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Visual Motion Caused by Movements of the Eye, Head and Body

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1 VISUAL MOTION ON THE RETINA RESULTING FROM SELF MOTION

1.1 Uses and Problems

Most of the chapters in this book up to this point have considered the processing of visual movement seen by an eye that is stable in space. Of course this never happens. The eyes are always in motion and most retinal image motion is caused by movement of the observer. Compensatory eye movements can often reduce the retinal movement but can never remove it completely. This chapter discusses the visual consequences of self motion including all motions of the eyes in space. The eyes can move both under the influence of the extraocular muscles and as a consequence of head movement. The head in turn can move both under the influence of the neck musculature and as a consequence of body movement. Normally the eyes move as a consequence of a combination of these causes.

It is misleading to think of the retinal image as primary when considering visual perception. This notion is easily dispelled by comparing the small, inverted, optically-distorted and blood-vessel-interrupted retinal image with the pristine quality of visual experience. Self motion is particularly removed from its retinal origins since it is derived from many sensory sources and can even arise independently of visual information. The traditional view that self motion contributes a distortion to the retinal image which must be hidden from perception is misleading.

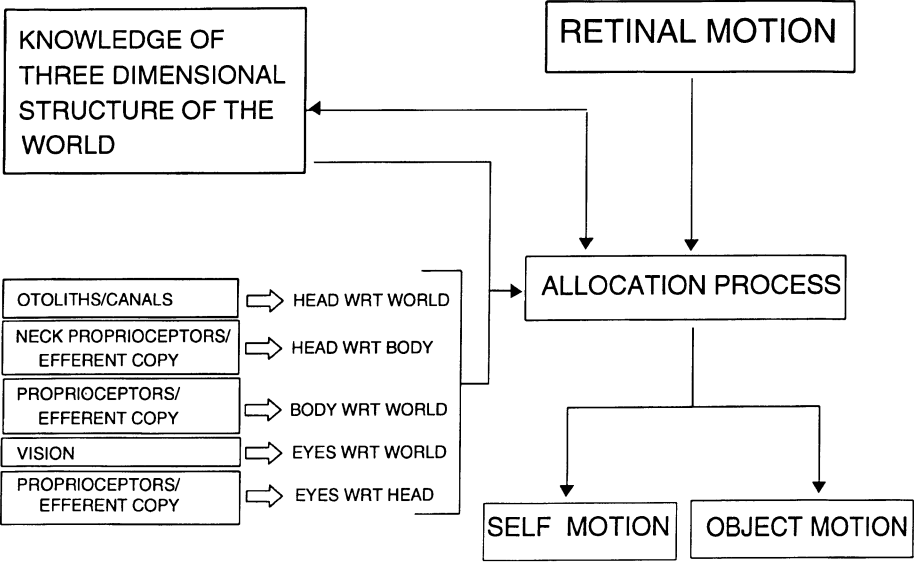Observers must distinguish between self- and externally-generated retinal motion to

Figure 1   The sources of information about self motion which can help in the allocation of retinal motion to self motion and object motion components. The various sources are shown as giving information with respect to (WRT) different reference frames. Information about the three-dimensional structure of the world is also required. There is a reciprocal relationship in which self motion helps in obtaining three-dimensional structure information and three-dimensional structure helps in obtaining self motion information.

use and perceive retinal motion appropriately. Three basic sources of information about self motion are available during natural movement: the visual consequences, the motor commands and signals from proprioceptors (Figure 1). Care must be taken to distinguish information that is *present* and information that is *used.*

Once retinal motion is attributed to self motion, it can provide important information about that self motion. This is *proprioceptive vision* (Simpson *et al.*, 1988a, 1988b; Nakayama, 1985; Harris & Jenkin, 1993). The same retinal motion is also important for determining the three-dimensional structure of the world: a topic which is beyond the scope of this chapter (see Regan, 1991, for a recent review). These concepts are interactive since a knowledge of the three-dimensional structure of the world is needed to interpret self motion information and vice versa.

1.2   Coordinate Systems, Units and Vectors

Understanding the consequences of self motion requires using appropriate coordinate systems and units. The literature is often confusing on this point with often one system used to describe visual movement but another to describe the self movement that created it. A coordinate system requires a reference frame and a geometry within that frame. Possible reference frames include the retina, the head, the body or some part of

external space. Possible geometries include the familiar Euclidean or Cartesian system of three orthogonal axes. This geometry is an arbitrary and biologically-implausible choice (Simpson et al., 1981, 1988a) and biological axes are much more likely to be non-orthogonal and non-linear. There is no 'correct' solution and representations in one system can always be converted into another. Often additional information is required for the conversion, however. For example, converting information relative to the retina into a head-referenced system requires information about the position of the eyes in the head. Schemes that claim to be 'independent of coordinate systems' (e.g. Viirre et al., 1986, p. 446) are misleading, merely referring to convenient mathematical techniques for moving between systems.

The choice of units is equally important. The motion of each eye in space is a combination of rotation and translation. The speed of rotation is the rate of change of angle (e.g. degrees/second) whereas the speed of a translation is the rate of change of distance (e.g. metres/second). Notice that neither of these units (or the units of angle, distance or time that make them up) is likely to have linear biological counterparts. Translational velocity can only be calculated using extraretinal information.

When talking about rotations, the terms 'horizontal', 'vertical' and 'torsion' are inherently inappropriate and reflect historical attempts to represent three-dimensional rotations on two-dimensional paper. A convenient method that avoids some of the pitfalls of these terms (see Tweed & Vilis, 1987; Carpenter, 1988) is to express the rotation as being about an axis of specified orientation. This is called a vectorial representation. Vectors can be usefully used not only to describe the rotation of the eye or head, but also when describing the retinal consequences (see Figure 2).

1.3   Allowing for the Contribution of Eye Movements

Dealing with self-generated sensory information is not a problem unique to vision; it is a general problem of all sensory systems. Distinguishing self-produced from external sounds is a similar problem. Once self-generated sensory stimuli have been identified, a possible way to handle them is to remove or 'cancel' them from the percept leaving any activity of external origin uncontaminated (Von Holst & Mittelstaedt, 1950).

When self- and externally-generated components are independent, as they are for sounds, removing the contribution of internally-generated stimuli is indeed often appropriate. For vision, however, the self-generated and external aspects of the retinal image interact: which external object features are present on which parts of which retina depends on the self-generated movements. The interaction between the internal and external components contains important information for interpreting both the internal and external generators. Although retinal image motion as a consequence of self motion presents a problem for clear vision and a challenge to interpretation of the image, simply 'cancelling' it and pretending that nothing has happened is not a valid solution – things that it is important to know about *have* happened. For example there might have been changes in the direction of heading. New areas of the visual scene might have come into view and so on.

A simple subtraction process of the motion of the eye from the retinal motion, as was implied by Von Holst and Mittelstaedt (1950), cannot in any case be adequate. Consider the coordinate and the unit systems involved. It is the eye movements in

three-dimensional space including both angular and linear components that need to be taken into account in the interpolation of the complex visual movement arising simultaneously on two retinae.

1.4   How Well Does the System Need to Work? Tolerance of Retinal Image Slip

Carpenter (1988), using Green and Campbell's (1965) data, calculates that visual acuity should be degraded by the equivalent of 2 dioptres of myopia for a 1 d/s movement. Potential visual degradation is often cited as a *raison d'être* for compensatory eye movements: to maintain a stable retinal image. When the head is kept still, image motion can be kept down to about 0.5 d/s by compensatory eye movements (Skavenski *et al.*, 1979). However, during normal head movement, image slippage, even at the fixation point, is often in excess of 5 d/s (Steinman & Collewijn, 1980; Steinman & Levinson, 1990; Sperling, 1990). Omnipresent retinal slip generates two obvious questions: Why is vision not degraded? And why is the image movement unnoticed?

Self-generated retinal slip does not seems to degrade vision as much as it should (Murphy, 1978; Westheimer & McKee, 1975, 1978; see Steinman & Levinson, 1990, for a comprehensive review). Movement of the image due to self motion alters the contrast sensitivity function (CSF): high spatial frequencies require more contrast to be detected and lower spatial frequencies are easier to see (Steinman *et al.*, 1985). The changes may actually be beneficial to vision (Tulunay-Keesey & VerHoeve, 1987). Compensatory eye movements may keep or introduce desirable movement, especially enhancing the visibility of large objects (Skavenski *et al.*, 1979; see Carpenter, 1991). The changes to the CSF during active motion are less pronounced than when the same movement is externally generated (cf. Steinman *et al.*, 1985; with Kelly, 1979).

There seems to be a general depression of motion sensitivity that accompanies self motion. Reduction in sensitivity is a well-known correlate of saccadic eye movement (where it is called saccadic suppression: section 2.5.2.1) but the reduction actually occurs during all types of self motion (see, for example, section 4.4). Physical factors such as blur and relative motion have an effect, but the extent of the difficulty of seeing object motion indicates a central suppression mechanism. It seems that detection of one kind of motion (self motion) affects the ability to detect other kinds of motion (object motion). Such an interaction suggests a common mechanism for *all* motion detection arising from both visual and non-visual sources.

2   HANDLING RETINAL MOTION DUE TO EYE MOVEMENT ALONE

The centre of rotation of the eye is essentially fixed in the head (but see Harris *et al.*, 1993a), and therefore, if the head does not move, the only movements of the eye with respect to the head, body or space are pure rotations. The sources of information which might be used to determine whether image motion was caused by eye rotation in the head are vision, efference copy of eye movement commands and proprioception from the extraocular muscles.

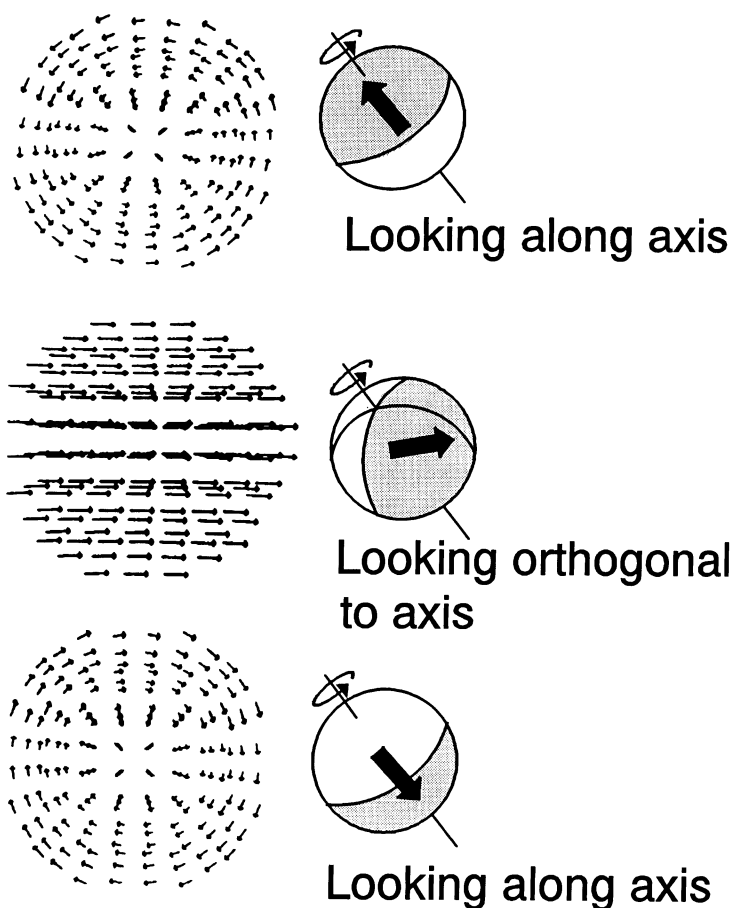Different perceptual tasks have different uses for eye movement information. The

Looking along axis

Looking orthogonal to axis

Looking along axis

Figure 2 The optic flow associated with pure rotation of the eye. On the left side of the figure, the small arrows trace out the paths of dots equally spaced in the visual field. The three circles are planar projections of the hemispherical view looking in different directions with respect to the axis of rotation. The views are shown shaded on the right-hand side of the figure. Describing the rotation needs only an instantaneous representation of the orientation of the axis and the velocity of rotation: a vectorial description. When looking along the axis (top and bottom sections of figure), the movement in the centre of the field is pure rotation, there is no translation of these features across the retina. When looking orthogonal to the axis of rotation (centre section), the motion in the centre of the field is pure translation. These planar projections of three dimensional events need careful interpretation. Remember that *the observer is at the centre of the circles* (in the plane of the paper). The arrows at the top and bottom of the centre circle represent the movement of dots pointed to by the axis of rotation: the same movement that is represented in the centre of the upper and lower circles. Similarly the arrows around the edges of the top and bottom circles represent the movement orthogonal to the axis: the same movement that is represented by the arrows in a horizontal line through the centre of the centre circle (left-hand side redrawn from Andersen, 1986, p. 54).

perception of a stable world needs to take into account the resulting position change. The perception of object movement during pursuit needs to take into account the eyes' velocity. The nature of the signals that drive smooth pursuit is considered in the chapter by Krauzlis. Eye-in-orbit information is important when the head *is* free to move too, in order to distinguish eye rotation from that of the head or body. Rotations of each of these have different perceptual and practical problems associated with them.

Optokinetic responses (OKN) to full-field motion normally represent the response to the visual consequences not of an eye movement but of a head movement. OKN is therefore considered below under head movements (section 3).

2.1   Visual Cues Concerning Eye Movement

The obvious visual cue that suggests that retinal motion was caused by eye rotation is that the entire field moves together at the same speed.[1] All parts of the field have a constant angular velocity added on to any existing movement. Because the retina is hemispherical, images from different parts of the visual field have different retinal motions depending on their visual direction with respect to the axis of rotation. The part of the image directly orthogonal to the axis translates across the retina whereas those parts of the image at the ends of the axes rotate and do not change their retinal locus (Figure 2). Full-field rotation above 0.5 deg/s is perceived by a stationary observer and the orientation of the axis can be judged to within 5 deg (Harris & Lott, 1993).

2.2   Efference Copy Describing Eye Movements

Evidence for the use of an efference copy of the motor signals controlling eye movements (Helmholtz, 1866; Sperry, 1950) is largely circumstantial. Other sources of information might be too slow. There is some evidence that compensation for saccadic eye movement commences before the movement itself (Duhamel *et al.*, 1992). However, the visual world is not very stable actually during eye movements: vision is suppressed during fast saccades and the world often seems to move around all over the place during slower pursuit movements.

A theoretical reason for proposing an efference copy is for engineering stability in the control of eye movements. Making an internal comparisons between the intended movement and the movement-carried-out-so-far allows an eye control system to function at high gain and therefore helps make fast and accurate eye movements

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[1] Actually, since the nodal point of the eye lies some 6.2 mm in front of the centre of rotation of the eye (Alpern, 1962), the consequences of even a pure rotation of the eye will be affected by translation of the nodal point. The effect of this translation depends on the distance of the object. For the image of an object at 25 cm, the displacement of the nodal point will alter the maximum velocity by 2.5% (cf. section 3.1. and Appendix A).

(Robinson, 1975; Guthrie *et al.*, 1983; Van Gisbergen *et al.*, 1981 but cf. Sparks, 1986).

For an efference copy to be useful, either for eye movement control or for perceptual cancellation, it has to describe the relevant eye movement fully in three dimensions and each eye has to be dealt with separately since they might be doing different things. Using a vectorial representation of eye-in-head information to interpret visual (eye-in-space) information needs considerable sophistication and some extraretinal information. Furthermore, a record of position deduced by keeping track of continuous movements is extremely vulnerable to cumulative error.

2.3 Proprioception Describing Eye Movements

When skeletal muscles are pulled, various associated proprioceptors are activated including joint receptors and muscle spindles (see Matthews, 1982). These signals are important for skeletal muscle control. Some component of the signal probably represents limb position and may underlie the sense of where limbs are in space (Roll *et al.*, 1991a,b). Using the proprioceptor system of skeletal musculature as an analogy, oculomotor proprioceptors have been proposed as a source of eye position information (Sherrington, 1918). The eye's motion is very different from the essentially one-dimensional movement of a hinged skeletal muscle joint, however, and the problem of defining reference points from which to describe the eye's position is formidable. The distribution and variation in type of proprioceptors in the oculomotor muscles is rich and unusual (Spencer & Porter, 1988) and there is a massive representation of oculomotor proprioception throughout the brain (Abrahams & Rose, 1975; Donaldson & Long, 1980; Batini *et al.*, 1974; Kimura *et al.*, 1991). Circumstances suggest that proprioception might carry useful information about the activity of extraocular muscles (Steinbach, 1987). Whether extraocular proprioceptive information under normal conditions is related to eye position, dynamic eye movement control or both, is unknown.

2.4 Comparison of Proprioception and Efference Copy Contributions

A stable world is perceived during fixation periods between eye movements when visual, efference copy and proprioceptive information are all available (Howard, 1993). The relative contribution of these three cues during and between eye movements has traditionally been assessed by looking at each one alone. There has been little work on the use of vision in this context, perhaps because it has been seen as the problem rather than the solution.

During attempted eye movements under paralysis, an efference copy should be present but without visual or proprioceptive signals about eye movement. If efference copy were used then, under these circumstances, visual motion should be perceived, as the presumed motion of the eye is subtracted from the unexpectedly stable image. Early experiments reported just such a phenomenon (Mach, 1886; Brindley & Merton, 1960; Kornmüller, 1931). But careful repetition, ensuring *complete* paralysis, found no illusory visual movement during attempted eye movements (Brindley *et al.*, 1976;

Stevens *et al.*, 1976). The expected brisk illusory motion of a stabilized image during normal saccades is also not experienced (Grüsser *et al.*, 1987). It seems that some other relevant signals are required to make use of an efference copy.

Pulling the eye around can be sensed without vision, presumably from proprioceptive information (Skavenski, 1972). By carefully manipulating an occluded eye with a finger while the unobstructed eye viewed a small fixation point in a dark room, Gauthier *et al.* (1990a, 1990b) and Bridgeman and Stark (1991) claimed, rather improbably, to be able to evoke the same proprioceptive inflow as might accompany a natural movement. Poked eye movements were perceived as 16% to 25% of their actual sizes. Pushing on the uncovered eye evoked both efferent (resisting the push) and afferent activity from which the efferent-only contribution could be calculated as indicating movement of 61% of the actual movement (Stark & Bridgeman, 1983, Bridgeman & Stark 1991). Bridgeman and Stark (1991) suggested that proprioceptive and efferent information might be additive although it is unclear what advantages such a combination might impart.

A dim spot fixated in front of a dark background appears to drift around ('*autokinesis*', Aubert, 1887; see Howard, 1982). Although a comprehensive explanation of autokinesis is lacking, the phenomenon suggests that, in the absence of both efference copy of movement commands and visual information, proprioceptive knowledge about eye position is inadequate to achieve visual stability.

2.5   Does it Work? How Good is Vision During Eye Movement?

There are two consequences of the successful division of the visual signal into internally- and externally-generated components. Firstly, the perceptual stability of the world is not disrupted by eye movements. Secondly, external object movement can be discerned during eye movements.

2.5.1   Judging eye position and world stability

The retina only has good resolution in the fovea. Knowledge of where the eyes are pointing compared with where they were pointing during previous fixations is required to relate sequentially foveated views in space. Knowledge of change-of-position, however, is not the same as knowledge about motion. Although position can be derived from motion, eye position is probably determined largely from information available when the eye is at rest (Howard, 1993). The eyes can be repositioned with an accuracy of 2–4 deg after a gaze change (Hansen & Skavenski, 1977; Lemij & Collewijn, 1989). This level of repeatability seems crude compared with our perception of features as being in precisely the same place every time we fixate them. But in fact target shifts of 2–4 deg during saccades are not detectable (Bridgeman, 1983).

Knowledge of eye position, even using visual, proprioceptive and efferent copy information, would be a very unreliable way to confirm that the world indeed did not move during saccades. Such a system would be fraught with missed movements and false positives.

2.5.2 Judging object motion perception during eye movements

2.5.2.1 During saccadic eye movements

One of the most obvious things about visual perception during saccades is that it is suppressed (Volkmann et al., 1978; Volkmann, 1986; Matin, 1974). Whilst a lot of the reduction in visual sensitivity can be attributed to the optical consequences of high-speed image movement (Carpenter, 1991), the effect is larger that can be accounted for by physical blur of the image, especially at low saccadic velocities (Burr et al., 1982) and some central suppression mechanism is required although its contribution during large saccades is 'feeble' (Carpenter, 1988). Here we are concerned with just one aspect: the ability to see motion during a saccade: that is, the success with which retinal and object motions can be disentangled.

The threshold for motion detection during saccadic eye movements increases linearly with both saccadic amplitude and velocity but is more closely correlated to amplitude (Bridgeman et al., 1975). Interestingly it does not matter which direction the displacement is in (Bridgeman & Stark, 1979; Ilg & Hoffmann, 1993) suggesting a generalized loss of sensitivity comparable to that seen during other self motions. The phenomenon may be explainable entirely by the high retinal speeds (and thus difficult discriminations) involved. Identical retinal stimuli were not compared in the eye moving and in the eye stationary controls. Brooks et al. (1980) found that when saccadic retinal velocities were accurately simulated on a stationary eye, motion discriminations were comparable to those during actual saccadic movements. More experiments and detailed reporting of the stimuli used is required before firm conclusions can be made about what happens during and following a saccade.

2.5.2.2 During smooth pursuit eye movements

How well is motion of the visual image that results from smooth pursuit eye movements compensated for? The question has two aspects: how well can we perceive the external motion of a pursued target and how well can we ignore (that is, assign to the consequence of the tracking eye movement) the retinal movement of everything else?

Two sources of information contribute to identifying the motion of a pursued object: (i) the visual movement of the object relative to its background and (ii) knowledge about the pursuit eye movement. The perceived speed of a pursued target moving in the fronto-parallel plane is only about 70% of the perceived speed of the same target when it is not pursued. The reduction of perceived velocity is independent of the presence of a background and is known as the *Aubert–Fleischl phenomenon* (Fleischl, 1882; Aubert, 1886, 1887; Gibson et al., 1957; Dichgans et al., 1969, 1975; Mack & Herman, 1972, 1973, 1978). The phenomenon suggests that efference copy and proprioceptive information about smooth pursuit together underestimate the eye velocity. Alternatively, estimates of the speed of targets that are not pursued may be too fast.

Judgements of *external* target movement should be in *linear* terms (m/s). The conversions from either the angular retinal velocity of targets that are not pursued or the angular eye velocity associated with targets that are pursued, to external linear movement requires distance information (see Gogel, 1982 and Appendix B). Perhaps the two assessments are equally accurate in angular terms but differ in their access to distance information. Targets presented during smooth pursuit can be hit accurately (Hansen, 1979) suggesting that at least some levels of perception can do the job.

And what of the other side of the coin, the appearance of the background?

If you move your finger back and forth at arms length, and follow it with your eyes, the appearance of the background is actually rather hard to describe. It appears to move, yet we know it isn't really moving; whereas during a saccade we have no sense at all that anything has moved except our gaze.

<div align="right">Carpenter (1988) p. 333</div>

The illusory movement of a stationary background as a pursued target passes in front of it is known as the *Filehne effect* (Filehne, 1922). The phenomenon is compatible with the velocity of pursuit eye movements being underestimated (Mack & Herman, 1973, 1978; Wertheim & Bles, 1984; Wertheim, 1985). If the eyes pursue a target accurately but are registered as moving at only 70% of their true velocity then the perceived target movement cannot account for all the relative motion present. The remaining 30% must be due to external movement.

Wertheim (1981), measured thresholds for imposed movement of the background during smooth pursuit. He found that background drift up to 10–15% of the eye velocity could not be distinguished from stationary backgrounds. Even suprathreshold movements of the background in either direction were underestimated (Wertheim & Van Gelder, 1990).

Taken together these observations suggest that knowledge of eye movements is used in the perceptual process. Vision, efference copy and proprioception contribute but the process is imprecise to say the least. The retinal motion that is actually due to eye movement but that is not attributed to this cause should be interpreted as indicating alarming movement of the outside world. Normally the problem is solved by suppression.

3   HANDLING RETINAL MOTION DUE TO HEAD ROTATION

The head's axis of rotation cannot pass through both eyes[2] and so head rotation, even with the rest of the body still, causes both rotation and translation of the eyes. Rotation and translation have their own distinctive retinal consequences. *Both* have to be correctly attributed to the head rotation that caused them in order to reveal any remaining motion of external origin.

During head rotation, some sources of information in addition to vision and oculomotor afferents and efferents are potentially available. These include (i) activity of the vestibular system, (ii) activity of neck proprioceptors, (iii) an efference copy of instructions to move the head and possibly (iv) activity of an efference copy of compensatory eye movement control signals. The possible existence of the latter signal does not necessarily follow from the existence of an efferent copy of pursuit and saccadic eye movements (Bedell, 1990).

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[2] The only exception, rotation about a horizontal axis through the centres of rotation of both eyes, actually does not occur naturally. The natural axis for pitch rotations of the head lies well behind the eyes and so even pitch of the head is normally associated with eye translation.
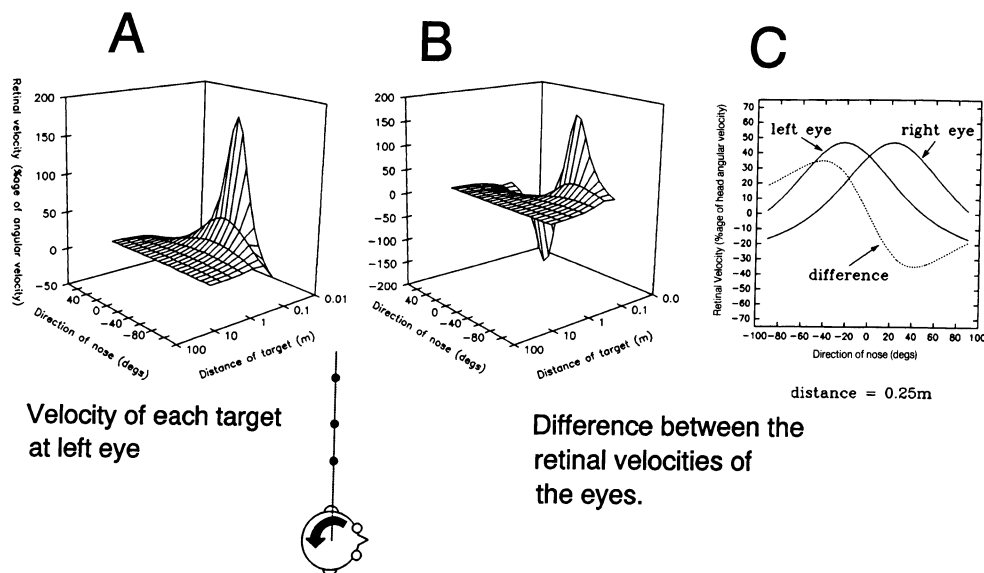
A

B

C

Velocity of each target
at left eye

Difference between the
retinal velocities of
the eyes.

distance = 0.25m

Figure 3   The angular retinal velocity introduced by the linear component of an angular head movement (see Appendix A for derivation). These retinal velocities are *in addition* to those due to the angular velocity. The velocity depends on the distance and eccentricity of each point and is plotted here as a percentage of the angular head velocity for objects from 0.125 to 8 m distant as the head sweeps through 180° as shown in the insert. *Panel A* shows a 3D plot of the effect of eccentricity and distance for objects seen with the left eye. Notice that at 12.5 cm (the closest object distance shown), the *additional* velocity reaches some 150% of the angular velocity when the object is in the direction pointed to by the line joining the eye and the centre of the head's rotation. Thus, during a head velocity with a peak of 200 deg/s, an object at that distance and eccentricity would have an angular velocity of 500 deg/s at the eye. *Panel B* plots the difference between the two eyes for the same X/Y values as panel A. There are dramatic differences (up to around 150% of the angular velocity or up to 300 deg/s for a 200 deg/s head movement) at quite modest eccentricities for close (0.125 m) targets. *Panel C* plots the retinal velocity for each eye and the difference between them for one distance (25 cm). At this distance the retinal velocities reach almost 50% of the head velocity. Thus, if the head had an angular velocity of 200 deg/s, corresponding to taking 900 ms to traverse the horizontal axis (from + to − 90 deg), the peak angular velocity in each eye (ignoring any compensatory eye movement) would be close to 300 deg/s and the difference would be about 70 deg/s alternating from fastest in the left eye as the object lined up with that eye to fastest in the right eye when the object lined up with that eye some 44 deg further on in the head movement. The difference between the two eyes would be zero when the object lined up with the subject's nose. Notice also that the angular speed of the object is actually reduced by the linear component at eccentricities greater than about 45 deg. (Interocular distance: 6 cm; eyes to centre of head rotation: 8 cm.)

3.1   Visual Cues Concerning Head Rotation

During a head rotation, the motion of each point on each retina is the vector sum of motion due to rotation and the motion due to translation of the eyes. The rotation component is equivalent to rotation around an axis passing through the eye, parallel to the head's rotation axis (see section 2.1 and Figure 2).

The direction of the translation component is tangential to the circle described by the movement of the eye in space and it follows that the direction is therefore *different for each eye* (Figure 3). The translation speed depends on the distance between the axis of rotation and the eye and on the rate of rotation.

The retinal consequences of translation depend on target distance. Since distance is not available from the retinal image, even from both retinal images, it follows that the direction and speed of eye translation cannot be deduced from retinal image movement alone. Objects at different distances have different retinal velocities generated by the translation component of head rotation which can be conveniently expressed as a percentage of the head rotation velocity (Figure 3). When the distance between the object and eye is large relative to the distance between the eye and the axis of rotation, this component of image movement during head rotation becomes negligible. The retinal velocity of distant points is determined exclusively by the angular rotation (see Figure 2). At close viewing distances the effects of the translation of the eye associated with head rotation can be dramatic (Figure 3, Appendix A).

Since the distances from a given point to each eye are usually different, the retinal velocities, as well as the translation direction, are usually different in the two eyes for each point (Figure 3C).

3.1.1 Assignment of visual motion to self motion (circularvection)

Visual motion compatible with head rotation often evokes the sensation of physical rotation even when the observer is stationary (*circularvection*: Mach, 1875; Fischer & Kornmüller, 1930; Howard, 1982). Circularvection can be used as an indicator of when visual movement is attributed to head rotation. Contrary to intuition, it is not necessary for a large part of the field to move (Brandt *et al.*, 1973) provided that the moving area is perceived as the background (Ohmi & Howard, 1987; Howard & Heckmann, 1989).

The speed of perceived circularvection, for a given angular velocity, depends on the perceived distance of the evoking stimulus (Wist *et al.*, 1975). The rate of head rotation during circularvection is derived from a retinal image whose movement, were it genuinely generated by a head rotation, is partly due to the rotation component and partly to the consequent translation of the eyes. Misperception of the relative contribution of translation arises from a misperception of depth. More systematic studies of the roles of the rotational and translational components of head rotation are needed.

3.2   Vestibular Cues Concerning Head Rotation

The vestibular system is an important proprioceptive sense for monitoring head movement. The system comprises two parts, the semicircular canals which transduce angular accelerations, and the otolith organs which transduce linear accelerations (see Benson, 1980; Wilson & Melvill Jones, 1979 for reviews)

3.2.1 Semicircular canals and head rotation

The semicircular canals provide important information about head rotation. Although the canals are activated by angular *acceleration*, they perform a mechanical integration so that they signal the head's angular *velocity* over the normal physiological range (Fernandez & Goldberg, 1971). There are three canals roughly orthogonal to each other and so the axis of rotation is mechanically broken down into three vectors. These three vectors are to some extent kept separate within the brain (e.g. vestibular nucleus; Curthoys & Markham, 1971) although there is convergence between signals coming from different canals (Baker *et al.*, 1984). Thus head rotation velocity and axis of rotation information are provided by the semicircular canal system during head rotation.

3.2.2 Otoliths and head rotation

The otolith system operates independently of the semicircular canals. Otoliths are sensitive to linear acceleration (Benson, 1980; Wilson & Melvill Jones, 1979). The system consists of arrays of hair cells that respond maximally when bent in a certain direction (Loe *et al.*, 1973). Thus, *which* hair cells respond provides the direction of an acceleration and *how much* they respond is related to the magnitude of the acceleration.

During a head rotation those otolithic hair cells tuned to directions radiating out from the rotation axis are activated by the centrifugal force. If the distance of the otoliths from the rotation axis were known, their activation under these circumstances could provide information about the rate, but not the direction, of the rotation. It is not known if this information is used when the axis is within the head, but when it is outside the head, as in eccentric rotation or as a component of curvilinear translation, the concurrent otolith activation does play a role (see section 4.4.1).

The otoliths can provide useful information about the rate and plane of head rotation when the axis of rotation is within the head but not orthogonal to gravity. Exactly which hair cells are most active at any one time depends on the head's orientation with respect to gravity. If the axis of rotation is tilted, orientation varies systematically as rotation proceeds. The associated ripple of otolith stimulation evokes strong compensatory eye movements in some species (monkeys: Raphan *et al.*, 1981; cats: Harris, 1987; Darlot & Denise, 1988) but not in man (Guedry, 1965; Harris & Barnes, 1985; Darlot *et al.*, 1988; Benson & Bodin, 1966).

3.3 Neck Muscle Proprioception and Head Rotation

Neck muscle proprioceptors might potentially provide head-on-body information although this system shares many of the difficulties of the extraocular proprioceptive system. The freedom of the head functionally to move in a ball-and-socket-like arrangement makes reference points difficult to define or discover. There is no monosynaptic reflex in neck muscles (Abrahams *et al.*, 1975a,b) suggesting an unusual innervation. Circumstantial evidence suggests that neck proprioceptors are

important since they are extensively represented in the brain (Boyle & Pompeiano, 1981a,b; Anastasopoulos & Mergner, 1982; Mergner *et al.*, 1985).

The contribution of neck proprioception to the sense of head movement and position has been investigated by holding the subject's head still in space and twisting the body beneath it (e.g. Mergner *et al.*, 1991) thus achieving the same relative displacement of the head-on-body as during a natural head movement. Visual, vestibular and efference copy sources are silent during these body-alone rotations. Eye movements and sensations of rotation are evoked which appear roughly in accord with the supposed head movement (*the cervico-ocular reflex*: Bles & Dejong, 1982). The difference between neck proprioceptor activity during these imposed neck twists and their activity during natural head movements, however, makes these experiments hard to interpret. Both vibratory stimulation of neck muscles (Biguer *et al.*, 1988; Roll *et al.*, 1991a,b) and rotation of the body beneath a stationary head (Mergner *et al.*, 1992a,b) causes illusory movements of a head-stationary visual target suggesting illusions of head movement (cf. section 3.5.2).

3.4   Efference Copy Concerning Head Rotation

Obviously, when the head is voluntarily rotated on the shoulders, motor command signals must be present in the brain. It might be useful to take an efference copy of these signals to act as a reference during movement control or to aid in assessing the direction of gaze in space. The use of efference copy for head movement control and monitoring has all the same problems as it does for eye movement control (difficulty of defining a frame of reference, cumulative error, etc.; cf. section 2.2). In addition, the head presents a potentially variable load to its muscles and so head position derived from the efferent commands is likely often to be inaccurate. Since the vestibular proprioceptive sense is so fast and effective (10 ms; Lisberger, 1984; Snyder & King, 1992) there can be little need for other sources of fast information about head position. One function of efferent copy of head motor commands might paradoxically be to keep track of the position of the *body* relative to the head since the primary spatial orientation detectors are in the head.

Predictable head movements evoke eye movements that are more efficient in their phase and gain relations to the visual stimulus than those evoked by unpredictable head movements (Barnes, 1991, 1992; Barnes & Lawson, 1992). This suggests that, at least under some circumstances, the oculomotor system can access a motor command in anticipation of the head movement.

3.5   Does it Work? How Good is Vision during Head Rotation?

The correct assignment of retinal movement to an ongoing head rotation allows the same two perceptual processes to occur that were potentially disrupted by movements of the eyes in the head. It allows the maintenance of perceptual stability of the world and the perception of external object motion despite the retinal movement that almost inevitably accompanies head movement.

Considerable extraretinal information is available concerning the head rotation.

Since a sensation of motion can be induced by vestibular information alone (see Benson, 1980), the canal signal might contribute centrally to the interpretation of visual movement. But it is important not to count the signal twice: if compensatory eye movements are effective at removing the angular component of the visual signal at source, then a central representation of the canal signal is only useful in providing a context for the remaining linear movements. Extraretinal distance information is essential since retinal movement of objects during translation of the eye depend on their distance from the eye. The dependence on distance has two consequences. Firstly, the accuracy with which motion can be interpreted as resulting from self motion depends on the accuracy of distance estimation as well as the accuracy of self movement estimation. And secondly, external object motion needs to be detected in the presence of many different retinal velocities associated with objects at different distances. These problems get worse in section 4 when unconstrained translations are considered.

3.5.1 The effect of eye movements compensatory for head rotation on retinal image motion

Head rotation causes retinal motion due to both the rotation and the associated translation of the eyes in space. Any contribution of rotation can theoretically be cancelled by ocular counter-rotation of appropriate speed and about the appropriate axis (with the caveat described in footnote 1). Complete removal of the angular component occurs when the vestibulo-ocular reflex (VOR) has unity gain (eye velocity output as a ratio of head velocity input). Although some animals routinely shown high gains to vestibular stimulation alone (e.g. cats: Harris, 1987; Blakemore & Donaghy, 1980), humans usually exhibit a much lower gain when measured in the dark (e.g. Barr *et al.*, 1976). The contribution of the VOR when other systems (e.g. vision) are present is more difficult to assess (Collewijn, 1989a, 1989b), but there is no doubt that, during natural active head rotation, the compensatory eye movements for the angular component are highly effective (light: Steinman *et al.*, 1985; dark: Tomlinson *et al.*, 1980).

Figure 3 shows that, due to the translation of the eyes during head rotation, the retinal images of objects at different distances have different angular velocities. Thus eye movements cannot completely stabilize the whole field at once. The background could be stabilized by counter-rotating the eyes at the rate of head rotation and any contribution of translation ignored. Alternatively the image of a particular target could be stabilized. Fixating a particular target results in retinal motion of the images of all features at other distances from the eye.

Even when fixating on distant targets, compensatory eye velocity does not perfectly compensate for retinal movement (Steinman *et al.*, 1985). But the distance of the target *is* taken into account and the speed of compensatory eye movements increases when closer targets are fixated (cats: Blakemore & Donaghy, 1980; monkeys: Viirre *et al.*, 1986; Snyder & King, 1992; humans: Biguer & Prablanc, 1981; Gresty & Bronstein, 1986; Hine & Thorn, 1987). Adjustment of eye velocity for target distance occurs in the dark and with too short a latency and at too high a speed for vision to play a role (Snyder & King, 1992; Snyder *et al.*, 1992). It is necessary to

postulate a central representation of target distance that can influence eye movements of vestibular origin.

The role of vision in generating eye movements that help maintain a stable image during head rotation may, under natural conditions, be restricted to long-duration, constant-velocity movements. Optokinetic eye movements experimentally evoked by full-field visual motion alone have two components, one which builds up quickly and another which builds up more slowly (Cohen *et al.*, 1977). The swift and efficient vestibularly-evoked response to head rotation does not usually require visual support (Miles, 1993) and leaves little role for vision. On the other hand the slow-build-up of a central representation of head velocity during long duration head rotation ('velocity store': Raphan *et al.*, 1979; 'delayed optokinetic nystagmus (OKN)': Miles, 1993) is ideally suited to smoothing over the inadequacies of the canals' response to long-duration stimuli.

To summarize: during natural head rotation, the motion due to the angular component can be effectively removed by the vestibulo-ocular reflex. The additional, distance-dependent translation component is also effectively removed for targets at the distance of regard but retinal movement of objects at other distances is inevitable and made worse by fixation of close targets.

3.5.2   *Judging object motion during head rotation*

Anecdotally, a swinging tree branch seems to move less if viewed while nodding or shaking one's head. Laboratory studies confirm this insensitivity: object movement as fast as 35% of the speed of self rotation is still perceived as earth-stationary (Wertheim & Bles, 1984; Wallach, 1985). The threshold for object motion is increased by up to three times during passive or active head movements (0.5–1.5 Hz: Probst & Wist, 1982; Probst *et al.*, 1986) and is also increased by circularvection or even just neck muscle stimulation (Probst *et al.*, 1986). Probst and his colleagues assumed that reflex eye movements kept the image completely stable during these measurements and therefore image motion on the retina could not contribute to the degradation. The retinal image is unlikely to be stable during head movements (see sections 1.4, 4.4.1) but the likely slippage seems unlikely to be enough to explain the considerable degradation reported: some kind of central suppression mechanism is required. There have been no supra-threshold measures of perceived velocity during head rotation.

Although motion sensitivity is reduced during head movement, an object that is actually observer-stationary seems to move slightly faster than the observer and in the same direction. The effect occurs with or without a background (*oculogyral effect*: Graybiel & Hupp, 1946; Elsner, 1971; Ross, 1974; Howard, 1982). During optokinetic stimulation a similar illusory movement of an observer-stationary target is seen (*induced motion*: Duncker, 1929). These illusory motions could reflect mis-estimates in the internal representation of reflex vestibular or optokinetic eye movements and their suppression by fixation (Raymond *et al.*, 1984; Whiteside *et al.*, 1965; Post *et al.*, 1984; Post & Leibowitz, 1985; Post, 1986 cf. section 2.5.2.2), but it is likely other factors are involved.

The targets associated with these illusory movements are observer-stationary, that is they are seen to be in orbit around the rotation axis and to be translating through space.

Their perceived linear velocity must be deduced from their angular velocity and perceived distance with respect to the centre of their orbit (not the eye). Mis-estimates of either of these parameters or errors in the deduction process will result in a mis-estimate of the target's linear velocity and might contribute to illusory movements.

Which of the various cues to head rotation is responsible for altering sensitivity to external motion? Is it that object motion detection is centrally attenuated (as during saccadic suppression) in response to the detection of head rotation? Or is all retinal motion channelled to the head movement processing system once a head movement has been detected and anything left over discarded (rather than being detected as object motion)? Or is it that the stimulus conditions are just too complex: object motion cannot be distinguished from or is masked by the other motion cues introduced by head rotation? The answers to these important questions await appropriate research programmes.

4   HANDLING RETINAL MOTION DUE TO BODY MOTION

Vision is an integrated part of behaviour. So the visual consequences of self motion normally include components due to movements of the eye, head and body together. Analysing retinal events during unrestrained body movement involves extracting the independent contributions of rotation and translation. Extracting each in the presence of the other, especially since some of each eye's translation is due to head rotation (section 3.1), is not trivial. The decomposition is important, however, because the components denote different things and need to be used differently. Rotation changes the visual direction of all objects except those at the end of the axis of rotation but does not change their distance from the centre of rotation. Translation changes the visual direction of all objects except those in the direction of travel and changes the distance to all points. Translation is also associated with various challenges to balance and locomotion guidance as well as the perceptual consequences of moving through the world.

Movements of the body generate extraretinal information that includes: (i) activity of the vestibular system, (ii) activity of proprioceptors from throughout the neck and body, and (iii) an efference copy of instructions to move the body.

Can these factors help interpret the movement of the retinal image due to body movement? How do they interact with information about eye and head rotations? Knowledge of head position in space contributes to the full description of the direction of the gaze in space needed to relate the location of a foveated point to other points in space.

4.1   Visual Cues Concerning Head Translation

The angular velocity of the image of each part of each object due to translation of the observer through space depends on its distance from the eye and the observer's speed and direction of heading with respect to that point. Since these parameters cannot be the same for any two points, translation introduces relative movement between the images of different objects on the retina (motion parallax). Since the parameters

cannot be the same for the two eyes' images of any single point in space, the angular velocity in each eye is different. The distribution of relative velocities within and between retinae contains useful information concerning the three-dimensional structure of space and the observer's movements within it (Regan & Beverley, 1979; Regan, 1992; see Chapter 12 by Cumming).

As an observer translates through space, objects move relative to the head and eye through an equal distance in the opposite direction. The movement produces a pattern of instantaneous velocities on the retina in directions that radiate out from the direction of travel. An example is given in Figure 6A and the velocities are plotted in detail in Figure 4 for points on a horizontal plane that transects the eyes during
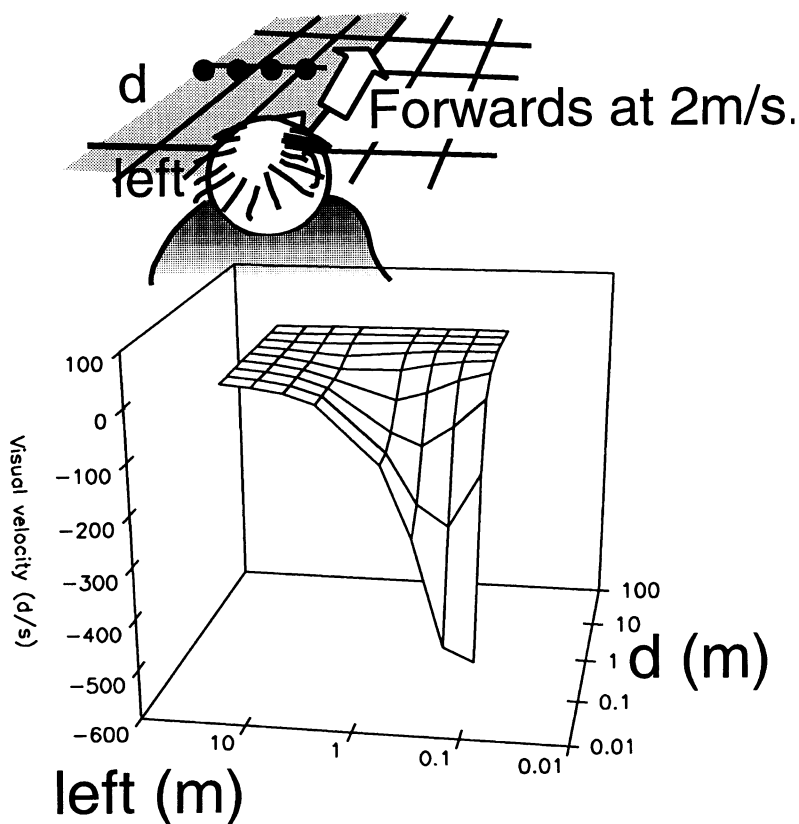

Figure 4 The angular velocity at the eye for points on a plane level with the head (inset) during forward motion at 2 m/s (fast walking speed, around 4 mph). Instantaneous angular velocities have been calculated for a logarithmically-spaced grid of points stretching from 0.1 m to the left of the subject out to 25.6 m and up to 25.6 m in front using the formulae described in Appendix B. The distance ahead ('d') and sideways ('left') have been plotted in metres on logarithmic scales. Although retinal angular velocities for distant objects are small, closer objects can reach high velocities. For example, an object 1.6 m forwards and off to the side by 1.6 m has a retinal velocity of 36 deg/s. An object at 0.1 m has a velocity in excess of 500 deg/s.
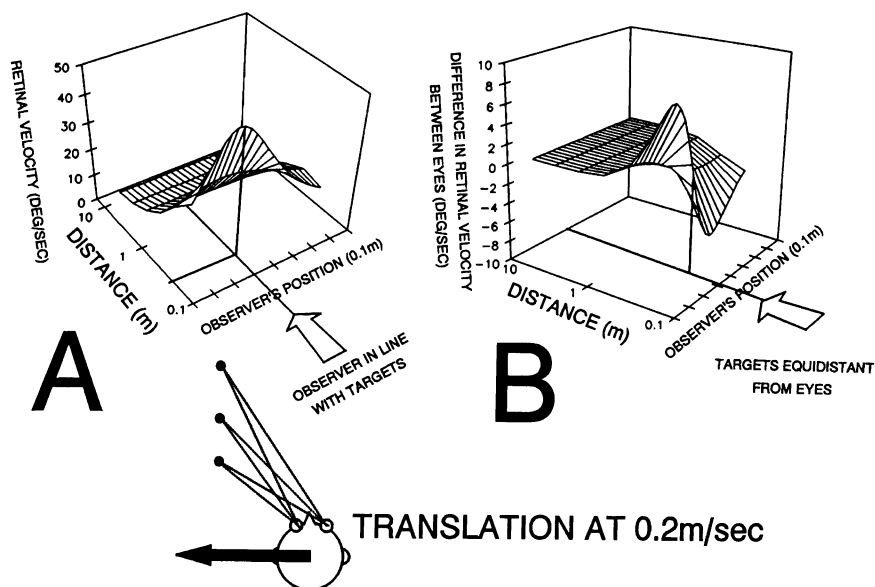
Figure 5 The effect of object distance and eccentricity during lateral translation. This is the effect of looking sideways while walking or out of the side window of a vehicle while travelling but has been calculated for the very slow speed of 0.2 m/s. The 'distance' axis is logarithmic. The 'observer's position' axis starts 0.2 m to the right of being lined up with the targets and ends 0.4 m on the other side (see inset). *Panel A* shows the retinal velocities for targets from 0.25 to 8 m distant. The maximum velocity for each target occurs when it is lined up with the observer. An object at 0.25 m has a retinal velocity in excess of 30 d/s. At 0.5 m, the velocity still exceeds 10 d/s. These retinal speeds are proportional to the translation velocity. *Panel B* shows the difference in retinal velocity between the two eyes for these same targets. The maximum differences occur approximately as the targets line up with one eye and then the other. (Interocular distance: 6 cm; eyes to centre of head rotation: 8 cm, as for Figure 3.)

forwards motion. The retinal speeds depend on the distance of each object from the eye. An object level with the eyes, 1.6 m forwards and 1.6 m to the left, for example, has a retinal velocity of 36 deg/s to the left when walking at 2 m/s. To fixate this object requires an eye rotation at 36 deg/s around an axis orthogonal to the plane defined by the direction of translation, the centre of rotation of the eye and the point in question. The retinal consequences of the eye rotation (section 2, Figures 2 and 6B) add to the existing retinal motion.

Translation in any direction produces a similar pattern of retinal movement with the motion of each point radiating out from the direction of travel. The retinal speed is zero for a point in the direction of travel and reaches a maximum when its visual direction is orthogonal to the direction of travel (Figure 5). Figure 5A plots the retinal velocities of a number of points arranged in a straight line that would correspond to those highlighted in the insert to Figure 4, but with the observer looking sideways rather than straight ahead and moving more slowly. The direction in which the eye is looking does not alter the distribution of retinal velocities although it will, of course,
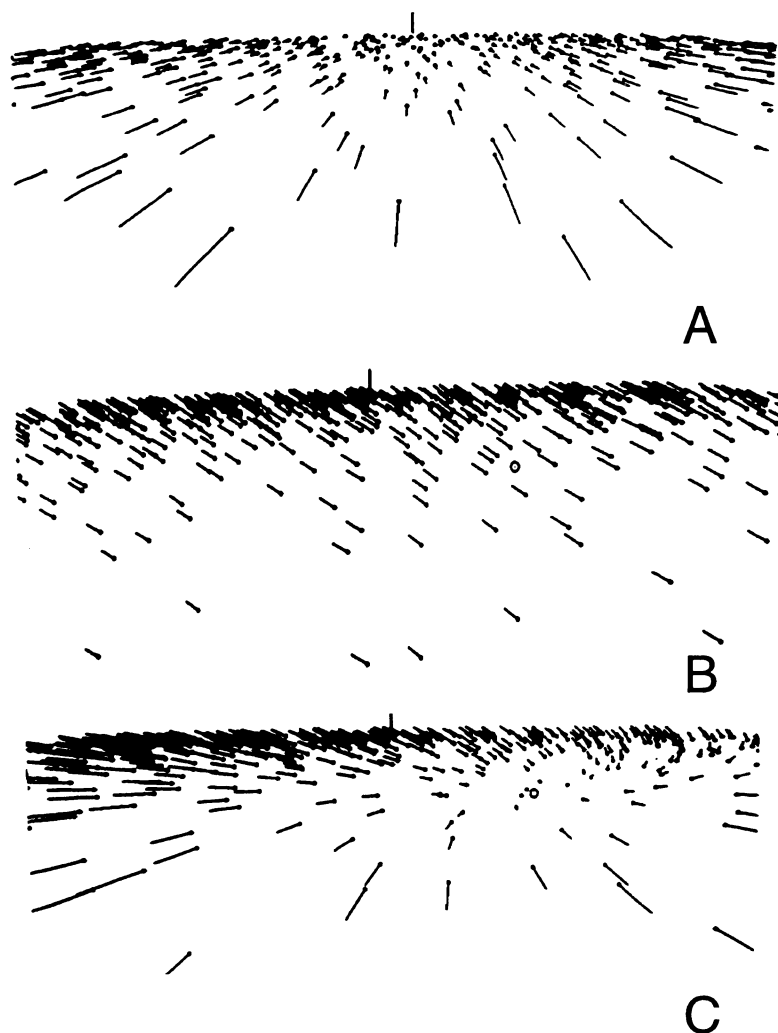
Figure 6   *Panel A* The pattern of optic flow on a stable retina produced by forwards translation across a ground plane. The point of heading is shown by the little flag pole in the centre. *Panel B* shows the effect of eye rotation alone on such a display. Compare the central region of the centre circle of Figure 2. *Panel C* shows the effect of having both rotation and translation present at the same time. This simulates the effect of fixating an earth-fixed point (shown by the circle) during translation towards the flag pole. It could also simulate translation along a curved path. The point fixated is quite distant so the rotation velocity is modest. Redrawn from Warren and Hannon (1990, Figure 1, p. 161).

determine which velocities fall on which part of the retina. The *difference* between the velocities in two eyes depends on the orientation of the head relative to the direction of travel (Figure 5B and Appendix B).

   Translation of the eye due to *translation* of the head and due to *rotation* of the head

generates identical instantaneous retinal image velocities, of course. But the two situations can be distinguished because, in the latter case, the direction of translation of each eye is tangential to the orbit and therefore is different (cf. section 3.1). The presence of rotation will also be independently identified both by its (non-translational) contribution to image movement and extraretinal cues (section 3).

Figure 6C shows what happens to the retinal image when angular (Figure 6B) and translation (Figure 6A) components are present at the same time. Although it may be mathematically possible to extract Figures 6A and 6B from 6C (Gibson, 1950, 1954; Koenderink & van Doorn, 1975; see Warren & Hannon, 1990 and Warren et al., 1991 for useful reviews), it would still be necessary to know the combination of eye, head and body rotation that caused the rotation contribution of Figure 6B. It requires extraretinal information to find that out.

4.1.1 Assignment of visual motion to self motion (linearvection)

The assignment of visual motion to linear self motion generates a *sensation* of self motion in a particular direction and with a particular velocity (*linearvection*: Fischer & Kornmüller, 1930; Berthoz et al., 1975; see Howard, 1982 and Miles & Wallman, 1993 for reviews). The pattern of retinal motion consistent with the linearvection might subsequently be calculated for each point using its perceived distance and deviations attributed to external movement.

Research into the extraction of information from optic flow caused by translation has concentrated on deriving the direction of heading of the observer. But optic flow provides information about rotation and translation in space and, as such, can be used to update the positions of *all* points in space, at least with respect to the eye (e.g. Rieser, 1983; Rieser et al., 1986). There is nothing special about the point that represents the direction of heading. In fact direction of heading seems particularly artificial information to extract from a small display which presents the same image to each eye[3] and which is often not associated with the sensation of self motion. Amazingly, however, the direction of heading can be extracted to within 1 deg from such displays simulating translation alone (Figure 6A: Warren, 1976; Royden et al., 1992a, 1992b; Warren & Hannon, 1990; Warren et al., 1991). In the presence of a rotation component above 2 deg/s, however, extraretinal information about the rotation is required for accurate heading judgement (Figure 6C: Royden et al., 1992a). Further experiments will undoubtedly show a role of vestibular and other sensory input in the interpretation of optic flow with many components.

4.2 Vestibular Cues Concerning Head Translation

An important cue that normally helps the rapid assignment of visual flow to linear translation is concurrent activity of the otoliths which transduce linear accelerations of

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[3] The images to the two eyes will actually be slightly different during stimulus presentations but the difference arises from the distance of the subject to the viewing screen rather than, as should be the case, the simulated distance of each dot in the display.

the head (see section 3.2.2). If the otoliths do not report head acceleration, as when only visual cues are provided to a stationary observer, linearvection is a very sluggish phenomenon (Howard, 1982). The canal system is not sensitive to linear translation (Goldberg & Fernandez, 1975) and so its levels of activity are not relevant here.

On earth, the otoliths are subjected to the constant acceleration of gravity. In addition, from time to time, the otoliths are subjected to accelerations generated by linear movement of the head. Applying two simultaneous accelerations to a body is exactly the same as applying a single acceleration of appropriate magnitude in their resultant direction. So the otolith system at any one time can only signal a single acceleration in a single direction from which the components of externally-generated gravity and self-generated motion must be deduced. This case is akin to the problem of identifying self-generated sounds (section 1.3) – unlike in the visual version of this problem, the two components do not interact. The components *can* be separated if at least one direction and one acceleration value are known. The use of extra-otolithic information such as tilt signalled by the canals (Guedry, 1974) or knowledge of the otolith's dynamics (Mayne, 1974) might help.

The eye movements evoked by linear acceleration of lower animals such as rabbits indicates that they attribute all otolith activity to the direction of gravity (Baarsma & Collewijn, 1975). But the eye movements of higher animals such as cats (Fukushima & Fukushima, 1991), monkeys (Paige & Tomko, 1991a,b) and humans (Paige, 1989; Baloh *et al.*, 1988; Berthoz *et al.*, 1987; Buizza *et al.*, 1979; Israel & Berthoz, 1989), during linear translation suggests that linear acceleration information can be extracted in those species. The decomposition is not perfect, however, and especially during high accelerations, perceptual confusion often arises between interpreting the otoliths as signalling an added linear acceleration or tilt (Guedry, 1974).

Interactions can occur between vision and otoliths where neither are able to operate unambiguously alone: the optic flow due to translation is difficult to disentangle from simultaneous rotation and otolithic information due to linear acceleration is difficult to disentangle from gravity. Together each helps reduce the other's ambiguities and rapid and appropriate sensations of movement through the environment result.

4.3 Other Cues Concerning Head Translation

There are many other potential sources of information in addition to vestibular and visual cues concerning body movements associated with head translation. Proprio-ceptors all over the body, for example in the legs and ankle joints, could contribute. Copies of relevant motor commands, such as to walk or run in a particular direction, might also be useful. How such high-level information might be represented in the brain and how it might be used in interpreting optic flow is unknown. Cognitive factors also play an important role (Howard, 1982) and expectancies can, for example, strongly influence whether the sensation of vection is experienced.

4.4   Does it Work? How Good is Vision during Head Translation?

The successful assignment of the appropriate components of retinal movement to head translation, when coupled with knowledge of eye and head rotations, means that

perceptual stability of the world and the perception of external object motion can continue during unrestrained movement in the real world.

Extraretinal distance information is particularly significant when dealing with the retinal consequences of free translation. The accuracy of motion assignment depends on the accuracy of distance estimation, and external object motion needs to be detected within a retinal image containing many different retinal velocities resulting from objects at different distances.

4.4.1   The effect of eye movements compensatory for head translation on retinal image motion

Compensatory eye movements tend to oppose retinal image movement that would otherwise result from head movement even if it is not appropriate to achieve stabilization (sections 1.4, 4.4.1). During head *rotation*, the dominant eye movement required is counter-rotation of both eyes at the same speed as the head rotation around axes parallel to the head rotation axis. During head *translation*, the compensatory eye movements required for retinal movement depend critically on the distance of the target being fixated and on its position with respect to the direction of travel. The eye movements required for fixation of close targets during translation are more like pursuit than reflex compensatory eye movements. The velocity for each eye needs to be updated continuously because the stimulus velocity varies with direction and distance which are themselves continuously changed by translation. Each eye needs to rotate around an axis orthogonal to the plane defined by the direction of translation, the centre of rotation of the eye and the point in question. For each point, the orientation of the required axis is different for each eye: the movements of each eye are geometrically required to be independent.

Only a part of each eye's image can possibly be stabilized at one time. The images of objects further away than a couple of metres usually require no stabilizing during translation at normal human speeds since they move on the retina at less than the speeds normally left by compensatory eye movements (Steinman & Collewijn, 1980; Sperling, 1990; Appendix B). The velocity of an eye movement that stabilizes one point (Figure 2) is added vectorially to the entire retinal image, speeding some points, slowing others and changing the direction of motion on the retina of most.

Compensatory eye movements evoked by linear motion are certainly sensitive to distance information (Baloh *et al.*, 1988; Israel & Berthoz, 1989; Post & Leibowitz, 1982; Schwarz & Miles, 1991; Paige, 1989; Schwarz *et al.*, 1989). Target distance might be obtained from accommodation or vergence angle (Demer, 1992; Schwarz *et al.*, 1989; Schwarz & Miles, 1991). In the absence of a new target the old distance estimate is retained for at least 250 ms as the modulator of eye velocity (Schwarz & Miles, 1991). Divergence of the eyes was occasionally seen in the dark during fixation of a remembered, earth-fixed target during lateral translation of the observer (Schwarz & Miles, 1991). Divergence is consistent with each eye following the target under separate control. The possibility of independent control should be investigated systematically by varying the position of the target and hence the movements of each eye needed to maintain fixation during translation movements.

Translation of the eyes can be along parallel straight lines or along curved paths. A special example of curvilinear translation is the path of the eyes as they transcribe an

orbit around the centre of rotation of the head (section 3). For each eye, the result is equivalent to translation in the direction tangential to the orbit and rotation about its own axis. The feature that distinguishes curvilinear from linear translation is that the simultaneous direction of translation of each eye is different. The difference reaches a maximum when rotation is about a point in between the two eyes and falls off as the distance from that point increases. Theoretically, if the direction and velocity of the translation of each eye could be deduced it would, by triangulation, provide full information about the rate of rotation and the location of the axis. Altering the position of the axis of rotation while keeping fixation distance constant (using increasingly eccentric rotations: Viirre et al., 1986; Gresty et al., 1987; Sargent & Paige, 1991; Snyder & King, 1992; Snyder et al., 1992) causes appropriate adjustments in eye velocity. The adjustment occurs in the dark, suggesting an otolithic contribution (see section 4.2).

Are the eye movements evoked by translation due to vestibular, visual or other drives? Miles (1993) suggested that the fast-build-up component of optokinetic nystagmus may be particularly useful in maintaining vision in the presence of many different retinal velocities because of the dominant role of the centre of the field in the generation of the eye movements (Brandt et al., 1973). But visually-driven eye movements can be easily confused by differences between the central and peripheral fields (Abadi & Pascal, 1991). The most accurate eye movements evoked by translation during body movements are in the light when multiple cues are available (Wall et al., 1992; Harris et al., 1993b; Solomon & Cohen, 1992a,b; Bles & Kotaka, 1986).

In conclusion, eye movements can never remove the retinal consequences of translation. They can be extremely accurate and resourceful in stabilizing one object's image but usually at the expense of the rest of the field. Their contribution to the optic flow over the rest of the image is additive. Their presence is thus potentially confusable with various other situations. Some extraretinal cues are certainly used to identify their contribution and others might theoretically do so but have yet to be systematically investigated.

4.4.2   Judging object motion during head translation

Perceptual thresholds for object motion are raised and object velocity is underestimated during head translation (Pavard & Berthoz, 1977; Berthoz & Droulez, 1982; Probst et al., 1984, 1986). The perceived direction of motion of objects is also distorted and the *accuracy* of direction judgements gets worse when the judgements are made during head translation (standard errors increased from $\pm$ 1.8° to $\pm$ 4.5°: Swanston & Wade, 1988; Swanston et al., 1992).

The uncorrectable retinal image motions associated with translational head movement probably contribute to the perceptual degradation under some conditions. But visual simulations of translation are not always associated with changes in motion thresholds suggesting that extraretinal factors are important and possibly the only contributors (Brenner, 1991a,b, 1993).

In addition to difficulties and misperceptions of external motion during head translation, illusory movement is often perceived in objects that are in fact stationary during the translation, for example the moon (*apparent concomitant motion*: Gogel,

1982; Gogel & Tietz, 1973; Post & Leibowitz, 1982; cf. section 3.5.2). Apparent concomitant motion presumably arises from the deduction of linear motion from angular retinal events using inaccurate distance information. The general reduced sensitivity to motion found during head movements probably reduces the confusion that might otherwise arise from such misassignments (Probst *et al.*, 1986).

5 CONCLUSIONS

The argument that considering a moving eye in a fixed head is the first step on the path towards looking at retinal image motion in the real world has introduced many misleading ideas which need to be revised – as when learning to touch-type after typing with one finger. Examples are the concepts of 'cancellation' (section 1.3), 'efference copy' (section 2.2) and describing eye movements as 'horizontal' or 'vertical' (section 1.2). These and related concepts become all but useless when applied to the unconstrained movements of normal behaviour.

This chapter has described the retinal consequences of self movement elaborating the effect of a nested chain of contributors including eye-in-orbit, head-on-shoulders, etc. Each leaves retinal trademarks such that they can, theoretically, be recovered from the conglomerate, especially in association with the appropriate extraretinal information. Little is known about whether some sources of movement information can be used for human performance. It is probable that information, although technically available perhaps in a single sense (e.g. the optic flow) is normally available through an interaction of the senses (e.g. otoliths and vision).

The extraction of different contributors to visual motion (e.g. eye rotation during translation) allows different tasks to be carried out simultaneously. Think of the sub-tasks involved in fixating a jogger while cycling around a corner. Features of the observer's self motion and relationship to space are available and are not irreversibly disrupted by the additional optic flow introduced by fixating a moving target. The multiple assignment of visual image movement must introduce some cumulative noise. Some movement is assigned to eye rotation, some to head rotation, some to translation of the eye resulting from head rotation, some to head translation and any remaining movement is available to be assigned to external causes. It is perhaps not surprising that object movement perception is poor under such conditions!

The retinal movements generated by self motion can be thought of as relative to the eye itself or relative to the images of other points. They can be thought of as instantaneous velocities or as patterns that change over time. This gives us four ways of describing the retinal events. It is likely that the same retinal information might be processed in more than one of these ways simultaneously. For example, relative motion between neighbouring retinal points is not sensitive to rotation since neighbouring points are affected similarly by rotation (Figure 2). Local differences therefore represent a technique for identifying translation relatively uncontaminated by the effects of rotation. Other processing systems that look for common features across the retina would be more suited to identify the rotation.

How well the brain uses self-motion information and its tolerances and fussiness are important both in understanding and in exploiting the visual system. The dependence of the retinal consequences of translation on the distance of each point from each eye

introduces a special challenge for proponents of virtual reality (VR). To experience virtual reality, the angular and linear accelerations of an observer's head are monitored and miniature television screens, mounted in goggles, provide a visual input. The screens simulate what an observer would see were they to move, with the patterns of head movement actually detected, around a computer-simulated landscape. As the head rotates to the left, the images are shifted by the program to the right. To simulate the relationships described in this chapter in which the movement of each point in each eye has motions attributable to several sources which depend on their perceived depth presents a formidable programming challenge.

   Perhaps if VR participants could be kept mobile enough, the consequent reduction in sensitivity to motion would keep players tolerant of program shortcomings in the same way that the brain is forgiving of the often unwanted and potentially confusing retinal motion present during natural self motion.

ACKNOWLEDGEMENTS

APPENDIX A   The Geometry of Retinal Velocities due to the Linear Displacement of the Eyes by an Angular Head Movement

Given:

$$\text{angular velocity} = \frac{\text{linear velocity} \times \cos^2 \text{ (eccentricity)}}{\text{perpendicular distance}} \quad \text{[rads/s]}$$

In this situation, therefore:

$$\dot{\theta}_E = \frac{\dot{M}.\cos^2(\theta_E)}{d} \quad \text{[rads/s]}$$

where:

$\dot{\theta}_E$ = angular velocity of eye [°/s]
$\dot{M}$ = linear velocity of eye [m/s]
    = head rotation rate × h [rads/s × m]
θ_E = eye position [°]
d = orthogonal distance to target (see Figure 7)

d and θ_E can be expressed in terms of dist_H (the distance from the head to the target), h (the distance between the axes of rotation of the head and eye) and θ_H (head position) (Figure 7).

$$d = \text{dist}_H.\cos(\theta_H) - h$$

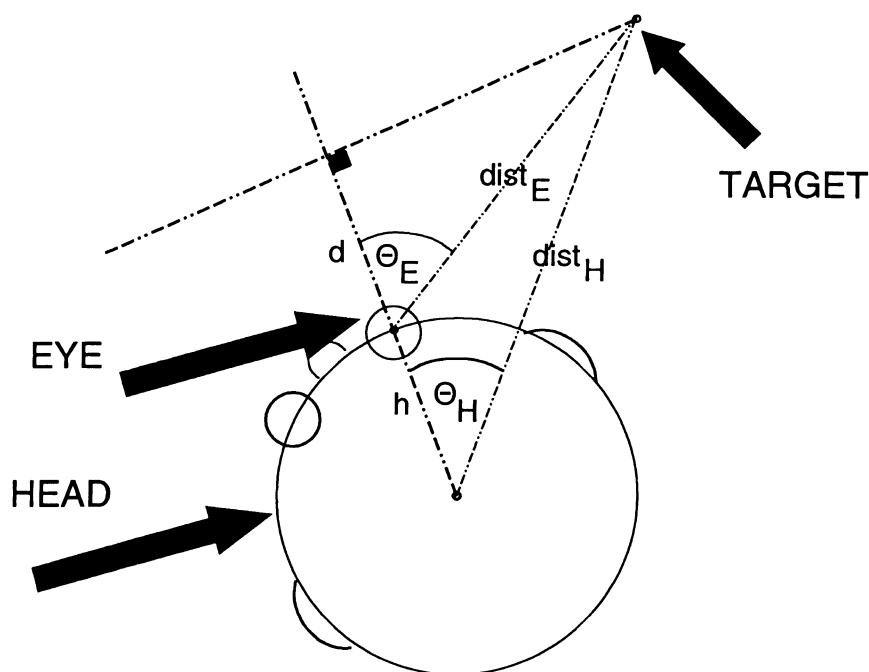$$\theta_E = \tan^{-1}\left(\frac{\text{dist}_H.\sin(\theta_H)}{d}\right)$$

Figure 7 The variables needed to analyse retinal motion of a target during head rotation. The target has a bearing θ_E and dist$_E$ from the centre of the eye and bearing θ_H and dist$_H$ from the centre of the head.

For a head rotation about an axis of fixed distance from the eyes (h) and of fixed distance from a target (dist$_H$), the only things that vary during rotation are the head velocity and the head position (θ_H).

The difference between the eyes (see Figure 8) is calculated by a simple increment to θ_H given by:

$$\Delta\theta_H = \pm \sin^{-1}\left(\frac{\text{interocular distance}}{2h}\right)$$

APPENDIX B   The Geometry of Retinal Velocities due to Linear Head Translations

Given:

$$\text{angular velocity} = \frac{\text{linear velocity} \times \cos^2 (\text{eccentricity})}{\text{closest distance}} \quad \text{[rads/s]}$$

$$\dot{\theta}_E = \frac{\dot{M}.\cos^2(\theta_E)}{cd}$$

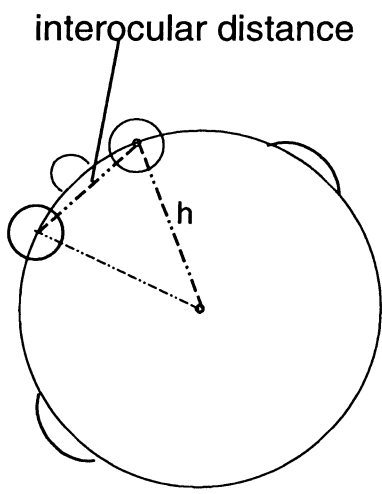**Figure 8** Interocular distance is the distance between the eyes. The eyes are 'h' from the centre of the head.

$$= \frac{\dot{M}.cd^2}{cd.\text{dist}^2_E}$$

$$= \frac{\dot{M}.cd}{dist^2_E}$$

Where

$\dot{\theta}_E$ = eye velocity [°/s]
cd = orthogonal distance (see Figure 9)
$\dot{M}$ = linear velocity of the eye [m/s]

For a given direction and speed of translation and for a given point of closest distance cd, the only thing that varies is distance from the eye (dist_E) (Figure 9).

$$\text{dist}_E = \sqrt{cd^2 + dx^2}$$

and dx varies linearly with the head translation

$$\Delta dx = \dot{M}.t$$

The maximum speed, θ_E occurs when $dx = 0$. For each eye, cd and the initial value of dx will be different depending on the interocular distance and the direction of travel, the orientation of the head relative to the direction of travel and the bearing of the target. But M and Δdx are the same resulting in different speeds at the two eyes and different times when $dx = 0$.
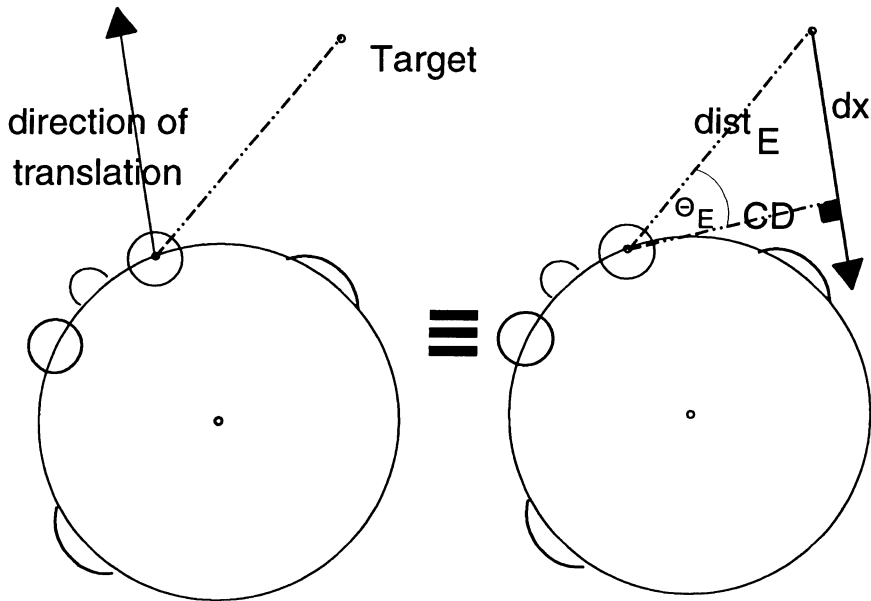
Figure 9 The variables needed to analyse the retinal motion of a target during translation. The target is at $dist_E$ from the eye. Translation of the eye past a stationary point (left side) is exactly equivalent to translation of a point past a stationary head (right side). *cd* indicates the closest approach that the target will make to that eye.

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