

SPATIAL VISION WITHIN EGOCENTRIC AND EXOCENTRIC FRAMES OF REFERENCE

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INTRODUCTION

It is remarkable that we are able to perceive a stable visual world and judge the directions, orientations and movements of visual objects given that images move on the retina, the eyes move in the head, the head moves on the body and the body moves in space. An understanding of the mechanisms underlying perceptual stability and spatial judgements requires precise definitions of relevant coordinate systems. An egocentric frame of reference is defined with respect to some part of the observer. There are four principal egocentric frames of reference, a station-point frame associated with the nodal point of the eye, an retinocentric frame associated with the retina, a headcentric frame associated with the head, and a bodycentric frame (torsocentric) associated with the torso. Additional egocentric frames can be defined with respect to any segment of the body. An egocentric task is one in which the position, orientation or motion of an object is judged with respect to an egocentric frame of reference. A proprioceptive task is a special kind of egocentric task in which the object being judged is also part of the body. An example of a proprioceptive task is that of directing the gaze toward the seen or unseen toe. An exocentric frame of reference is external to the observer. Geographical coordinates and the direction of gravity are examples of exocentric frames of reference. These various frames of reference are listed in Table 1, together with examples of judgements of each type.

The Station-Point Frame

We start with an illuminated three-dimensional scene of fixed objects, the visual world. A station point is defined with respect to some arbitrary coordinate system anchored in the world. Any optical system has two nodal points which have the geometrical property that all light rays passing through the first emerge from the second without having changed direction. The nodal points of the human eye are close together and can be regarded as one nodal point situated near the centre of the eye. The nodal point is a geometrical abstraction, light rays do not necessarily pass through it. The nodal point of the eye is the visual station point.

The visual surroundings or ambient array is the set of light sources and reflecting surfaces which surround the station point and from which light rays can reach the station point. The spherical array of light rays that reach the station point constitutes the station-point frame of reference. Within this frame of reference the distance of any point in the ambient array from the station point and the angle subtended at the nodal point by any pair of points in the ambient array can be specified. The station-point frame of reference itself contains no natural fiducial lines for specifying orientation or direction, since a point has no defined orientation. It is therefore meaningless to talk about the effects of

rotating the station point or rotating the ambient array round the station point. Every linear motion of the station point changes the distances of points and the angular subtense of pairs of points in the ambient array. The ambient array is sometimes thought of as the projection of the ambient array onto a fixed surface, usually a spherical surface centered on nodal point. This simply means that distances to points in the visual surroundings are not directly specified in this form of the ambient array, although the ambient array may contain enough information to allow distances to be recovered.

Visual attributes which may be defined in terms of the station-point frame of reference include (1) what is in view from a given place, (2) the relative directions (angular subtense) of two or more objects, (3) the distance of an object, (4) the relative angular velocities of moving objects, (5) velocity flow fields created by linear motion of the station point, expressed as a set of differential directed angular velocities and (6) the set of objects which define the locus of zero parallax (heading direction) in a three-dimensional array of objects as the station point is moved along a linear path. Judgements of these attributes are station-point judgements.

The Retinocentric Frame

We now add a pupil, lens, retina and associated structures of an eye. For a given position and orientation of the eye, the bundle of light rays which enter the pupil is the optic array and the portion of the ambient array from which these light rays originate is the distal visual stimulus, or field of view. For most purposes we can assume that the optic array projects onto a spherical retina centered on the nodal point. A visual line is any line which passes through the pupil and nodal point from a point in the distal stimulus to its image on the retina. The visual axis is the visual line through the fixation point and the centre of the fovea. A three-dimensional polar coordinate system centered on the nodal point can be used to specify the retinocentric distance, position, and direction of any object. An object's distance is its distance from the nodal point. Its eccentricity is the angle between its visual line and the visual axis. Its meridional direction is the angle between the plane containing the visual line of the object and the visual axis and the plane containing the visual axis and the retinal meridian which is vertical when the head is in a normal upright posture. These three-dimensional coordinates project onto the surface of the retina as two-dimensional polar coordinates, with the fovea as origin for eccentricity and the normally vertical meridian as the fiducial line for meridional direction. This is the retinocentric frame of reference. Note that the linear velocity of an image is proportional to the angular velocity of the object relative to the eye. This retinal coordinate system may be projected through the nodal point onto the concave surface of a perimeter or onto a tangent screen, which allows one to specify the oculocentric eccentricity and meridional angle of a stimulus on a chart. For certain purposes it may be more convenient to specify retinocentric positions in terms of elevation and azimuth or longitude and latitude. For instance, longitude and latitude are useful when describing the retinal flow field created by linear motion over a flat surface because the flow vectors conform to lines of longitude. The visual axis provides a natural reference which allows one to specify the direction of gaze with respect to selected landmarks in the ambient array.

Visual attributes which may be defined in terms of the retinocentric frame of reference include: (1) the eccentricity and meridional direction of an object (its visual direction relative to the fovea and the prime retinal meridian), (2) the orientation of a line, relative to prime retinal meridian. These are absolute retinocentric visual features. Relative retinocentric features involve only the specification of the relative positions, orientations or motions of images on the retina. Example are (1) the shape of a

retinal image (2) the retinal velocity of an image and hence the angular velocity of an object moving with respect to the eye. (3) the angular velocity of the eye with respect to a stationary object, and (4) retinal flow fields created by translations of the eye with respect to an ambient array. For a perfectly spherical retina relative retinocentric features are geometrically equivalent to those defined in terms of the ambient array projected onto a spherical surface.

All absolute retinocentric attributes change when the eye rotates with respect to a fixed nodal point and distal display. However, absolute retinocentric features are not necessarily affected by all types of eye rotation. For instance, the retinocentric direction of an object is invariant when the eye rotates about the visual line of the object. The eyes rotate as if about an axis at right angles to the meridian along which the gaze moves (Listing's law). An interesting consequence of this fact is that the retinocentric orientation a line is invariant when the gaze moves along the line (Howard, 1982, p. 185). For a spherical retina and distortion-free optical system, relative oculocentric attributes, such as the shape of the retinal image, are not affected by any rotations of the eye. If the retina were not spherical this would not be true and the task of shape perception would be more complex.

The station-point and retinocentric frames of reference are both oculocentric frames of reference.

The Headcentric Frame

We now add a head. The orientation of an eye in the head about each of three axes may be specified objectively in terms of either the Fick (latitude and longitude), the Helmholtz (elevation and azimuth) or the Listing (polar) coordinate system (see Howard, 1982 for details). The headcentric position of a visual object may be specified in terms of angles of elevation relative to a transverse plane through the eyes and angles of azimuth relative to the median plane of the head. The headcentric orientation of an object is usually specified with respect to the the normally vertical axis of the head. The head is defined as being vertical when the line from the ear hole to the angle of the eye socket and the line joining the two pupils are both horizontal. Particular headcentric spatial features of objects may be defined in terms of the types of head motion that leave them unchanged. If we assume that the centre of rotation of the eye is the same as the nodal point then the headcentric position of an object is the vector sum its retinocentric position and the position of the eye in the head. For instance, if an object is 10° to the left of the fixation point and the eye is elevated 10° then the headcentric position of the object is about 14.1° along the upper left diagonal with respect to the eye socket. Similar arguments apply to the headcentric orientation and motion of an object. Of course the coordinate systems used for specifying retinocentric position and eye position must correspond. Visual attributes that may be defined in headcentric terms include (1) the direction of an approaching object relative to the head, (2) the direction of gaze in the head, (3) an object's inclination to the mid-head axis and (4) a shape defined by the path an eye follows when pursuing a light spot.

The Bodycentric Frame

We now add a body. The bodycentric (torsocentric) position, orientation or movement of an object may be specified with reference to any of the three principal axes or planes of the body. The defining characteristic of bodycentric attributes is that they are affected by specific types of body motion.

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, as indicated in the second column of Table 1. But this is not all. For certain types of bodycentric judgement the observer must appreciate the lengths of body parts, in addition to their angular positions. For instance, a person can place the finger tip of the hidden hand on a visual target only if the length of the arm is taken into account. Conscious knowledge is not involved, but rather the implicit knowledge of the body that is denoted by the term body schema. 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.

Examples of bodycentric attributes include 1) the direction of an object relative to a part of the body. This would need to be appreciated by a person who wished to direct the hidden hand towards an object, 2) motions of an object with respect to a part of the body and 3) the inclination of an object relative to the mid-body axis.

The Exocentric Frame

Finally, the exocentric position, orientation or movement of an object are specified with respect to coordinates external to the body. The defining characteristic of exocentric spatial attributes is that they are not affected by changes in the position or orientation of the observer or any part of the observer. Exocentric attributes may be absolute or relative. Absolute exocentric attributes are defined with respect to a coordinate system which is assumed to be fixed in inertial space. Examples of extrinsic coordinate systems are the one-dimensional gravitational coordinate, the two-dimensional geographical coordinates and a set of three-dimensional Cartesian coordinates. Absolute exocentric attributes include (1) the gravitational orientation of a line, (2) the compass direction of an arrow and (3) the movements of an object within a defined space.

Relative exocentric attributes are defined in terms of the position, orientation or motion of one object relative to another or of parts of an object relative to other parts. The reference frame is now intrinsic to the object or set of objects being judged. The distinction is analogous to that between extrinsic and intrinsic geometries. Relative exocentric attributes include (1) the shape of an object (the relative dispositions of parts), (2) rotation of an object relative to an intrinsic axis. For instance, the rotation of an aircraft about the yaw, roll or pitch axis and (3) the motion of one object relative to another.

Exocentric judgements about an isolated visual object can be with respect to a frame of reference provided by memory, as when we relate the position of a light to the remembered positions of the contents of a room. Otherwise, the exocentric position of an isolated visual object can be specified with respect to a frame of reference supplied by a second sense organ. Thus we can judge the position of a light in relation to a frame of reference provided by sounds or by things we touch or we can judge the orientation of a line in terms of stimulation registered by the vestibular organs. These are all intersensory tasks.

In theory, the variance of performance on an intersensory task should equal the sum of the variances of directional tasks that involve the separate component senses. A multisensory task is one in which the position, orientation or movement of an object is detected by more than one sense organ at the same time. For instance, we perform a multisensory task when we determine the headcentric direction of an object both by sight and by the sound that it makes. Given that the observer believes that the seen and heard object is one, the variance of performance on a multisensory task should, theoretically, be less the variance of performance on tasks using only one or other of the component senses (see Howard, 1982, Chapter, 11 for more details on the distinction between intersensory and multisensory tasks).

Finally there are cases where the frame of reference is external but the object is the self. I shall refer to them as semi-exocentric frames of reference. Examples of semi-exocentric attributes include (1) the position of an observer on a map (2) the compass direction of an observer with respect to an object (3) the position of an observer with respect to being under or over something. Note that, unlike purely exocentric attributes, semi-exocentric attributes vary with changes in the location of the observer.

In what follows I shall discuss the extent to which perceptual judgements 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.

PERCEPTUAL JUDGEMENTS WITHIN THE OCULOCENTRIC FRAME

The subjective registration of the station-point or retinocentric features of an object depend 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 and stable mapping onto the retina and visual cortex.

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 Reikosh, 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, page 501 for a more detailed discussion of this subject).

The movement aftereffect 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.

PERCEPTUAL JUDGEMENTS WITHIN THE HEADCENTRIC FRAME

A person making headcentric visual judgements must take account of both oculocentric and eye-in-head information. The question of how and to what extent people make accurate use of eye-in-head information when making headcentric judgements is a complex one. One complication arises because the two eyes are in different positions. The visual system must construct a headcentric frame of reference that is common to both eyes. It can be shown that people judge the headcentric directions of an object as if the eyes were superimposed in the median plane of the head, somewhere between the actual positions of the two eyes. This is known as the cyclopean eye, or visual egocentre (See Howard, 1982 for a fuller discussion of all these issues).

A misjudgment of the headcentric direction or motion of a visual object can 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.

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. 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.

The Oculogyral Illusion

The oculogyral illusion may be defined as the apparent movement of a visual object induced by stimulation of the semicircular canals of the vestibular system (Graybiel and Hupp, 1946). The best visual object is a small point of light in 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 is the headcentric component of the oculogyral illusion.

Whiteside et al. (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 vestibulo-ocular reflex (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 et al. (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 et al. 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 requires them only to imagine that it is stationary with respect to the head. We had already found 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 by Howard et al. (1988).

Subjects in total darkness were subjected to a rotary acceleration of the whole body of $14^\circ/\text{s}^2$ to a terminal velocity of $70^\circ/\text{s}$, 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 see a moving display, but they could totally inhibit the response only after about 30s, 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.

PERCEPTUAL JUDGEMENTS WITHIN THE EXOCENTRIC FRAME

Information about the position, orientation and movement of the body in inertial space is provided by the normally stationary visual surroundings, by proprioception and by the otolith organs and semicircular canals of the vestibular system. The otolith organs respond to the pitch and roll of the head with respect to gravity but provide no information about the 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 semicircular 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 signal from the canals can provide information about the position of the body but only with respect to a remembered initial position.

Vection

Vection is an illusion of self motion induced by looking at a large moving display. For instance, illusory self rotation, or circularvection, 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 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). Judgements about the motion of the self with respect to an external frame of reference are semi-exocentric judgements since they involve an external frame and a reference to the self. 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.

Vection for different postures and axes of rotation

If the vection axis is vertical, the sensation of self rotation is continuous and 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 et al. 1975). There are three vection axes with respect to the body (yaw, roll and pitch) and in each case the vection axis can be either vertical or horizontal. Of these six stimulus conditions only three had been investigated. We decided to measure vection and illusory body tilt under all six conditions (Howard et al., 1987). The subject was suspended in various postures within a large sphere that could be rotated about a vertical or horizontal axis. The magnitude of vection and of illusory body tilt were measured for yaw, pitch and roll vection for both vertical and horizontal orientations of each axis (see Figure 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 illusory body tilt was about 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 et al. 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 subjects were primed to expect that their bodies might really tilt. In most subjects, illusory backwards tilt accompanying by pitch vection was much stronger than illusory forward tilt. Only two of our 16 subjects showed the opposite asymmetry, that was also reported by Young et al. (1975).

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 et al. (1975) found that vection was not affected by stationary objects in front of the moving display but was reduced when the objects were 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 et al. (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 their appearance.

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 circular vection 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 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. Furthermore, vection sensations are not 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, and this is detected just as well by retinal image motion as by motion of the eyes.

Vection and the central-peripheral and near-far placement of stimuli

It has been reported that circular vection is much more effectively induced by a moving scene confined to the peripheral retina than by one confined to the central retina (Brandt et al. 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 weak vection evoked by it.

Howard and Heckmann (1989) 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 54° by 44° 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 15cm in front of or 15cm 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 $30^\circ/\text{s}$ 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 circular vection.

The results are shown in Figure 3. They reveal that vection was driven better by the peripheral stimulus acting alone than by the central stimulus acting alone. Indeed it was driven just as well by a

moving peripheral display with the center black or visible and stationary as by a full-field display. However,vection was reduced when the central display moved in a direction opposite to that of the peripheral display. When the peripheral display was visible but stationary the direction ofvection was determined by the central display but only when it was 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 moving central display was nearer than the stationary surround, a small amount ofvection was evident in the same direction as the motion of the central display. We believe that the motion of the center induced apparent motion in the stationary surround, which in turn causedvection. We call this 'induced-motionvection. These experiments are a confirmation and extension of experiments conducted by Howard et al. (1987).

Induced Visual Motion, an Oculocentric, Headcentric and Exocentric Phenomenon

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. In a commonly studied form of induced motion the stationary object is seen within a frame which moves from side to side. In this stimulus configuration the moving frame changes in eccentricity and this may be responsible for some of the illusory motion of the stationary object. In order to study the effects of relative motion alone it is best to present the stationary object on a large moving background that either fills the visual field or remains within the confines of a stationary boundary.

We have evidence that induced visual motion occurs within the oculocentric, the headcentric and the exocentric system and that the mechanisms in the three cases are very different. As an oculocentric effect, it could be due to contrast between oculocentric motion-detectors. As a headcentric effect, it could be due to misregistration of eye movements. This could occur in the following way. Optokinetic nystagmus (OKN) induced by the moving background is inhibited 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 available, this should create an illusion of movement in a direction opposite to that of the background motion. This explanation, which I proposed in Howard (1982, p. 303) is analogous to that proposed by Whiteside et al. to account for the oculogyral illusion. It has been championed more recently by Post, and Leibowitz (1985), Post (1986) and Post and Heckmann (1986).

Induced visual motion can also be an exocentric illusion. It has been explained above 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.

We have recently devised psychophysical tests which can be used to dissociate the oculocentric, headcentric and exocentric forms of induced visual motion. These tests will now be described.

The key to measuring the oculocentric component of induced visual motion is to have two inducing displays moving in opposite directions, with a stationary test object on or near each. 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. The apparent velocity of this induced motion was only about 0.1°/s. This display is not ideal for measuring oculocentric induced visual motion since the outward and inward motion of the two induction lines mimics visual looming produced by forward body motion. An outwardly expanding textured surface is known to induce forward linear vection (Andersen and Braunstein, 1985; Ohmi and Howard, 1988).

A better stimulus for measuring oculocentric induced visual motion is that shown in Figure 4a. The two inducing stimuli move in a shearing fashion which does not mimic visual looming. If the gaze is directed at the boundary between the two moving displays, neither optokinetic nystagmus nor vection should occur. Any perceived relative motion between the two test spots must reflect oculocentric induced motion since headcentric or exocentric induced motion would affect the two objects in the same way. The task of judging the relative velocity of the test spots is simplified by using a procedure described by Wallach et al. (1978). The two test spots were moved vertically at a velocity of 2°/s with periodic fast returns and subjects estimated the apparent inclination of the path motion of one spot relative to that of the other spot. The apparent direction of motion of each spot is the resultant of its actual vertical motion and its apparent horizontal motion. With this display we have found the velocity of oculocentric induced motion to be about the same as that reported by Nakayama and Tyler.

The next step is to isolate the headcentric component of induced visual motion. Since the oculocentric component is confined to the region of the inducing stimulus, placing the test dot on a black band, as shown in Figure 4b, ensures that this form of induced motion will not occur. Again subjects judged the apparent slant of the path of a vertically moving spot, but this time pursuing it with the eyes. In a series of experiments we have shown that the apparent slant of the track is determined by headcentric induced motion and is not influenced by exocentric induced motion. This is probably because the frame of reference for judging the vertical is carried with the illusory motion of the body. The magnitude of headcentric induced motion was found to be about 2°/s, which is considerably larger than oculocentric induced motion (Heckmann and Howard, 1989; Post and Heckmann, 1986).

Finally we measured exocentric induced visual motion by having subjects estimate the velocity of illusory self motion induced by the motion of a large moving display. By definition this is a measure of the exocentric induced visual motion. People readily experience 100% vection at stimulus velocities of up to 60°/s and stationary visual objects appear to move in space at the same velocity as the apparent movement of the body. Thus exocentric induced visual motion can be many times larger than headcentric induced motion which in turn is several times larger than oculocentric visual motion.

The task of distinguishing between oculocentric, headcentric and exocentric components of any perceptual phenomenon and the task of discovering which sensory or cognitive processes may be responsible for a given phenomenon, require tests and procedures specifically designed for each case.

REFERENCES

- Andersen, G. J. and Braunstein, M. L. (1985) Induced self-motion in central vision. *J. Exp. Psychol., Hum. Percept. Perform.*, 11, 122-132.
- Barr, C. C., Schulthies, L. W. and Robinson, D.A. (1976) Voluntary, non- visual control of the human vestibulo-ocular reflex. *Acta Otolaryngol.*, 81, 365-375.
- Benson, A. J. and Barnes, G. R. (1978) Vision during angular oscillation: The dynamic interaction of visual and vestibular mechanism. *Aviat. space environ. Med.*, 49, 340-345.
- Brandt, T., Dichgans, T. and Koenig, E. (1973) Differential effects of central versus peripheral vision on egocentric and exocentric motion perception. *Exp. Brain Res.*, 16, 476-491.
- Brandt, T., Wist, E. R. and Dichgans, J. (1975) Foreground and background in dynamic spatial orientation. *Percept. Psychophys.*, 17, 497-503.
- Cohen, H. B. (1966) Some critical factors in prism adaptation. *Amer. J. Psychol.*, 79, 285-290.
- Duncker, K. (1929) Uber induzierte Bewegung. *Psychol Forsch.*, 22, 180-259.
- Fredrickson, J. M. and Schwan, D. W. F. (1977) Vestibulo-cortical projection. In R. F. Naunton (Ed.) *The Vestibular System*. New York: Academic Press, pp 203-210.
- Graybiel, A. and Hupp D. I. (1946) The oculo-gyral illusion. *J. Aviat. Med*, 17, 3-27.
- Heckmann, T. and Howard, I. P. (1989) Induced visual motion: dissociation of exocentric and head-centric components. *Invest. Ophthal. Vis. Sci.*, 30 (ARVO Abs.), 323.
- Held, R., Dichgans, J. and Bauer, J. (1975) Characteristics of moving visual areas influencing spatial orientation. *Vision Res.*, 15, 357-365.
- Held, R. and Rekosh, J. (1963) Motor-sensoly feedback and geometry of visual space. *Science*, 141, 722-723.
- Hill, A. L. (1972) Direction constancy. *Percept. Psychophys.*, 11, 175-178.
- Howard, I. P. (1982) *Human Visual Orientation*. Chichester; Wiley. pp 388-397.
- Howard, I. P. and Anstis, T. (1974) Muscular and joint-receptor components in postural persistence. *J. exp. Psychol.*, 103, 167-170.
- Howard, I. P., Cheung, B. and Landolt, J. (1977) Influence of vection axis and body posture on visually-induced self rotation and tilt. *Proceedings of the AGARD Conference on Motion Cues in Flight Simulation and Simulator Sickness*. Brussels.

- Howard, I. P., Giaschi, D. and Murasugi, C. M. (1988) Inhibition of optokinetic and vestibular nystagmus by head-fixed stimuli. *Exp. Brain Res.*, Submitted for publication.
- Howard, I. P. and Heckmann, T. (1989) Circular vection as a function of the relative sizes, distances and positions of two competing visual displays. *Perception*, in press.
- Howard, I. P., Ohmi, M., Simpson, W. and Landolt, J. (1987) Vection and the spatial disposition of competing moving displays. *Proceedings of the AGARD Conference on Motion Cues in Flight Simulation and Simulator Sickness*. Brussels.
- Kohler, W. and Wallach, H. (1944) Figural aftereffects: An investigation of visual processes. *Proc. Amer. Philos. Soc.*, 88, 269-357.
- McKinley, P.A. and Peterson, B. W. (1985) Voluntary modulation of the vestibuloocular reflex in humans and its relation to smooth pursuit. *Exp. Brain Res.*, 60, 454-464.
- Melvill Jones, G., Berthoz, A. and Segal, B. (1984) Adaptive modification of the vestibulo-ocular reflex by mental effort in darkness. *Brain Res.*, 56, 149-153.
- Morgan, C. L. (1978) Constancy of egocentric visual direction. *Percept Psychophys.*, 23, 61-68.
- Nakayama, K. and Tyler, C.W. (1978) Relative motion induced between stationary lines. *Vision Res.*, 18, 1663-1668.
- Ohmi, M., Howard, I. P. and Landolt, J. P. (1987) Circular vection as a function of foreground-background relationships. *Perception*, 16, 17-22.
- Ohmi, M. and Howard, I. P. (1988) Effect of stationary objects on illusory forward self motion induced by a looming display. *Perception*, 17, 5-12.
- Paap, K. R. and Ebenholtz, S. M. (1976) Perceptual consequences of potentiation in the extraocular muscles: An alternative explanation for adaptation to wedge prisms. *J. exp. Psychol.*, 2, 457-468.
- Post, R. B. (1986) Induced motion considered as a visually induced oculogyral illusion. *Perception*, 15, 131-138.
- Post, R. B. and Heckmann, T. (1986) Induced motion and apparent straight ahead during prolonged stimulation. *Percept. Psychophys.*, 40: 263-270.
- Post, R. B. and Leibowitz, H. W. (1985) A revised analysis of the role of efference in motion perception. *Perception*, 14, 631-643.
- Tomlinson, R. D. and Robinson, D.A. (1981) Is the vestibulo-ocular reflex cancelled by smooth pursuit? In Fuchs, A. and Becker, J. (Eds.) *Progress in Oculomotor Research*. Elsevier: North Holland.

Waespe, W. and Henn, V. (1978) Conflicting visual-vestibular stimulation and vestibular nucleus activity in alert monkeys. *Exp. Brain Res*, 33, 203-211.

Wallach, H., Bacon, J. and Schulman, P., 1978, Adaptation in motion perception: alteration of induced motion. *Percept. Psychophys.*, 24: 509-514.

Whiteside, T. C. D., Graybiel, A. and Niven, J. I. (1965) Visual illusions of movement. *Brain*, 88, 193-210.

Young, L. R., Oman, C. M. and Dichgans, J. M. (1975) Influence of head orientation on visually induced pitch and roll sensations. *Aviat. space and environ. Med.*, 46, 246-269.

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Table 1. Frames of Reference for Visual Spatial Judgements.

O signifies the object, the position or orientation of which is being judged or set
RF signifies the reference frame with respect to which the object is being judged or set

Frame of reference	Sensory components	Examples of tasks
Proprioceptive		
O and RF internal		
Non-visual	Sense of position of body parts	Point to the unseen toe
Purely visual	Locations of images of body parts	Align two seen parts of the body
Intersensory	Location of image plus proprioception	Point unseen finger to seen toe
Egocentric		
O external, RF internal		
Station point	Abstract or inferred	Specify objects visible from a vantage point
Retinocentric	Retinal local sign plus retinal landmark	Fixate an object. Place line on retinal meridian
Headcentric	Eye position + retinal local sign	Place an object in the median plane of the head
Bodycentric		
Purely visual	Relative retinal location	Align a stick to the seen toe
Intersensory	neck + eye position + retinal local sign	Point stick to the unseen toe. Place an object to left of the body
Semi-exocentric		
O internal, RF external		
Purely visual	Relative retinal location	Align self with two objects
Intersensory	Seen part of body and gravity senses	Point upwards
Exocentric		
O and RF external		
Absolute	Vision with appropriate reference frame	Judge geographical directions
Relative	Relative retinal location with appropriate constancies	Align three object. Judge the shape of an object
Intersensory	Visual and non-visual stimuli compared	Set a line vertical. point line to unseen sound

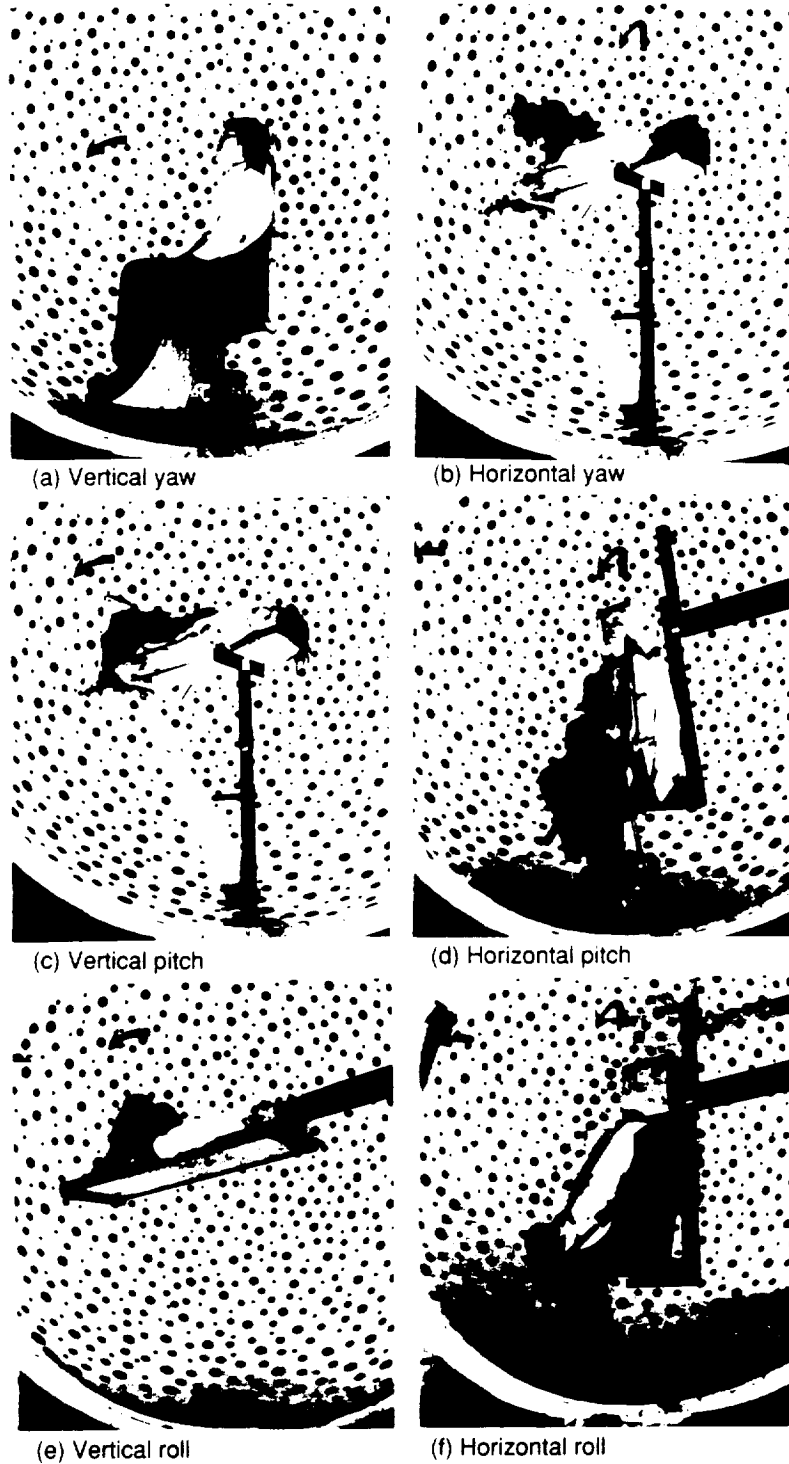


Figure 1. Stimulus conditions. Yaw denotes stimulus rotation about the mid-body axis, pitch about the y-body axis and roll about the visual axis. Vertical and horizontal refer to the orientation of the axis of scene rotation.

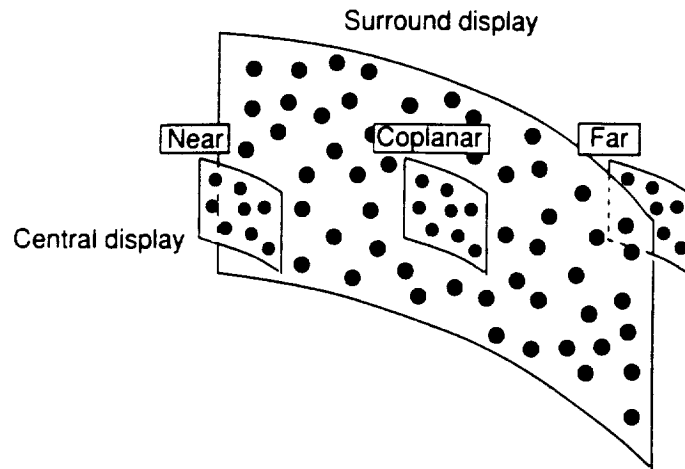


Figure 2. A diagrammatic representation of the displays used by Howard, Simpson and Landolt (1987) to study the interaction between central-peripheral and far-near placement of two displays in generating circularvection. The two displays could be moved in the same or in opposite directions, or one of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

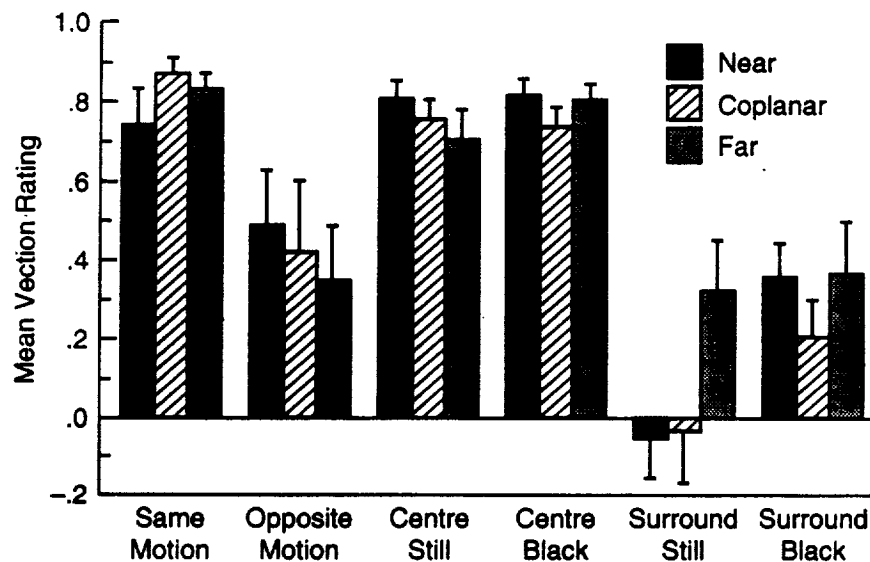


Figure 3. Mean vection ratings of nine subjects plotted as a function of the relative depth between the central and peripheral parts of the display and the type of display. A vection rating of 1.0 signifies full vection in a direction opposite to the motion of the display. When the two parts of the display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

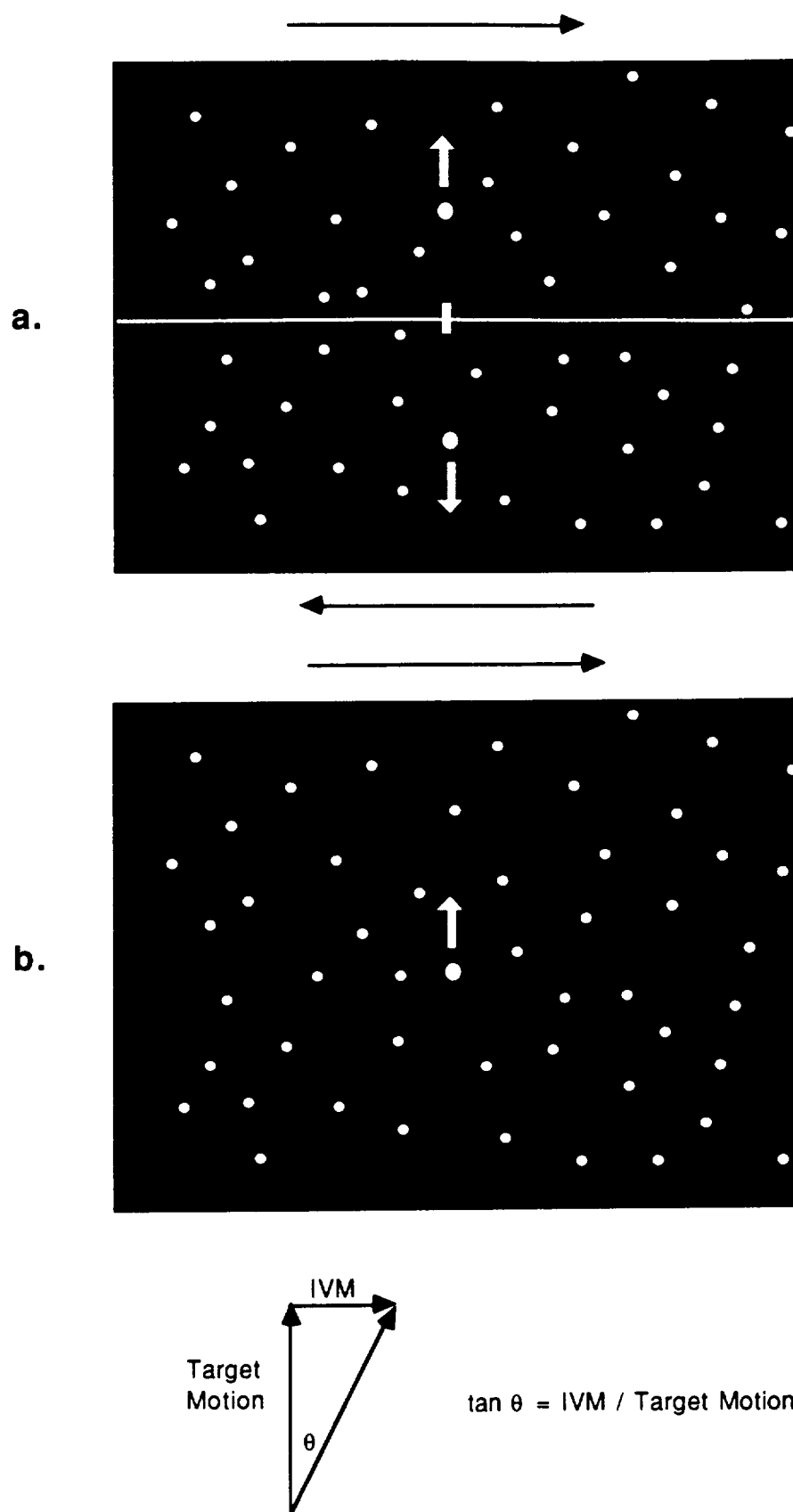


Figure 4. Stimuli for measuring components of induced visual motion: (a) Oculocentric component; (b) headcentric component.

