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N90-22928

SPATIAL VISION WITHIN EGOCENTRIC AND EXOCENTRIC FRAMES OF REFERENCE

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1. INTRODUCTION

Our ability to perceive a stable visual world and judge the directions, orientations and movements of visual objects is remarkable given that the images of objects may move on the retina, the eyes may move in the head, the head may move on the body, and the body may move in space. An understanding of the mechanisms involved requires that definitions of relevant coordinate systems be as precise as possible. An *egocentric* frame of reference is defined with respect to some part of the observer. When both the object being judged and the reference frame are parts of the body, we have a *proprioceptive* task. If the object being judged is external to the body, its position, orientation and movement may be judged with respect to any of three principal egocentric coordinate systems, an *oculocentric* frame associated with the eye, a *headcentric* frame associated with the head and a *bodycentric* frame associated with the torso. A reference frame external to the body is an *exocentric* frame. In an exocentric task the object being judged may be part of the body, as when a person points north, or it may be external to the body, as when a person judges the direction of one object with respect to another. In addition there are reference frames which combine egocentric and exocentric elements. For instance, when we say that an object is north of us, we use our own body as the origin of a directional scale which is also anchored to the world. The same is true when a person says that something is above the head. Such frames may be referred to as *heterocentric* frames of reference. These various frames of reference are listed in table 1 together with examples of judgments of each type.

Polar coordinates based on meridional angles and angles of eccentricity are commonly used for the objective specification of the oculocentric position of a visual object. The subjective registration of the oculocentric position of an object depends on the local sign mechanism of the visual system. This is the mechanism whereby, for a given position of the eye, each region of the visual field has a unique (one-to-one) and stable mapping onto the retina and visual cortex. In a nominal local sign system, stimulation of each retinal location evokes an identifiable response, but the set of responses is not metrically organized. In an ordinal local sign system, values such as up and down or left and right are specified, and in an interval system, distances between objects may be specified. Quantitative judgments about the oculocentric location of an isolated object require a ratio local sign system, that is, one in which there is a built-in reference point and fiducial line, such as the fovea and the normally vertical meridian.

The headcentric position, orientation or movement of a visual object may be objectively specified in terms of its angle of elevation relative to a transverse plane through the eyes, and its angle of azimuth relative to the median plane of the head. A person making headcentric visual judgments must take account of both oculocentric and eye-in-head information. The bodycentric (torsocentric) position or movement of an object may be objectively specified in terms of the median plane of the head and some arbitrary transverse plane of the body. If no part of the body is in view, bodycentric judgments require the observer to take account of oculocentric information, eye-in-head information and information from the neck joints and muscles regarding the position of the head on the body. Thus the oculocentric, headcentric and bodycentric reference systems form a hierarchical, or nested, set of egocentric frames as indicated in the second column of table 1. If the body as well as the object being judged is in view, bodycentric judgments are much simpler since they can be done on a purely visual basis without the need to know the positions of the eyes or head. Eye-in-head and head-on-body information provided by afferent or efferent neural signals can, at least in theory, provide nominal, ordinal, interval, or ratio metrics.

Finally, the exocentric position, orientation, or movement of an object is specified with respect to arbitrary coordinates external to the body. Exocentric judgments about an isolated visual object require the observer to take account of oculocentric, eye-in-head and head-on-body information and, in addition, information regarding the position or movement of the body with respect to an external frame. This may involve associating the position of a seen object with, for instance, the position of the noise that it is making. This is a multisensory task. In other cases it may involve relating the position of an object detected by one sense organ with the position of another object detected by a second sense organ. This is an intersensory task (see Howard, 1982, Chapter 11, for more details on this distinction). The vestibular system is the only sense organ that provides direct information about the attitude and movement of the body in inertial space. The otolith organs respond to the static and dynamic pitch and roll of the head with respect to gravity; they provide no information about rotation or position of the head around the vertical axis. The otolith organs also respond to linear acceleration of the body along each of three orthogonal axes, but cannot distinguish between head tilt and linear acceleration. The semi-circular canals provide information about body rotation in inertial space about each of three orthogonal axes. But if rotation is continued at a constant angular velocity, the input from the canals soon ceases. The integral of the motion signal from the canals can provide information about the position of the body, but only with respect to a remembered initial position. If there are two point-objects in view at the same time, exocentric judgments of the distance between them and their relative motion are possible using only oculocentric information. At least three point-objects are required for exocentric visual judgments of direction or orientation based solely on oculocentric information.

In what follows I shall discuss the extent to which perceptual judgments within egocentric and exocentric frames of reference are subject to illusory disturbances and long-term modifications. I shall argue that well-known spatial illusions, such as the oculogyral illusion and induced visual motion have usually been discussed without proper attention being paid to the frame of reference within which they occur, and that this has led to the construction of inadequate theories and inappropriate procedures for testing them.

2. THE OCULOCENTRIC FRAME

Any misperception of the oculocentric position or movement of a visual object can arise only as a result of some disturbance of the retinal local sign system or of the oculocentric motion-detecting system. In a geometrical illusion, lines are apparently distorted or displaced when seen in the context of a larger pattern. In a figural aftereffect, a visual test object seen in the neighborhood of a previously seen inspection object appears displaced away from the position of the inspection object. Such effects operate only over distances of about one degree of visual angle, and the apparent displacement rarely exceeds a visual angle of a few minutes of arc (Kohler and Wallach, 1944). We must conclude that the local sign system is relatively immutable. This is not surprising, since the system depends basically on the anatomy of the visual pathways. Several claims have been made that oculocentric distortions of visual space can be induced by pointing with hidden hand to visual targets seen through displacing prisms (Cohen, 1966; Held and Rekosh, 1963). Others have claimed that these effects were artifactual, and we are left with no convincing evidence that oculocentric shifts can be induced in this way. (See Howard, 1982, p, 501 for a more detailed discussion of this subject.)

The movement after effect is a well-known example of what is almost certainly an oculocentric disturbance of the perception of motion. I will not discuss this topic here.

3. THE HEADCENTRIC FRAME

A misjudgment of the headcentric direction or motion of a visual object could arise from a misregistration of the position or motion of either the retinal image or the eyes. In this section I shall consider only phenomena due to misregistration of the position or movement of the eyes.

3.1 Illusory Shifts of Headcentric Visual Direction

Deviations of the apparent straight ahead due to misregistered eye position are easy to demonstrate. If the eyes are held in an eccentric position, a visual target must be displaced several degrees in the direction of the eccentric gaze to be perceived as straight ahead. When the observer attempts to look straight ahead after holding the eyes off to one side, the gaze is displaced several degrees in the direction of the previous eye deviation. Attempts to point to visual targets with unseen hand are displaced in the opposite direction. The magnitude of these deviations has been shown to depend on the duration of eye deviation and to be a linear function of the eccentricity of gaze (Hill, 1972; Morgan, 1978; Paap and Ebenholtz, 1976). Similar deviations of bodycentric visual direction occur during and after holding the head in an eccentric posture (Howard and Anstis, 1974). It has never been settled whether these effects are due to changes in afference or to changes in efference associated with holding the eyes in a given posture (see Howard, 1982, for a discussion of this issue). Whatever the cause of these effects, it is evident that the headcentric system is more labile than the oculocentric system. This is what one would expect, because headcentric tasks require the neural integration of information from more than one sense organ.

3.2 The Oculogyral Illusion

The oculogyral illusion may be defined as the apparent movement of a visual object while the semicircular canals of the vestibular system are being stimulated (Graybiel and Hupp, 1946). The best visual object is a small point of light in otherwise dark surroundings and fixed with respect to the head. When the vestibular organs are stimulated, as for instance by accelerating the body about the mid-body axis, the point of light appears to race in the direction of body rotation. The oculogyral illusion also occurs when the body is stationary, but the vestibular organs signal that it is turning. This happens, for instance, in the 20 or 30 seconds after the body has been brought to rest after being rotated. It is not surprising that a point of light attached to the body should appear to move in space when the observer feels that the body is rotating. I shall refer to this perceived motion of the light with the body as the exocentric component of the oculogyral illusion. The exocentric component is not very interesting because it is difficult to see how a rotating person could do other than perceive a light which is attached to the body as moving in space. But even casual observation of the oculogyral illusion reveals that the light appears to move with respect to the head in the direction of body acceleration. This headcentric motion of the light is the headcentric component of the oculogyral illusion.

Whiteside, Graybiel and Niven (1965) proposed that the headcentric component of the oculogyral illusion is due to the effects of unregistered efference associated with the vestibulo-ocular response (VOR) The idea is that when the subject fixates the point of light, VOR engendered by body acceleration is inhibited by voluntary innervation. The voluntary innervation is fully registered by the perceptual system, but the VOR efference is not, and this asymmetry in registered efference causes the subject to perceive the eyes as moving in the direction of body rotation. This misperception of the movement of the eyes is interpreted by the subject as a headcentric movement of the fixated light. To support this theory, we need evidence that the efference associated with VOR is not fully registered by the perceptual system responsible for making judgments about the headcentric movement of visual objects.

For frequencies of sinusoidal head rotation up to about 0.5 Hz, the VOR is almost totally inhibited if the attention is directed to a visual object fixed with respect to the head (Benson and Barnes, 1978). The most obvious theory is that VOR suppression by a stationary object is due to cancellation of the VOR by an equal and opposite smooth pursuit generated by the retinal slip signal arising from the stationary light. This cannot be the whole story because Barr, Schulthies and Robinson (1976) reported that the gain of VOR produced by sinusoidal body rotations decreased to about 0.4 when subjects imagined that they were looking at an object rotating with them. It looks as though VOR efference can be at least partially cancelled or switched off even without the aid of visual error signals (McKinley and Peterson, 1985; Melvill Jones, Berthoz and Segal, 1984). Tomlinson and Robinson (1981) were concerned to account for how an imaginary object can inhibit VOR, but for our present purposes, the more important point is that VOR is not totally inhibited. Perhaps an imagined object is not a satisfactory stimulus for revealing the extent of voluntary control over VOR. We wondered whether an afterimage might be a better stimulus because it relieves subjects of the task of imagining an object and only requires them to imagine that it is stationary with respect to the head. We had already found optokinetic nystagmus (OKN) to be totally inhibited by an afterimage, even though it was not inhibited by an imaginary object. The results of all these experiments are reported in Howard, Giaschi and Murasugi (1988).

Subjects in total darkness were subjected to a rotary acceleration of the whole body of $14^\circ/s^2$ to a terminal velocity of 70°/s, which was maintained for 60 s. In one condition subjects were asked to carry out mental arithmetic. In a second condition they were asked to imagine an object rotating with the body, and in a third condition, an afterimage was impressed on both eyes just before the trial began and the subject was asked to imagine that it was moving with the body. The same set of conditions was repeated, but with lights on, so that the stationary OKN display filled the visual field. Under these conditions both VOR and OKN are evoked at the same time.

In all conditions the velocity of the slow phase of each nystagmic beat was plotted as a function of time from the instant that the body reached its steady-state velocity. For none of the subjects was VOR totally inhibited at any time during any of the trial periods. For the OKN plus VOR condition, subjects could initially inhibit the nystagmus only partially, even though they could see a moving display, but they could totally inhibit the response after about 30 s, when the VOR signal had subsided.

We propose that VOR is not completely inhibited by an afterimage seen in the dark because the mechanism used to assess the headcentric motion of visual objects does not have full access to efference associated with VOR. Thus the system has no way of knowing when the eyes are stationary. The component of the VOR which cannot be inhibited by attending to an afterimage gives an estimate of the extent to which VOR efference is unregistered by the system responsible for generating voluntary eye movements and for giving rise to the headcentric component of the oculogyral illusion.

4. THE EXOCENTRIC FRAME

4.1 Vection

Vection is an illusion of self-motion induced by looking at a large moving display and is the clearest example of an exocentric illusion. For instance, illusory self-rotation, or circular-vection, is induced when an upright subject observes the inside of a large vertical cylinder rotating about the mid-body axis (yaw axis). For much of the time the cylinder seems to be stationary in exocentric space and the body feels as if it is moving in a direction opposite to that of the visual display. Similar illusions of self-motion may be induced by visual displays rotating about the visual axis (roll axis) or about an axis passing through the two ears (pitch axis) (Dichgans and Brandt, 1978). Rotation of a natural scene with respect to the head is normally due to head rotation, and the vestibular system is an unreliable indicator of self-rotation except during and just after acceleration. Therefore it is not surprising that scene rotation is interpreted as self-rotation, even when the body is not rotating. There is a conjunction of visual and vestibular inputs into the vestibular nuclei (Waespe and Henn, 1978) and the parietal cortex (Fredrickson and Schwarz, 1977), which probably explains why visual inputs can so closely mimic the effects of vestibular inputs.

4.1.1 *Vection for different postures and axes of rotation* – If the vection axis is vertical, the sensation of self-rotation is continuous and is usually at the full velocity of the stimulus motion. If the vection axis is horizontal, the illusory motion of the body is restrained by the absence of utricular inputs that would arise if the body were actually rotating. Under these circumstances a weakened but still continuous sensation of body rotation is accompanied by a paradoxical sensation that the body has tilted only through a certain angle (Held, Dichgans and Bauer, 1975). Howard, Cheung and Landolt (1987) suspended a subject in various postures within a large sphere that could be rotated about a vertical or horizontal axis and measured the magnitude of vection and illusory body tilt for yaw, pitch and roll vection for both vertical and horizontal orientations of each axis (fig. 1).

For body rotation about both vertical and horizontal axes, yaw vection was stronger than pitch vection, which was stronger than roll vection. When the vection axis was vertical, sensations of body motion were continuous and usually at, or close to, the full velocity of the rotating visual field. When the vection axis was horizontal, the sensations of body motion were still continuous, but were reduced in magnitude. Also, for vection about horizontal axes, sensations of continuous body motion were accompanied by sensations of illusory yaw, roll, or pitch of the body away from the vertical posture. The mean body tilt was over 20°, but the body was often reported to have tilted by as much as 90°. Two subjects in a second experiment reported sensations of having rotated full circle. Held, Dichgans and Bauer (1975) reported a mean illusory body tilt of 14°. We obtained larger degrees of body tilt, probably because our display filled the entire visual field and because subjects were primed to expect that their bodies might really tilt. In most subjects, illusory backwards tilt produced by pitch vection about a horizontal axis was much stronger than illusory forward tilt. Only two of our 16 subjects showed the opposite asymmetry; that was also reported by Young, Oman and Dichgans (1975).

4.1.2 *Vection and the relative distances of competing displays* – The more distant parts of a natural scene are less likely to rotate with a person than are nearer parts of a scene, so that the headcentric motion of more distant parts provides a more reliable indicator of self-rotation than does motion of nearer objects. It follows that circularvection should be related to the motion of the more distant of two superimposed displays. In line with this expectation Brandt, Wist, and Dichgans (1975) found that vection was not affected by a stationary object in front of the moving display, but was reduced when the object was seen beyond the display. Depth was created by binocular disparity in this experiment, and there is some doubt whether depth was the crucial factor as opposed to the perceived foreground-background relationships of the competing stimuli. Furthermore, the two elements of the display differed in size as well as distance.

Ohmi, Howard and Landolt (1987) conducted an experiment using a background cylindrical display of randomly placed dots which rotated around the subject, and a similar stationary display mounted on a transparent cylinder which could be set at various distances between the subject and the moving display. The absence of binocular cues to depth allowed the perceived depth order of the two displays to reverse spontaneously, even when they were well separated in depth. Subjects were asked to focus alternately on the near display and the far display while reporting the onset or offset of vection. They were also asked to report any apparent reversal of the depth order of the two displays, which was easy to notice because of a slight difference in appearance of the two displays.

In all cases vection was experienced whenever the display that was perceived as the more distant was moving and was never experienced whenever the display perceived as more distant was stationary. Thus circular vection is totally under the control of whichever of two similar displays is perceived as background. This dominance of the background display does not depend on depth cues, because circularvection is dominated by a display that appears more distant, even when it is nearer. We think that perceived distance is not the crucial property of that part of the scene interpreted as background. When subjects focused on the moving display, optokinetic pursuit movements of the eyes occurred, and when they focused on the stationary display, the eyes were stationary. But such a change in the plane of focus had no effect on whether or not vection was experienced, as long as the apparent depth order of the two displays did not change.

Thus sensations of self rotation are induced by those motion signals that are most reliably associated with actual body rotation—namely, signals arising from that part of the scene perceived as background. Vection sensations are not tied to depth cues, which makes sense because depth cues can be ambiguous. Nor are vection sensations tied to whether the eyes pursue one part of the scene or another, which also makes sense because it is headcentric visual motion that indicates self-motion, which is just as well detected by retinal image motion as by motion of the eyes.

4.1.3 *Circularvection and the central-peripheral and near-far placement of stimuli* – It has been reported that circularvection is much more effectively induced by a moving scene confined to the peripheral retina than by one confined to the central retina (Brandt, Dichgans and Koenig, 1973). In these studies, the central retina was occluded by a dark disc which may have predisposed subjects to see the peripheral display as background, and it may have been this, rather than its peripheral position, which caused it to induce strong vection. Similarly, when the stimulus was confined to the central retina, subjects may have been predisposed to see it as a figure against a ground, which may have accounted for the small amount of vection evoked by it.

Howard et al. (1987) conducted an experiment to test this idea. The apparatus is depicted in figure 2. The subject sat at the center of a vertical cylinder covered with randomly arranged black opaque dots. A 28° square display of dots above the subject's head was reflected by a sheet of transparent plastic onto a matching black occluder in the center of the large display. The central display could be moved so that it appeared to be suspended in front of, in the same plane as, or beyond the peripheral display. In the latter position it appeared as if seen through a square hole. In some conditions, one of the displays moved from right to left or from left to right at 25°/s while the other was occluded. In other conditions both displays were visible, but only one moved and in still other conditions, both displays moved, either in the same direction or in opposite directions. In each condition subjects looked at the center of the display and rated the direction and strength of circularvection.

The results are shown in figure 3. They reveal that, all things being equal, vection is driven better by peripheral stimuli than by a 28° central stimulus Indeed, it is driven just as well by a moving peripheral display with the center black or visible and stationary as it is by a full-field display. However, if the center of the display is moving in a direction opposite to that of the peripheral part, then vection is reduced. Thus a moving central display can weaken the effect of a moving peripheral display, but not to the extent of reversing vection. If the peripheral part of the display is visible but stationary, then the direction of vection is determined by the central part of the display, but only if the moving central field is farther away than the surround. This result is understandable when we realize that this sort of stimulation is produced, for example, when an observer looks out of the window of a moving vehicle. The moving field seen through the window indicates that the viewer is carried along with the part of the scene surrounding the window on the inside. When the surround is black, vection is still controlled by the movement of the central display, even when it is coplanar with or in front of the surround. The reason for this is probably that a central display in front of a black surround provided virtually no cues to its location in depth and subjects perceived it as being beyond the surrounding black display.

4.2 Induced Visual Motion

Induced visual motion occurs when one observes a small stationary object against a larger moving background and was first described in detail by Duncker (1929). For instance, the moon appears to move when seen through moving clouds. There is a form of induced motion in which the stationary object is seen against a frame which moves across it. In this stimulus configuration, the moving frame becomes increasingly eccentric and this may be responsible for some of the illusory motion of the stationary object. I do not wish to consider the asymmetry effect, so the stimulus I shall consider is one in which the stationary object is seen against a large moving background that either fills the visual field or remains within the confines of a stationary boundary.

Induced visual motion could occur within the oculocentric, the headcentric or the exocentric system. As an oculocentric effect, it could be due to contrast between oculocentric motion detectors. I shall argue that this is not a major cause of the illusion.

As a headcentric effect, induced visual motion could be due to OKN induced by inhibition of the moving background by voluntary fixation on the stationary object. If the efference associated with OKN were not available to the perceptual system, but the efference associated with voluntary fixation were, this should create an illusion of movement in a direction opposite to that of the background motion. This explanation, which I proposed in 1982, is analogous to that proposed by Whiteside, Graybiel and Niven (1965) to account for the oculogyral illusion. It has been championed more recently by Post and Leibowitz (1985) and Post (1986). I believe that the evidence reviewed below shows that this is not the main cause of induced visual motion.

Induced visual motion could be an exocentric illusion. It has been explained that inspection of a large moving background induces an illusion of self-motion accompanied by an impression that the background is not moving. A small object fixed with respect to the observer should appear to move with the observer and therefore to move with respect to the exocentric frame provided by the perceptually stationary background. This possibility was mentioned by Duncker and is, I suggest, the major cause of induced visual motion. I shall now review evidence in favour of this explanation of induced visual motion.

4.2.1 *Inhibition of OKN is neither necessary nor sufficient for induced motion* – In the experiment on circularvection described in section 4.1.2, Ohmi, Howard, and Landolt (1987) showed that vection occurred whenever the more distant of two displays was moving, but never when the more distant display was stationary. When the more distant display moved, vection occurred both when the subjects converged on the moving display and had OKN, and when they converged on the stationary nearer display and inhibited OKN. The important point in the present context is that the nearer stationary display appeared to move with the subject (exocentrically) whenever there was vection, but appeared perfectly stationary when there was no vection. Thus, induced visual motion came and went with vection and did not depend on whether or not OKN was inhibited. McConkie and Farber (1979) reported that a visual display perceived as background induced visual motion in an otherwise similar display perceived as foreground, although they did not relate this to changes in vection.

The theory that ascribes induced visual motion to contrast between oculocentric motion detectors cannot account for these results, because the same relative motion was present when the far display moved and the near display did not, as when the near display moved and the far one did not. According to the oculocentric theory there should have been induced motion in both cases rather than only in the first.

The headcentric theory of induced visual motion that explains the effect in terms of inhibition of involuntary OKN by voluntary efference cannot account for these results either, because induced motion occurred whether or not OKN was inhibited. Furthermore, when a stationary display was seen as the background to a moving display, vection did not occur, even when subjects attended to the stationary display and inhibited OKN. Thus, whether or not OKN was inhibited had no bearing on whether induced visual motion occurred under these circumstances.

Vection is an exocentric phenomenon, and induced visual motion of stationary elements of the visual display comes and goes with saturated vection. The stationary elements simply look as if they are rotating with the body, not slower and not faster. If vection is fully saturated, the moving scene appears stationary and the body and stationary elements of the scene appear to move exocentrically at the full velocity of the inducing field. Under these circumstances induced visual motion is complete. For instance, if a large scene rotates at 60°/s, induced visual motion of a stationary object is also that velocity. All this suggests that induced visual motion can be an exocentric effect coupled to vection. Headcentric induced motion may occur in other conditions.

The exocentric theory of induced visual motion nicely explains why there is no loss of accuracy in pointing with unseen hand to a visual target subjected to induced visual motion (Bacon, Gordon and Schulman, 1982; Bridgeman, Kirsch and Sperling, 1981). A headcentric theory of induced motion predicts that pointing would deviate, since any misperception of gaze should be reflected in the bodycentric task of pointing. On the exocentric theory, there should be no loss in pointing accuracy, since pointing is a bodycentric task.

It might be objected that when a single stationary object is placed against a small moving display it exhibits induced motion, although there is no discernable illusion of self-motion. I think this is because the visual consequences of vestibular stimulation have a lower threshold than the sensations of body motion. For instance, it is well known that the oculogyral illusion induced by actual body rotation gives a more sensitive measure of vestibular thresholds than do sensations of body motion (Miller and Graybiel, 1975). When the inducing field is small, induced visual motion is only a fraction of the velocity of the inducing field, but as the size of the inducing field is increased, vection becomes evident and induced visual motion more pronounced until, when the field is sufficiently large, both vection and induced visual motion attain the full value of the velocity of the moving field. When vection and induced visual motion are saturated, the objectively stationary object appears to move in exocentric space at the same velocity as the body, neither getting ahead nor lagging behind. In other words, with large inducing fields there is no perceptible headcentric component of induced visual motion. The stationary object may appear to be headcentrically displaced in the direction of motion of the background, but that is a displacement effect, not an illusory motion. This effect may be related to the well-known fact that, in the absence of a fixation point, the eyes deviate in the direction of the fast phases of OKN (Brecher, et al., 1972; Heckmann and Post, 1986). It is possible that when a visual display is accelerating, the increasing deviation of gaze induces an apparent motion in a stationary object. However, I am dealing here only with illusory visual motion induced by visual displays moving at constant velocity.

4.2.2 *Evidence that OKN efference is perceptually registered* – The fact that a headcentric component of induced visual motion may be absent suggests that efference associated with OKN is available to the perceptual system, unlike that associated with VOR. We recently produced evidence that this is so (Howard, Giaschi and Murasugi, 1988).

Optokinetic nystagmus is induced when a person looks at a moving textured surface. The response cannot be inhibited by voluntary effort, as long as the eyes remain converged on the moving display (Howard and Gonzalez, 1987). However, the response is totally inhibited if attention is directed to a stationary object superimposed on the center of the display (Murasugi, Howard, and Ohmi, 1986). If the attention is directed to an afterimage imposed on the fovea, OKN may be totally inhibited (Viefhues, 1958; Murasugi, Howard and Ohmi, 1984: Wyatt and Pola, 1984). If the afterimage is regarded as fixed in space, then OKN is inhibited and the after image appears stationary. If the afterimage is regarded as moving with the moving display, then OKN is fully restored. It is easy to understand how a real stationary object allows a person to inhibit OKN; any movement of the eyes with respect to the stationary object generates both a misfoveation (position) signal and a retinal slip (velocity) signal. However, these error signals are not provided by an afterimage, so that some other error signal or an open-loop signal must be used in this case. The effect cannot be due to occlusion of the moving display by the afterimage because OKN was only partially reduced when the center of the display was occluded by a black horizontal band. The more OKN is inhibited, the more the eyes lag behind the moving display and the greater is the relative motion between afterimage and display. However, although relative motion is minimum when OKN gain is one, it has no maximum value because it would continue to increase if the eyes were to move in a direction opposite to that of the display. In other words, the degree of relative motion between afterimage and moving display does not indicate when the eye velocity is zero. A partial loss of gain of OKN found in some subjects when imagining a head-fixed object is presumably due to the injection of a voluntary command into the eye movement signal. But this effect accounts for only a small part of the complete suppression of OKN by an afterimage.

The inhibition of OKN by an afterimage could be due to the production of a voluntary efferent command of opposite sign which cancels the OKN efference signal. If the voluntary mechanism had only partial access to the efference controlling OKN, then it would not be able to produce a matching command and bring the eyes to a stop and at the same time perceive the afterimage as stationary with respect to the head. An object imagined in the plane of the display is ineffective, and this must be because it provides no confirming impression of a stationary object once OKN efference has been cancelled. In the absence of such an object, there is an overriding necessity to stabilize the image of the moving stimulus.

4.2.3 *Induced visual motion in several directions simultaneously* – Visual motion has been reported to be induced by stimuli moving simultaneously in two directions. For instance, Nakayama and Tyler (1978) reported that a pair of parallel lines pulsing in and out in opposite directions induced an apparent pulsation of a pair of stationary lines placed between them. However, the apparent velocity of this induced motion was only about 0.1°/s and the effect may have been an oculocentric effect akin to the figural aftereffects. But in any case, the exocentric theory of induced visual motion can account for induced visual motion in more than one direction. For instance, an outwardly expanding textured surface induces forward linear vection (Anderson and Braunstein, 1985). Ohmi and Howard (1988) found that forward linear vection induced by a looming display, and the accompanying induced visual motion of a superimposed stationary display occurred only if the looming display appeared more distant than the stationary display. According to the oculocentric theory of induced visual motion, the depth order of the two displays should not matter. A theory of induced visual motion based on the inhibition OKN cannot account for induced visual motion produced by looming displays, since such displays do not invoke OKN.

It is possible that there is a headcentric component to induced visual motion under certain circumstances, such as when a visual display is accelerating or becoming more eccentric. But the above evidence strongly suggests that the major part of induced visual motion induced by large moving fields under steady conditions is exocentric and is a simple consequence of vection. Visual motion induced under these circumstances can be 100% of the velocity of the inducing field. Furthermore, visual motion may be induced in a stationary display that fills the visual field if the display is perceived as a foreground in front of a large moving background.

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TABLE 1.– FRAMES OF REFERENCE FOR VISUAL SPATIAL JUDGMENTS. RF IS SHORT FOR REFERENCE FRAME AND O IS SHORT FOR STIMULUS OBJECT

TYPE	SENSORY COMPONENTS	EXAMPLES
EGOCENTRIC O and RF internal		
PROPRIOCEPTIVE	Sense of position of body parts	Point to the toe
EGOCENTRIC O external, RF internal		
OCULOCENTRIC	Retinal local sign (plus stereo vision)	Fixate an object, Place a line on a retinal meridian
HEADCENTRIC	Eye position + local sign	Place an object in the median plane of the head
BODYCENTRIC (Body not in view)	Neck + eye position + local sign	Align a stick to the unseen toe. Place object to left of body
BODYCENTRIC (Body in view)	Relative local sign	Align a stick to the seen toe
EXOCENTRIC O internal, RF external	Sensed body part and external reference	Align the arm with gravity. Point North
EXOCENTRIC O and RF external		
SINGLE POINT OR LINE	No exocentric judgments possible	
VISUAL OBJECTS	Relative local sign	Place object A East of object B. Align three objects
MULTISENSORY	One object detected by two senses	Associate the sight and sound of object
INTERSENSORY	Visual and non-visual objects compared	Set a line vertical. Point a line to an unseen sound
HETEROCENTRIC RF internal-external		
GEOGRAPHICAL	Object-to-self plus landmark	Judge that an object is East of the self
GRAVITATIONAL	Object-to-self plus gravity	Judge that an object is above the head

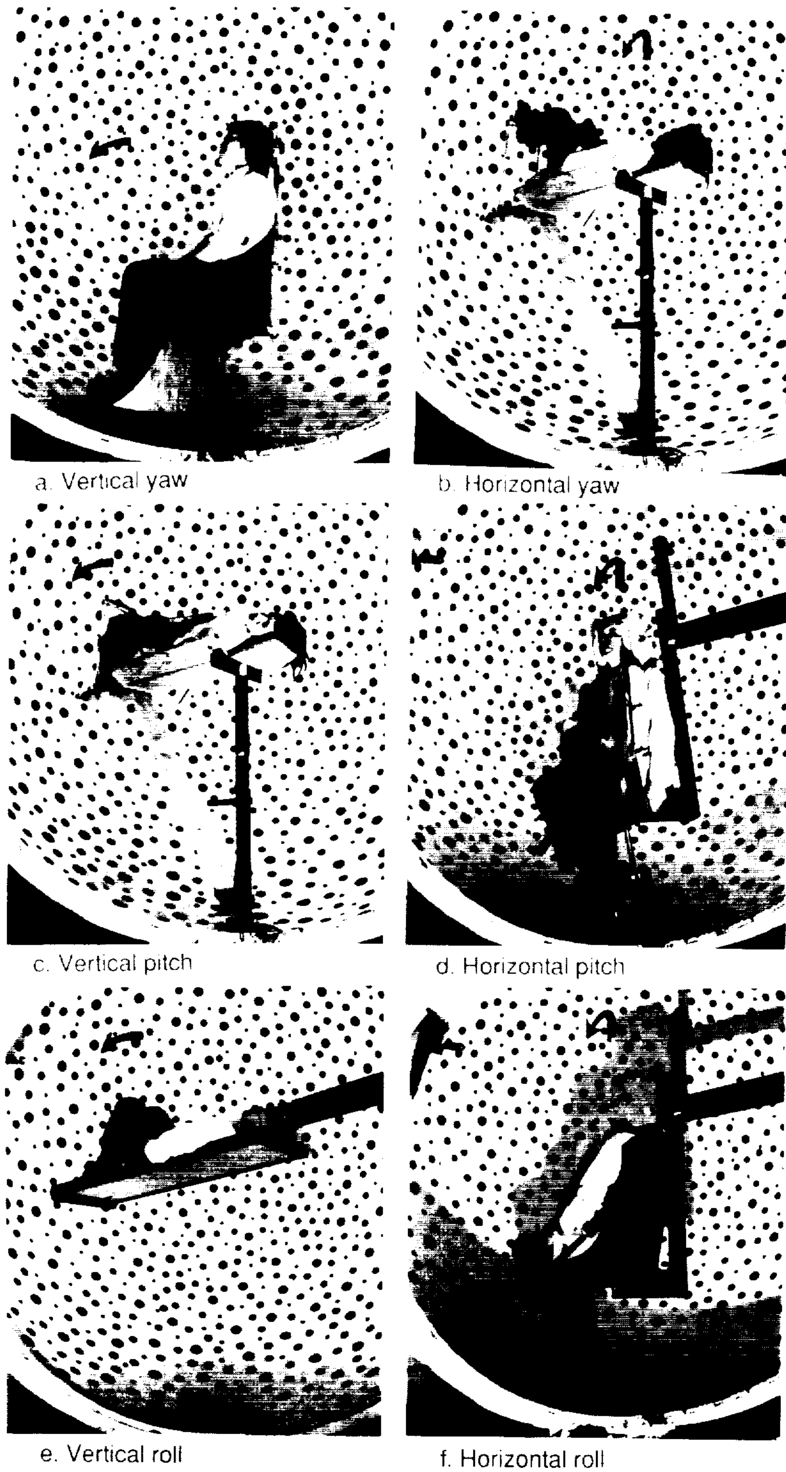

Figure 1.– The set of postures and vection axes use by Howard, Cheung and Landolt (1987) to study vection and illusory body tilt. The subject is seen through the open door of the 3m diameter sphere which could be rotated about either the vertical or horizontal axis. The subject was supported in different postures by air cushions and straps (not shown) so as to produce the six possible combinations of vection axis (yaw, pitch and roll) and gravitational orientation of the axis.

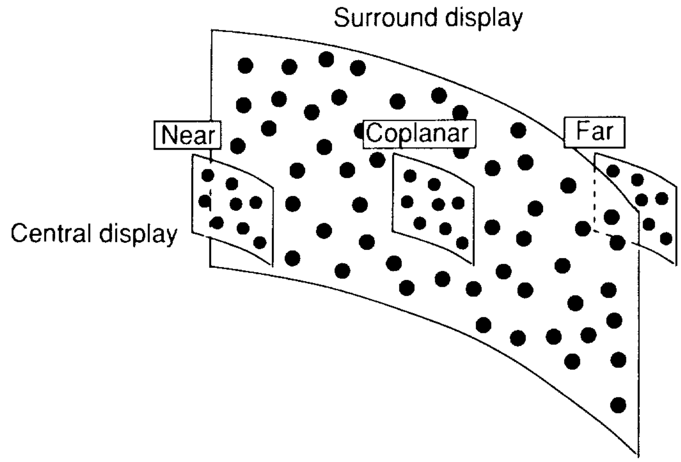

Figure 2.– A diagrammatic representation of the displays use by Howard, Simpson and Landolt (1987) to study the interaction between central-peripheral and far-near placement of two displays in generating circularvection. The two displays could be moved in the same or in opposite directions, or one of them could be stationary or blacked out.

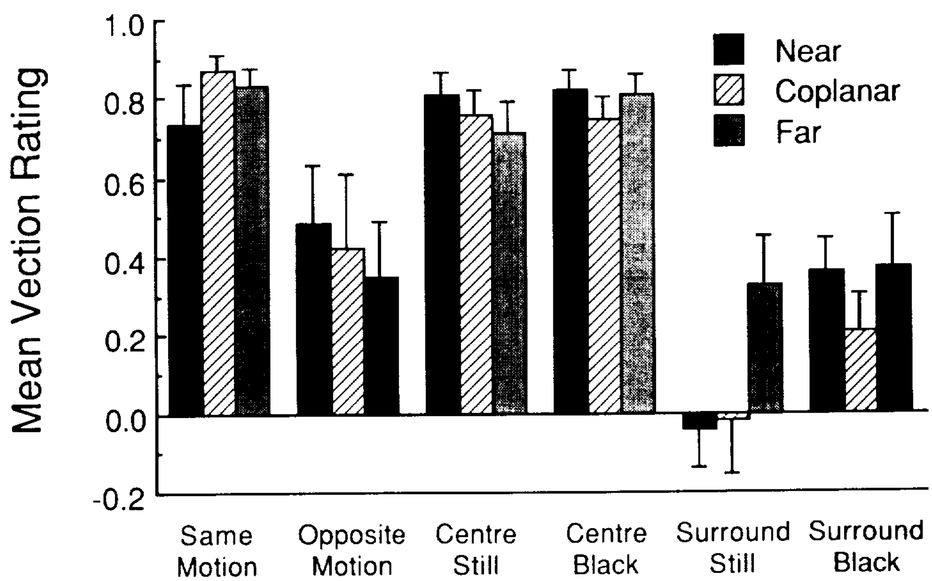

Figure 3.– Mean vection ratings of nine subjects plotted as a function of the relative depth between the central and peripheral parts of the display and the type of display. A vection rating of 1.0 signifies full vection in a direction opposite to the motion of the display. When the two parts of the display moved in opposite directions, the motion of the peripheral part was taken a reference. The error bars are standard errors of the mean.

COMMENTS ON TALK BY IAN HOWARD

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Induced visual motion is the name assigned a group of phenomena which can be described with more or less the same words: "illusory motion of stationary contours opposite the direction of moving ones." As Dr. Howard has pointed out, it is possible that oculocentric, headcentric and exocentric mechanisms generate experiences which may be described by the words "induced visual motion." We have found Dr. Howard's framework very helpful in organizing our thoughts about the multiple sources of these apparently similar phenomena. We also accept that some forms of induced visual motion may depend on vection and cannot be explained by suppression of nystagmus (e.g., phenomenal tilt of a stationary stimulus during roll vection induced by a contoured disc rotating in a frontal plane). We are less certain than Dr. Howard, however, that there is only one mechanism for induced visual motion.

In Dr. Howard's study, phenomenal motion of a stationary display which was positioned in front of a moving display occurred only when there was vection. We have reliably obtained induced visual motion of small fixation targets in the complete absence of vection (Post and Heckmann, 1987; Post and Chaderjian, 1988; Heckmann and Post, 1988). Dr. Howard would likely explain this finding with his statement that "...visual consequences of vestibular stimulation have a lower threshold than sensations of bodily motion." We agree wholeheartedly: optokinetic afternystagmus (OKAN), which is a good indicator of the vestibular effects of visual stimulation, has been found at moving-contour velocities too low to elicit vection (Koenig, Dichgans and Schmucker, 1982). We have also reliably obtained OKAN after exposure to a moving-contour stimulus which elicits no vection (Heckmann and Post, 1988). In fact, induced visual motion may be elicited by a single moving dot stimulus (Post and Chaderjian, 1988) which is not capable of producing vection.

If induced visual motion occurs because a perceptually registered voluntary signal for fixation opposes an unregistered involuntary signal for optokinetic nystagmus, then the illusion should reflect known dynamic properties of the optokinetic system. That is, the magnitude of induced visual motion will be proportional to the nystagmus signal being opposed. Induced visual motion should therefore vary across stimulation in the same way that nystagmus varies, but have the opposite directional sign. Our efforts to disconfirm this prediction have so far failed. Induced visual motion is correlated with OKAN of opposite directional sign across variations in stimulus illuminance and velocity (Post, 1986). The magnitude of induced visual motion increases along with the slow-phase velocity of OKAN with increasing stimulus duration. The illusion also decays and reverses direction along with OKAN after stimulus termination. Further, both responses show an increased tendency to reverse direction following stimulation in the presence of a fixation target rather than after stimulation without fixation (Heckmann and Post, 1988).

Induced visual motion is not the only motion illusion involving visual fixation of moving or stationary targets which can potentially be explained by interaction of voluntary and involuntary eye-movement signals. These illusions include autokinesis, the Aubert-Fleischel effect, the Filehne Illusion, and several others (Post and Leibowitz, 1985). Induced visual motion, however, provides a particularly good model for testing the eye-movement hypothesis, since a good deal is known about the dynamics of visually induced involuntary eye movements. We have not been so much interested in "championing" a particular explanation of induced visual motion, therefore, as we have been to test the existence and applicability of a particular mechanism. Of course, since we are using a well-known illusion as our model, we must also explore the applicability of alternative explanations of induced visual motion to our results.

With further reference to the origin of induced visual motion in vection, therefore, we recently reported a dissociation between the two illusions (Post and Heckmann, 1987). Briefly, fixation of a target located 10° left of the midline during exposure to rightward-moving background contours reliably increased the magnitude of induced visual motion. This finding is consistent with the idea that extra voluntary efference is needed to maintain a leftward as compared to a straight-ahead gaze during rightward motion of background contours. Vection, however, was reduced when a fixation target was made available, and further reduced when the target was placed 10° left of the midline. We emphasize that this dissociation does not reject the idea that some form of induced visual motion originates with vection, only the idea that all of induced visual motion originates with vection.

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