suggest, tentatively, that the hierarchy of geometric properties within the framework of Euclidean geometry may be an embodied constraint on the system that realigns maps.

THE ROLE OF EFFERENCE IN SPACE CONSTANCY

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Reflecting distinctions made in lesioned animals and brain-damaged humans, two modes of visual processing can be identified in normal humans. A "cognitive" system is assessed with perceptual measures requiring a symbolic relationship between target location and behavioral response. A second, "sensorimotor" system, serving visually guided behavior, is assessed with open-loop pointing or looking measures involving a 1:1 isomorphic relationship between target position and response.

The sensorimotor system requires an egocentric calibration, while the cognitive system relies largely on an image-centered metric. Thus the role of oculomotor efference can be expected to differ in the two systems. Experiments in my laboratory and others have revealed that the sensorimotor system relies more on efference-copy mechanisms than does the cognitive system. Pressing on the side of the eye to separate gaze position from efference, we have shown that the sensorimotor calibration is always affected by efference copy, even in a structured visual field, while cognitive judgments are influenced about equally by efference copy and by visual context.

Double dissociation experiments have changed spatial information independently in only one system, or only the other. The cognitive system is subject to many spatial illusions that have little effect on the sensorimotor system, while the latter's memory for positions of objects no longer present is limited.

THE MAINTENANCE OF SPATIAL ACCURACY BY VISUAL NEURONS IN THE MONKEY CEREBRAL CORTEX

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Humans (Hallett and Lightstone, 1976) and monkeys (Mays and Sparks, 1980) can make accurate saccadic eye movements to visual targets even when there is a dissociation between the retinal location of the target and the direction of the eye movement necessary to acquire it. Such a dissonance is established by a double-step task in which two stimuli, A and B, are flashed sequentially within a saccadic reaction time and the subject is obliged to make successive saccades from the fixation point to A and then from A to B. The saccade from A to B cannot be computed from the retinal location of the second target, but requires knowledge either of the target position in space or the metrics of the intervening saccade.

A subset of visual neurons in the posterior parietal cortex and frontal cortices of the rhesus monkey discharge after the first and before the second saccade in the double-step task when this second saccade matches the saccade necessary to acquire a stimulus in the neuron's receptive field. We argue that this discharge represents a transformation of the visual signal from retinal to motor coordinates: 1) The activity in the double-step task cannot be a premovement discharge since these neurons do not necessarily discharge when the monkey makes a similar learned saccade without a visual stimulus; 2) The discharge cannot be postsaccadic activity related to the first saccade since the neurons do not discharge after that saccade when it is performed in isolation; 3) The discharge cannot code the spatial location of the target since the neurons do not discharge when the monkey makes a saccade to the second target directly from the fixation point. We conclude that this activity represents a visual response to a stimulus that can be acquired by a saccade of specific direction and amplitude regardless of the retinal location of that stimulus. These neurons thus have visual receptive fields coded in motor coordinates but do not explicitly represent target position in space.

One possible explanation for this phenomenon is that the transformation from retinal to motor coordinates is effected by a discharge corollary to the intervening saccade which effectively performs a vector subtraction of the dimensions of the first saccade from the retinal location of the target. However, analysis of error trials in double-step tasks (in which the monkey either reversed the order of the saccades or made a saccade directly to the second target) shows that the cells discharge in response to the second target whenever it appeared in the context of the double-step task, and not only when the monkey actually made the first saccade. Thus the neural processes underlying this coordinate transformation have access to processing that precedes the actual performance of the intervening movement and are not dependent upon the movement actually taking place.

This transformation provides a mechanism whereby the oculomotor system can function accurately in space without ever requiring the representation, by a single neuron or by a distributed ensemble, of the absolute position of a stimulus in a suparetinal coordinate system. All of the signals necessary to implement a transformation from retinal to motor coordinates have been observed in the frontal and parietal cortices. This is especially convenient because signals in brainstem structures such as the superior colliculus and pontine and mesencephalic burst regions code amplitude and direction of saccade rather than target position in space. Such a direct transformation obviates the need for an explicit, head-centered representation of space.

VISUAL-VESTIBULAR INTERACTIONS IN PERCEIVED STABILITY

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The vestibulo-ocular reflex (VOR) serves to stabilize the retinal image when the head moves. However the vestibular organs do not respond to low-frequency or steady motion of the head. Under these circumstances the visually-driven optokinetic response (OKN) supplements VOR. The sense of self motion must also rely on visual inputs when the head moves slowly or steadily. The sense of self motion engendered by visual motion is known asvection and, when the body is not actually moving,vection is said to be illusory. We have been investigating how visual-vestibular interactions that influence visual stability and the sense of self motion have become adapted to the demands of stereoscopic vision. We have shown that the conditions that evoke OKN are very different from those that evokevection, even though the two responses are both mediated by the movement of large visual displays. OKN is evoked only by moving displays which lie within the plane of binocular convergence. This mechanism ensures that parallax motion signals arising from outside the plane of convergence do not disrupt OKN when a person moves linearly through a three-dimensional world.vection, on the other hand, is triggered by those parts of a visual scene which are, or are perceived to be, more distant, whether or not they fall within the plane of convergence. This makes ecological sense because the motion of more distant parts of a natural scene is a more reliable indicator of self motion than is that of nearer parts of a scene. This difference between the rules governing OKN andvection has enabled us to distinguish between three types of induced visual motion (IM), that is, illusory visual motion of a test target seen against a moving induction display. These types of IM form a nested hierarchy. Oculocentric IM occurs within a retinal frame of reference and is due to some form of contrast between visual motion detectors. Headcentric IM occurs within a headcentric frame of reference and includes effects due to misregistration of eye movements. Exocentric IM occurs within an external frame of reference and includes the apparent motion of stationary objects that accompanies illusory self motion. We have found tests for each of these forms of IM and have revealed their respective magnitudes.

EFFECTS OF CHANGING TARGET LOCATION ON PREHENSION MOVEMENTS

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Prehension involves processing information in two hypothesized visuomotor channels: one for extrinsic object properties (e.g., the spatial location of objects) and one for intrinsic objects (e.g., shape and size). The present study asked how the two motor components that correspond to these channels (transport and grasp, respectively) are related. One way to address this question is to create a situation where unexpected changes occur at the input level of one of the visuomotor channels, and to observe how the movement reorganizes. If transport and grasp are independent components, then changing the object location, for example, should affect only the transport, not the grasp component. Subjects were requested to reach, grasp and lift as accurately as possible one of three dowels using the distal pads of the thumb and index finger. On certain trials, upon movement initiation towards the middle dowel, the dowel was made to instantaneously change its location to one of the two other positions, requiring the subject to reorient the hand to the new dowel location. Results consisted of comparing the movement characteristics of the transport and grasp components of these perturbed movements with appropriate control movements.

Kinematics of the wrist trajectory showed fast adjustments, within 100 ms, to the change of dowel position. This duration seems to correspond to the minimum delay required within the visuomotor system for visual and/or proprioceptive reafferents to influence the ongoing movement. In addition, these delays are much shorter than has been found for conditions where object location changes before movement initiation (approximately 300 ms). The faster times may relate to the dynamic character of the deviant limb position signals, with the only constraint being the physiological delays for visual and kinesthetic signals to influence the movement.

A spatiotemporal variability analysis of the movement trajectories for non-perturbed trials showed variability to be greatest during the acceleration part of the movement, interpreted as due to control by a relatively inaccurate directional coding mechanism. Control during the deceleration phase, marked by low trajectory variability, was seen to be due to a sensorimotor process, using motor output signals, and resulting in an optimized trajectory supporting a successful grasp.

Analysis of the grasp component of prehension showed that perturbing object location influenced the movement of the fingers suggesting a kinematic coupling of the two components. However, forthcoming work shows that, when object size changes, and location remains constant, there is a clear temporal dissociation of the two components of prehension. Collectively, these results suggest that the two visuomotor channels have different time constraints with the time-constant of the channel activated by the perturbation constraining the timing of the other.

EFFERENCE COPY IN THE CONTROL OF THE VESTIBULO-OCULAR REFLEX

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Many experiments suggest that the brain uses "corollary discharge" or "efference copy" signals of eye position to localize objects with respect to the body or to direct eye movements. The origin and nature of these signals is usually not specified. For example, the vestibulo-ocular reflex (VOR), which stabilizes retinal images during head movements, is modulated inversely with viewing distance. Since vergence angle is also modulated inversely with viewing distance, it has been suggested that "vergence state" is used to modify the VOR. We compared the temporal relationship between changes in vergence and changes in the VOR to help characterize the source of such a signal. On the one hand, if a corollary discharge of the motor output of the vergence system modulates the VOR, then we would expect that changes in the VOR would be coincident with changes in vergence angle. On the other hand, if sensory cues encoding target distance modulate the VOR, then we would expect that changes in the VOR would lead changes in vergence angle.

Four rhesus monkeys, each equipped with two scleral search coils to monitor the movements of both eyes, were trained to fixate LED targets. Trials began with fixation of a target 13.5, 18 or 36 cm from the eyes. After at least 0.6 s of fixation, a vergence movement was evoked by lighting a near (9 cm) or far (220 cm) LED. Randomly, before, during or after the vergence movement, the monkey was briefly rotated (0.5 d/s/ms acceleration to 20 d/s) to the right or left. This pulse of head velocity provided a near-instantaneous assay of VOR response.

The amplitude of the VOR changed systematically during the course of vergence eye movements. These changes anticipated changes in vergence by as much as 100 ms, suggesting that sensory cues encoding target distance drive VOR modulation.

LOTZE'S LOCAL SIGN: A MECHANISM FOR JUDGING DISTANCE

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"The space relations of impressions pass as such into the soul, ...each impression is conveyed to it by a distinct fibre, and the fibres reach the seat of the soul with their relative situation wholly undisturbed." H. R. Lotze (1885).

In order to properly order stimuli in visual space, and to program saccadic eye movements, H.R. Lotze proposed that each retinal element has a position label, or local sign. Evidence will be presented to suggest that in peripheral vision, a point can be localized with a precision better than 1% of the target eccentricity. This precision is similar to the separation of on-pBeta ganglion cells in the retinal periphery (Wassle et al., 1990), suggesting that the position of each peripheral ganglion cell is indeed labeled.

The notion of local signs has important consequences for the encoding of position. In position acuity tasks (e.g., Vernier acuity and spatial interval discrimination), over a wide range of target separations, thresholds are proportional to the separation of the features. This is Weber's law for position. We argue that two distinct processes constrain position acuity, and each leads to Weber's law: i) when the target separation is small, position acuity is limited by the output of size tuned filters. Weber's law obtains as a consequence of using larger filters for targets with larger separations. The outputs of these localized filters can give rise to the fine position thresholds known as hyperacuity thresholds. ii) when the target separation is large, the eccentricity of the targets, i.e., the local signs, constrain position discrimination. Position discrimination experiments on iso-eccentric arcs (where separation and eccentricity can be pitted against each other) suggest that both processes constrain position judgments.

The notion of local signs also has important consequences for programming of saccadic eye-movements. Although it is widely held that the precision of saccadic eye movements is limited by the motor system, recent eye movement data (van Opstal and van Gisbergen, 1989), suggests that the precision of saccadic eye movements to peripheral targets can be almost as precise as the localization of a point in the periphery. Thus, the precision of saccadic eye movements may be primarily limited by the sensory limitations in encoding the position of peripheral targets, i.e., by Lotze's local sign.

VISUAL MOTION SIGNALS SUPPORTING STABILIZATION OF GAZE BY PURSUIT EYE MOVEMENTS

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Eye movements stabilize the images of moving objects by rotating the eyes at the velocity of the object. It has long been known that visual motion drives pursuit, and recent anatomical and neuropsychological studies suggest that visual motion signals carried by neurons in area MT (V5) of the macaque's extrastriate cortex are critical for the generation of pursuit. The goal of our study was to reveal the dynamic properties of signals that are actually used for pursuit and to determine whether those signals are available in MT.

In one series of experiments, we recorded the pursuit eye movements of a trained rhesus monkey in response to the motion of a small target. Stimuli were steps or ramps of target velocity, which provided stimuli moving at constant speed or constant acceleration. We analyzed only the first 100 ms of pursuit so that we use the open-loop response of the pursuit system as a probe for the properties of visual signals that drive pursuit. Steps of target velocity elicited eye acceleration that could be dissected into two components. An early "motion onset transient" dominated the first 40 ms of pursuit and was driven by the impulse of target acceleration at the onset of motion. A later steady-state response had a magnitude that was linearly related to target speed. The motion onset transient was affected by varying the motion onset delay, defined as the period when the tracking target was stationary and visible before it started moving. It was not evident if the target was moving when it came on, but became larger as the motion onset delay was increased to 200 ms. Ramps of target velocity revealed a third component of eye acceleration that was related to smooth target acceleration and could not be accounted for by either the motion onset transient or the steady-state target velocity component.

In a second series of experiments we recorded single MT units in anesthetized, paralyzed Cynomolgus monkeys, and analyzed the responses elicited by moving texture targets of variable speed and direction of motion. To analyze response dynamics, we modulated target speed with suitable pulses, steps, and ramps. We paid particular attention to the time course of the responses of MT neurons so that we could compare the signals they carry to those used by pursuit. As we expected, almost all MT units were selective for the direction and speed of stimulus motion. Most units also gave brisk responses to target acceleration. Analysis of these responses reveals that they result from the action of two mechanisms within MT receptive fields. The first is the spatio-temporal tuning of the unit, which gives it speed selectivity. When stimulus speed increases to and then past the preferred speed, the resulting excitation profile is a shaped pulse, causing a transient response during acceleration. The second mechanism enhances responses to changes in excitation level, such as those occurring during target acceleration. This mechanism can be modeled as a filter shaping the time course of response to a degree that varies among units. These two mechanisms combine to generate acceleration-related responses in MT neurons, without explicitly creating acceleration-tuned receptive fields. The two mechanisms also cause MT cells to emit a motion onset transient followed by sustained firing in response to steps of target speed. The amplitude of the motion onset transient of MT cells, like that in pursuit, increases as motion onset delay is increased. Our results show that MT neurons carry motion signals that can explain the contributions of target speed and acceleration to the generation of pursuit eye movements.

CALIBRATION OF SIMPLE VISUAL SYSTEMS BY COMPARISON ACROSS EYE MOVEMENTS

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A visual system is geometrically calibrated if its estimates of the spatial properties of a scene are accurate: straight lines are judged straight, angles are correctly estimated, collinear line segments are perceived to fall on a common line. I describe calibration methods for a model visual system whose photoreceptors are initially at unknown locations. The methods can also compensate for optical distortions that are equivalent to remapping of receptor locations (e.g., spherical aberration). The methods work by comparing visual input across eye/head movements; they require no explicit feedback, and no knowledge about the particular contents of a scene.

It's likely that no biological visual system is ever perfectly calibrated, but considerable evidence exists that biological visual systems do compensate for optical distortions and initial uncertainty about the position of photoreceptors in the retinal photoreceptor lattice. Recent anatomical work, for example, demonstrates apparent disorder in the retinal lattice outside central fovea, increasing with eccentricity. Further, the optics of the eye change throughout the lifespan, suggesting that calibration may continue in the adult.

Previous work in visual neural development suggests a variety of sources of information that drive calibration, and there are computational models of visual neural development based on these cues. Yet, although biological visual systems are known to require patterned visual stimulation to achieve normal organization, none of these models requires such stimulation to function. Further, while these models could in principle compensate for disorder in the retinal lattice, none of them clearly addresses the problem of compensation for optical distortion.

I describe two methods for calibrating a simple linear visual system that work by comparing visual input across eye/head movements. These methods can organize the receptive fields of a simple visual system so as to compensate for irregularities in the retinal photoreceptor lattice and optical irregularities equivalent to distortions in the lattice. They require no explicit feedback, and no knowledge about the particular contents of a scene, but instead work by 'asserting' that the internal representation of the scene behaves in a prespecified way under eye and head movements. I demonstrate that these methods can be used to calibrate a simple, linear visual system and I discuss the implications of this work for other models of visual processing.

SURFACE PERCEPTION FROM DISPARITY AND PARALLAX INFORMATION

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Most work on binocular stereopsis (psychophysical, computational and physiological) has assumed that the initial representation of disparity is in terms of the horizontal (and possibly the vertical) differences between corresponding *points* in the images (e.g. Julesz, 1971; p. 144). An alternative conception, which brings out the formal similarity between motion parallax and binocular disparity as sources of 3-D information, is to consider the *local differential structure* in the transformation needed to map one eye's image onto the other (Koenderink and van Doorn, 1976). In particular, the amount of deformation between corresponding regions in the two binocular images (or the amount of *deformation* over time in the case of the parallax transformation) provides information about the local slant of 3-D surfaces. The existence of (i) a similar and marked anisotropy in the perception of 3-D surfaces from either disparity or parallax information (Rogers and Graham, 1983) and (ii) an analogous "induced effect" (Ogle, 1950) in the parallax domain (Rogers and Koenderink, 19986) are both consistent with this alternative conceptualization. Furthermore, Cagenello and Rogers (1988, 1989) have shown that the orientation of line elements superimposed on stereoscopic surfaces has a significant effect on their perceived slant and curvature. The latter result is consistent with Koenderink's suggestion that an approximation to deformation could be computed by monitoring the *orientation differences* between corresponding line elements at two or more orientations in the two eyes' images (in the case of binocular stereopsis) or the *changes of orientation* of local line elements occurring over time (in the case of motion parallax).

Although attractive and consistent with much of the empirical evidence, the deformation hypothesis does not account for several recent observations. First, stereoscopic images related by a vertical shear transformation are seen to have the *opposite* direction of slant to that specified by the local deformation. Second, stereoscopic images related by a pure rotation generate the impression of surface slant with a magnitude comparable to that produced by images related by a simple horizontal shear, even though there is no deformation between the two images. These results suggest that the human visual system might rely on the simpler strategy of extracting the orientation differences between corresponding binocular elements, rather than computing the true differential structure of disparity and flow fields.

MOTOR CORTICAL CONTRIBUTIONS TO SKILLED MOVEMENT

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Unitary activity recorded in the proximal-arm area of primary motor cortex activity is sensitive to the direction that the contralateral arm moves. The tuning function that relates activity to direction is broadly tuned for many cells, spanning the entire directional domain, with the peak firing rate in a single "preferred direction." This suggests that these cells are all coding movement direction simultaneously during movement. A vector in each cell's preferred direction was scaled by the cell's discharge rate to represent its contribution to the population. The response of the entire population of these cells recorded during several behavioral tasks can be represented by adding vectors in each cell's preferred direction. The "population vectors," resulting from the addition of these individual vectors, point in the direction of movement.

Rhesus monkeys were trained to trace with their index fingers sine waves of different amplitudes and spatial frequencies generated on a computer monitor. These animals learned the task by following a circle as it moved along a randomly selected sinusoidal pattern. By adjusting the size of the circle and the maximum time allowed to reach the circle, the monkeys were conditioned (with a liquid reward) to make smooth and accurate movements.

Motor cortical activity recorded during this task was dependent on the direction the monkey was to move its finger 100-150 msec later. Population vectors (using the responses of 238 cells) calculated throughout the task ($n=100$) pointed along the tangent of the corresponding part of the trajectory. Since the direction of the population vector corresponded to the tangent of the movement, it seems likely that the motor cortex is using a relative coordinate system representing instantaneous direction. The length of each population vector calculated in the task corresponded to the speed of movement, again suggesting that these skilled movements are represented incrementally in the activity of motor cortical neurons. This work is supported by NIH (NS-26375).

HUMAN EYE MUSCLE PROPRIOCEPTION: ITS EXISTENCE AND ITS RAISON D' ETRE

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We have measured changes in eye-hand coordination following surgery on, or pharmacological weakening of, eye muscles. By preventing vision in the operated eye until the moment of testing, or in ruling out efferent (corollary discharge) contributions to eye position sensing, we have found evidence for the use of an afferent (proprioceptive) signal in determining the position of the eye in the orbit.

Our latest studies of resting eye position in anesthetized and paralyzed patients have shown that the direction of gravity influences this resting position. Our findings indicate that the center of rotation of the eye is actually in front of its center of mass. Eye muscles, therefore, operate under changing loads as the head changes its orientation with respect to gravity and thus are like other skeletal muscles in having a need for proprioceptors. Our finding may also be playing a role in the space motion sickness that some astronauts experience in microgravity. Finally, the vexing species differences concerning the presence of eye muscle spindles may be related to the need for them, i.e., animals with no spindles may have eyes with coincident centers of rotation and mass.

NAVIGATION FROM OPTICAL FLOW

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Gibson (1950) first proposed that patterns of optical flow produced at a moving eye specify the observer's direction of self-motion, or heading. Such information is critical for navigation in complex environments. In this vein, I argue that different flow morphologies specify different classes of observer movement, including linear translation, circular movement, combined translation and rotation (as with pursuit eye movements during locomotion), and combined circular movement and rotation. Recent experiments with random-dot displays, in which observers judged whether they would pass to the right or left of a target, demonstrate that the visual system can use such information to determine heading.

(1) *Translation*: Observers perceive translational heading with an accuracy of 1 deg, in both planar and 3D environments. There are no effects of dot density down to 3 dots, and a 2-frame dot life is sufficient. This indicates that judgments are based on the radial structure of the velocity field, rather than a local focus of expansion. In addition, the visual system can tolerate large amounts of noise in local vector direction or magnitude, indicating spatial pooling over the field. A neural network model with these characteristics is discussed.

(2) *Circular movement*: Observers perceive their future curved path with an accuracy of 1.5 deg (for a target 16m ahead), in both planar and 3D environments. There are no effects of dot density down to 2 dots, but a 3-frame dot life is necessary; the instantaneous velocity field is both theoretically and empirically insufficient. This is consistent with an analysis showing that the *change in direction of motion* of 2 elements over 3 frames is sufficient to specify circular heading.

(3) *Translation and rotation*: Observers can judge translational heading in displays that simulate the optical effects of a combined translation and eye rotation with an accuracy of 1.5 deg. This indicates that translational and rotational components can be decomposed on the basis of optical flow alone, without the contribution of an extra-retinal signal. Further, the decomposition is possible with a ground surface and a 3D cloud, but not with movement toward a wall surface. This pattern of results is inconsistent with general discrete models, least-squares models, and differential models (such as *div* and *curl*) that assume a continuous field, but consistent with a theory based on relative motion between neighboring elements at different depths. A neural network model that exhibits similar behavior is discussed.

The resulting heading direction is given in both retinal coordinates (anatomical position on the retina) and environmental coordinates (ordinal position relative to environmental surfaces). It could also be used to steer locomotion, for a change in heading direction (desired heading - current heading) could be made by effecting an equivalent change in the direction of shear force against the ground (desired force - current force) without transformation to body coordinates. This avoids the problem of local sign and coordinate transformations in a multi-degree-of-freedom system.

"SEE AS THOU WAST WANT TO SEE" **AFTEREFFECTS AND THE RECALIBRATION OF VISUAL PERCEPTS**

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Many visual processes in the central nervous system attempt to infer properties of the external world on the basis of input from earlier neural stages. For example, an opponent color mechanism might infer the amount of redness or greenness by comparing the inputs from L and M cone pathways. Variations in the input cause variations in the inference. There are two sources of variation in neural input: 1) A change in the distal stimulus and 2) a change internal to the visual system. A visual process is interested in the first source of variation and misled by the second. Thus, if the L cone input is somehow damaged and weakened, the opponent mechanism will interpret the preponderance of M-cone input as an indication of "greenness."

Since vegetative changes in the visual system are unavoidable and since the consequences are unacceptable, the visual system has developed measures to correct for internal errors. This is not an altogether trivial matter. A visual process has access only to visual information. It must decide if that information reflects the state of the external world or an internal problem requiring correction. An opponent color mechanism must be able to differentiate between a visual system that is looking at the grass while cutting the lawn and a system suffering a failure in the L-cone pathway.

Traditional models of error-correcting mechanisms do not make this distinction. They will correct for systematic bias in the input but are indifferent to the cause of that bias. The thesis of this talk is that the human visual system is not indifferent to this distinction. Internal and external sources of variation will produce different changes in the neural input. Components of the visual system are designed to self-correct in response to internal sources. If external stimuli are designed to mimic an internal source of variation, the result is a long-term aftereffect. For example, color and orientation are generally uncorrelated in visual stimuli. A correlation might be a sign of internal error. If we create a correlation by presenting red vertical and green horizontal gratings, the result is a long term aftereffect known as the McCollough effect. It can last for days following minutes of adaptation. If subjects are shown red vertical and red horizontal gratings, then there is no correlation between color and orientation and, even though either stimulus alone will produce an effect, little or no aftereffect is seen.

Different visual processes have different filters to distinguish internal from external variation. For example, there are both short and long term tilt aftereffects (TAE). Four minutes of sustained tilt adaptation will produce about four minutes of TAE. Four minutes of intermittent adaptation can produce a TAE lasting weeks. In this case, we believe that a single, unusual stimulus is not a sign of internal change. However, if many samples show a systematic bias as is the case in intermittent stimulation, the system can be fooled into recalibration.

In sum, we believe that the components of the visual system adjust themselves to correct for changes internal to the visual system. They protect themselves from wanton recalibration by placing a filter between the input and the adjustment mechanism. The filter is designed to pass only stimuli that are unlikely to occur in normal viewing and may be different for different components of the visual system.

SPATIAL ORIENTATION IN WEIGHTLESSNESS

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Although fundamental visual acuity appears unaffected by weightlessness and the most common visual illusions from space are easily explainable, there remain several interesting problems in spatial orientation in the absence of a gravity reference direction. This paper touches on three aspects of the question:

(1) Dynamic spatial orientation, based upon the interpretation of information from moving visual scenes (vection), vestibular stimuli and localized tactile inputs, is dramatically changed in orbit as the irrelevant otolith cues are ignored and visual as well as tactile cues begin to dominate.

(2) Static orientation can produce some remarkable illusions in the absence of a gravity reference vector, especially when the astronaut is confronted with familiar objects (the equipment racks, another crewmember, the earth) in unusual orientations. The "inversion illusion" and others are discussed and related to space motion sickness.

(3) Teleoperation involves a complex spatial transformation from the TV scene taken by a camera on a remote manipulator to the fixed display in front of the astronaut. Special issues are raised when the sensory-motor adaptation process must take place in the absence of a reference gravity vector.