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Motor learning in the non-visual control of spatial orientation during locomotion

by

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Abstract

This study investigated the *adaptive* characteristics of a novel “Podokinetic” (PK) somatosensory/motor system suitable for controlling locomotor trajectory by referencing body orientation to the stance foot on the ground. Adaptive remodeling was achieved by “stepping-in-place” on a rotating disc for up to an hour. Afterwards, when trying to step-in-place without turning while blindfolded and on solid ground, subjects *subconsciously* rotated themselves at well above vestibular sensory threshold. This response, termed “Podokinetic After Rotation” (PKAR), proved to be linearly related to stimulus magnitude and decayed exponentially with a time constant of 5-10 minutes. Vestibular/Podokinetic interaction was investigated by comparing compensatory eye movement produced by *consciously* generated self-rotation, and that of *subconsciously* generated PKAR of similar angular velocity. Before adaptation the PK-generated oculomotor response linearly summed with VOR. After adaptation (and during PKAR), the PK-oculomotor response disappeared, leaving an intact VOR.

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Chapter 1 : INTRODUCTION

General Introduction

This thesis asks how spatial orientation is achieved during low velocity, long duration changes in the trajectory of natural human locomotion. Sensory information from the visual, vestibular, and somatosensory systems serve brainstem control of reflex ocular stabilization and the spinal control of spatial orientation and postural equilibrium. The flow diagram shown in Fig 1.1 depicts the three components of spatial orientation important to the present studies.

Although all three components are normally available during locomotion, Glasauer et al (1994) have shown that vision is not required to walk accurately for short distances along a straight pathway. Furthermore, Takei et al (1996) have recently shown that blindfolded subjects walking twice around a previously seen circular path of about 3 meters diameter can follow the path quite accurately. Under these circumstances the vestibular signal becomes misleading due to the long duration of rotation incurred. How is it that we can walk around a previously seen pathway at slow velocity with such accuracy without the necessity of visual or vestibular input? It seems likely that an alternate system that utilizes somatosensory and/or locomotor information provides spatial orientation during normal walking. In the present studies we investigate the contributions made by such a somatosensory/locomotor system and its interaction with the vestibular system.

Feedback of the control of trajectory during locomotion is monitored online by the central nervous system. Adaptive adjustment of central parameters that control output, such as neural gain, is necessary to enable longer term changes of the relevant reflexes to

match the behavioral demands of development, growth and pathological interference. The studies within this thesis examine the effects of adaptation of a somatosensory/motor system, which we have termed the “podokinetic” system, on oculomotor and locomotor output within the low frequency, low velocity range of movement likely to be encountered in the trajectory of locomotion.

The biophysics of the vestibular system during slow prolonged curved locomotion

During brief high frequency head rotations associated with stepping during locomotion, the semi-circular canals accurately transduce instantaneous head angular velocity relative to space (Grossman et al, 1989). However, during the prolonged low velocity angular movement incurred almost continuously as one moves about the environment, the biophysics of the canals lead to an exponential decay of the peripheral sensory signal. Several features of the peripheral vestibular canal response are relevant to the present studies, and will be reviewed briefly.

Located within the petrous portion of the temporal bones on either side of the head lie the vestibular labyrinths as shown in Fig 1.2a. Three approximately orthogonal semi-circular canals (anterior, posterior, and horizontal) and two otolith organs (the saccule and utricle) are contained on each side. The diagram in Fig 1.2b illustrates the relation of the three canals to the utricle on one side. A cross section of one of the canals is shown in the inset in Fig 1.2b. The small endolymphatic canal within each bony labyrinth is surrounded by perilymph acting as a fluid bath. It is the flow of endolymph within this canal which leads to mechano-neural transduction in the sensory receptor cells. At three adjacent poles entering the utricle are the ampullar structures which contain the cupular membrane and

sensory epithelium of each canal responsible for this transduction. Because of this arrangement, the semi-circular canals act as continuous circular tubes of fluid with a flexible diaphragm (the cupula) across the lumen.

Horizontal head rotation leads primarily to stimulation of the lateral semi-circular canals of the peripheral vestibular sense organs as shown in Figs 1.2a & b, although because of the overlap in activity between the three orthogonal canal pairs, most rotational head movements activate all three canal pairs to some degree (Melvill Jones, 1991). Several important elements of the biophysics of the semi-circular canals contribute to the vestibular system's role in spatial orientation during locomotion. Since the present studies are limited to angular head movement in a horizontal plane, the contributions of the otolith organs, which respond to linear acceleration, are not examined.

To examine the mechanical response of the lateral canal, a simplified canal can be described as a thin circular tube filled with endolymph and lying close to an earth-horizontal plane when the head is erect. Although endolymph has physical properties akin to water, its relative fluid flow is microscopic due to the very small canal diameter of around 300 microns. This introduces scale effects that lead to heavy predominance of viscous opposition to any inertially driven fluid flow. As a result, fluid and cupular displacements are limited to very small values. For example, it has been estimated that even a high angular velocity stimulus of 500 °/s would deflect the cupula through no more than 1° of arc (Wilson & Melvill Jones, 1979). An important consequence of this high ratio of viscous to inertial forces is that the inertial force acting on the fluid mass is closely proportional to angular acceleration of the canal.

In accord with Newtonian principles, the resulting relative fluid flow within the canal is opposed by an equal and opposite force due to viscous drag. However, whereas the inertial driving force is proportional to angular *acceleration* of the canal, the (equal) opposing viscous force is proportional to the *velocity* of the induced relative fluid flow within the canal. Thus to a close approximation we may write:

Head angular acceleration is proportional to velocity of relative endolymph flow.

Given zero initial conditions, we may integrate this equation with respect to time, to derive the conclusion that:

Head angular velocity is proportional to fluid displacement within the canal.

The canal system thus emerges as an angular velocity transducer, whereby cupular deflection reflects instantaneous head angular velocity relative to inertial space.

However, cupular deflection invokes a proportionate elastic restoring force. Consequently, although the initial response to a step change in head angular velocity is a proportionate cupular deflection, during subsequent constant velocity rotation the endolymph is forced exponentially back to its starting position. This feature accounts for the pattern of canal response idealized in Fig 1.3, as well as the familiar post-rotational vestibular response on suddenly stopping a continuous rotation.

The step velocity response described above in the time domain can also be described in the frequency domain to illustrate the dynamic characteristics of the canal response in terms of natural movement. Fig 1.4 shows a classical Bode plot of idealized cupular displacement as a function of instantaneous head angular velocity over a range of frequencies of sinusoidal rotational head movement likely to be encountered during natural movement. The main feature here is that the canal's velocity transducing characteristic is

only valid during relatively high frequency head movements. In the lower frequency range both the gain and phase of response vary according to stimulus frequency, due to the cupula's elastic restoring characteristics mentioned above.

The elastic restoring force of the deflected cupula tends to drive the endolymph back to its initial position with a force proportional to cupular displacement. Due to rate dependent viscous opposition to the resulting fluid flow, the time course of this restoration is exponential. Recording from primary afferent neurons of the alert monkey, Fernandez & Goldberg (1971) estimated a restoring time constant of around 5 seconds, which is probably extended in humans to around 7 seconds (see Fig 1.3). The time constant is further extended to 15 - 20 seconds by brainstem mechanisms. However, even with the prolonged central time constant, the vestibular system cannot account for the control of spatial orientation during the low velocity, long duration movements that occur when walking round a curved pathway (Gordon et al, 1995). Returning to the study by Takei et al (1996) in which blindfolded subjects were able to walk along previously seen circular pathways; if their trajectory was determined by the decaying vestibular signals available, they would describe a spiraling pathway of increasing diameter as the vestibular information attenuated over time. Instead, the trajectories remained of fairly constant diameter indicating that vestibular input was not dictating spatial orientation under these circumstances. It would seem that we must then look to a somatosensory/motor control system.

The contribution of somatosensory/motor information for spatial orientation

When walking along a curved pathway, cutaneous stimulation occurs when the foot contacts the ground during each stance phase. As the trunk turns relative to the foot on the ground, proprioceptive information is obtained from muscle spindles, tendon organs, and joint capsule mechanoreceptors. Performance is monitored online using feedback of this sensory information. While feedback permits relatively slow monitoring of ongoing movement, feed forward control is needed to control faster movements and may involve the internal generation of an efferent copy of the motor command to permit information about a planned movement to be received prior to the motor event (Kandel et al, 1991). For example, Boyle et al (1996) found that medial vestibulospinal neurons in squirrel monkeys carry signals of head velocity related to passive head movement, but do not encode head velocity during self-generated head movements. The authors suggest that a mechanism such as an efference copy signaling the active head movement may cancel the vestibular signal of that movement. Spatial orientation during natural movements such as walking along a curved pathway may rely on such feedback and feed forward mechanisms to provide information from somatosensory and motor systems. We examined these systems during conditions in which they are likely to play an important role in spatial orientation, i.e. during slow prolonged curved locomotion.

The sensory information described in Fig 1.1 may be integrated to create an internal model of the body in space. In the absence of vision and when the support surface is stable, proprioceptive and cutaneous information from the legs and feet provide the most reliable information about trunk position relative to space (Nasher, 1977; Horak & MacPherson, 1995). Trunk orientation in space during locomotion may be best

represented by integrating this proprioceptive information derived from the trunk turning relative to the foot on the stable ground with vestibular information derived from head rotation relative to space.

The results of several studies involving the sensation of self rotation relative to space (circularvection) provide evidence for integration of vestibular and proprioceptive information under dynamic postural conditions. For example, arthrokinetic stimulation resulting from arm movements induced by following a rotating drum with the hand generates an illusion of self-rotation (Brandt et al, 1977). Apparent stepping around on a rotating platform (i.e. the subject does not turn relative to space) also generates the illusion of circularvection (Bles & De Wit, 1978). This illusion derives from rotation of the stance foot relative to the stationary trunk. Similarly, purely optokinetic stimulation, in which a drum rotates around a stationary subject in the light, leads to circularvection (Dichans & Brandt, 1978). Although there is no actual self-motion in these situations, compensatory eye movements are generated that match the perception of self-motion.

The outcome of somatosensory and vestibular system integration appears to depend on the motor context of the movement. Guedry & Benson (1983) examined nystagmus and self motion perception following passive and self-generated movements that were otherwise identical. They demonstrated that when a self-generated stopping force was imposed on a passively induced rotation, post-rotational sensation of self-motion was strongly suppressed but post-rotational evoked nystagmus remained unchanged. These results are in contrast to those mentioned above relating to arthrokinetic or optokinetic stimulation, in which the compensatory eye movements matched the perception of self-motion. When, instead of passively induced rotation, these

subjects used self-generated lower limb movements to rotate, both per-rotational nystagmus and self-motion perception were augmented. Thus, it appears that active motor drive influences the resulting oculomotor and perceptual response.

Similarly, during active running around a circular platform in the dark (which generates combined vestibular and somatosensory/motor stimulation) compensatory eye and head nystagmus were demonstrated in monkeys (Solomon & Cohen, 1992). The authors reported gaze compensation with close to unity gain for periods up to two minutes, and with long time constants compared to the same animals following passive rotation in the dark. One monkey was trained to run-in-place while the platform was counter-rotated underneath. Gaze gains were initially greater than unity, and then remained close to unity over the next 30 seconds. It was inferred that some aspect of active locomotion, likely somatosensory feedback, was responsible for activating velocity storage that produced continuous nystagmus during running (Solomon & Cohen, 1992). The present studies are intended to measure compensatory eye movements in human subjects during active self-generated “stepping around” in the dark, and to compare these results to those obtained in response to passively induced rotation.

Interaction of “top-down” vestibular stimulation and “bottom-up” proprioceptive information may contribute to spatial orientation during locomotion

Under conditions of passively induced rotation in humans, Mergner and colleagues (1991,1993) have examined self-motion perception derived from the interaction of “top-down” vestibular stimulation, and “bottom-up” proprioceptive information from the trunk turning relative to the foot on the ground. They have shown that the proprioceptive signal

is free of the dynamics that give the vestibular system its high-pass characteristics (see Fig 1.4). Whereas the velocity threshold for the vestibular system is on the order of 1 - 3 °/s (Guedry et al, 1974; Fernandez & Goldberg, 1971; Wilson & Melvill Jones, 1979; Mergner et al, 1993), the velocity threshold for detection of self-motion derived from the "bottom-up" proprioceptive system is 0.2 - 1.0 °/s. The authors have demonstrated (Mergner et al, 1991,1993) that a low threshold signal derived from the trunk turning relative to the foot is summed linearly with the high-pass vestibular signal of head rotation in space. As a result, the low frequency content of the rotation is faithfully represented and perception of trunk-re-space movement is veridical.

Perception of trunk-re-space movement has been shown to be based on the low threshold proprioceptive signal of trunk-re-foot movement alone when the feet are stationary (Mergner et al, 1993). Therefore when walking on solid ground, self-motion perception may rely on the "bottom-up" proprioceptive input to control for the stationarity of external references. Reliance on "bottom-up" inputs rather than vestibularly derived space references may avoid the potential disadvantages of the high threshold and high-pass properties of the vestibular system.

The present studies investigate the influence of the "bottom-up" somatosensory pathway on locomotor and oculomotor output and perception of self-motion during low frequency and velocity angular movement.

Motor learning and adaptation

The finesse of control in everyday movement demands active adaptive maintenance of controlling parameters such as neural gain; as is known to occur in vestibular ocular-

motor control (Melvill Jones, 1977; Miles & Eighmy, 1980; Robinson, 1976; Berthoz & Melvill Jones, 1986). For example, in patients with chronic bilateral vestibular loss, proprioceptive input contributes to the mechanisms that compensate for the loss (Bles et al, 1984). In these patients the gain of neck proprioception in the perception of head and trunk movement was shown to be modified (Schweigart et al, 1993). For example, during trunk rotation under a stationary head patients perceived that their trunk was stationary.

Adaptation in response to functional changes in the central nervous system has been shown to be context specific. In 1977, Melvill Jones showed that the vestibular ocular reflex (VOR) of normal subjects could be effectively reversed by prolonged wearing of reversing prism goggles. Miles & Braithwaite (1980) showed that the VOR gain of normal subjects was modified appropriately by wearing 2X magnifying goggles. Berthoz et al (1981) further demonstrated that subjects who wore prism goggles which altered the visual image in two planes of movement but not the third, had appropriate adaptive VOR responses in the altered planes but no changes in the unaltered one. Similarly, when subjects wearing prism goggles during motor learning of an overhand throwing task were asked to perform a different motor task (i.e. underhand throwing), no evidence of a carry over of improved performance from the previously learned task to the new one was evident (Thatch et al, 1992c).

Problem Formulation

During slow velocity, long duration horizontal directional changes of walking, the high pass characteristics of the vestibular system make it ineffective as a source of spatial orientation. Conversely, trunk rotation relative to the space stable foot on solid ground

provides proprioceptive input that is free of such frequency dependent characteristics (Mergner et al, 1991,1993). This "bottom-up" somatosensory signal is well suited to provide non-visual input for spatial orientation, and to control curvature of trajectory during natural locomotion. We term this the Podokinetic (PK) system since it employs information derived from trunk rotation relative to the stance foot on the space stable ground. We propose that it is employed for controlling body orientation relative to space during natural locomotion.

Presumably, such a system must be auto-adaptive in a manner akin to the VOR (Gonshor & Melvill Jones, 1976a & b; Melvill Jones, 1977; Robinson, 1976). Also, maintenance of neural gains and adaptation within the PK system would likely be context specific. The present experiments make use of putative adaptive capabilities of the PK system in order to characterise that system.

Additionally, optokinetic and arthrokinetic studies have demonstrated that integration of sensory information is used for spatial orientation under natural conditions. We propose that the PK system is a primary contributor to spatial orientation and is capable of interaction with visual and vestibular input according to task and context.

The objective of the proposed studies is to investigate the adaptive somatosensory/motor system controlling trunk orientation relative to space during locomotion. The specific experimental aims are: 1) to characterise the short-term and long-term adaptive responses of this system over a range of stimulus velocities and durations, and 2) to investigate putative interactions between the podokinetic and vestibular systems in the control of reflex compensatory eye movements.

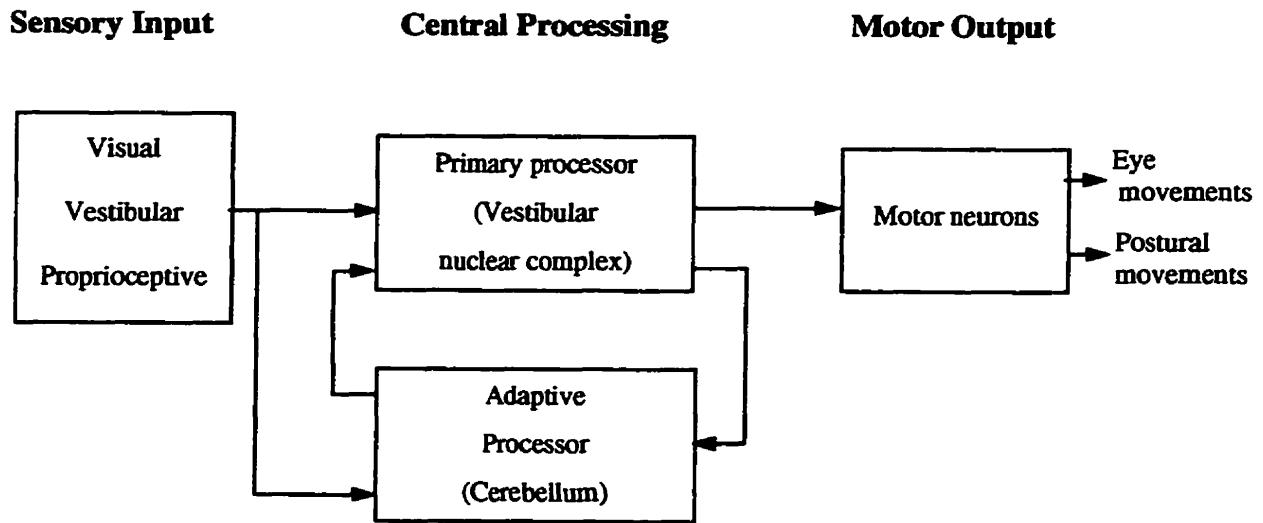


Fig. 1.1 Flow diagram of the major sensory systems contributing to the control of compensatory eye and postural movements important in spatial orientation. Sensory input from visual, vestibular, and somatosensory sources are used to control both ocular and postural motor output. Feedback from these movements is monitored online by the central nervous system, and parametric feedback control is used when longer term adjustment is required. Adapted from: Hain TC, Hillman MA (1994) Anatomy and physiology of the normal vestibular system. In: Vestibular Rehabilitation. Contemporary Perspectives in Rehabilitation (editor-in-chief SL Wolf) F.A. Davies, Philadelphia.

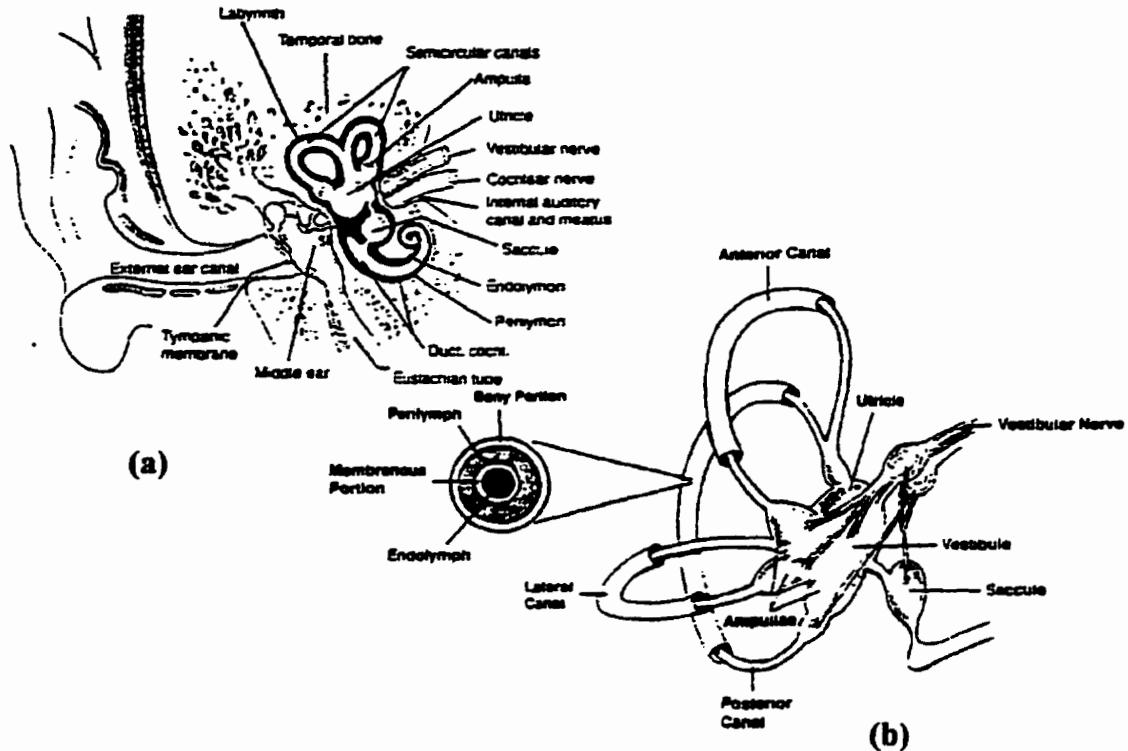


Fig. 1.2 Diagrammatic drawing of the Vestibular Apparatus. (a) Anatomy of the peripheral vestibular system in relation to the ear and temporal bone on one side of the head. Note that only two of the three semicircular canals are illustrated. (b) The membranous and bony labyrinths of one peripheral vestibular apparatus. Note that one end of each canal is widened to form an ampulla which contains the cupular membrane and sensory epithelium responsible for mechano-neural transduction. The figure inset shows a cross section of one bony labyrinth illustrating the small diameter of the membranous labyrinth filled with endolymphatic fluid, and surrounded by perilymph. The present studies are concerned with angular movement of the head in an earth-horizontal plane, which primarily stimulates the lateral semicircular canals. The biophysical properties of the canal pertinent to the present studies are discussed further in the text. Adapted from: Hain TC, Hillman MA (1994) Anatomy and physiology of the normal vestibular system. In: Vestibular Rehabilitation. Contemporary Perspectives in Rehabilitation (editor-in-chief SL Wolf) F.A. Davies, Philadelphia.

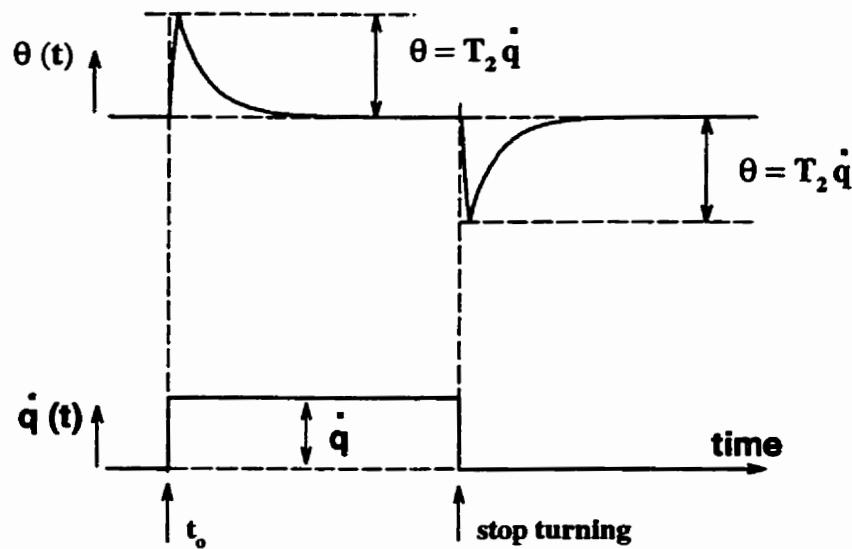


Fig. 1.3 Theoretical response of a semicircular canal to a step velocity input. The angular cupular displacement relative to the canal (θ) and neural signal (*top, solid curve*) in response to a step head velocity (\dot{q}) input (*bottom*), as a function of time (t). The dashed line above the top trace shows the ideal cupular response as a perfect rate sensor. Cupular displacement in response to prolonged rotation at constant velocity (*top, solid curve*) demonstrates an exponential decay of the neural signal with a time constant (T_2) of about 7 sec due to the elastic restoring force of the cupular membrane. The response is identical in the other direction for similarly stopping the stimulus. See text. Reproduced from: Melvill Jones, 1991, Eye Movements in Vision and Visual Dysfunction., Ed R.H.S. Carpenter., General Ed J.R. Cronly-Dillon., Macmillan Press.

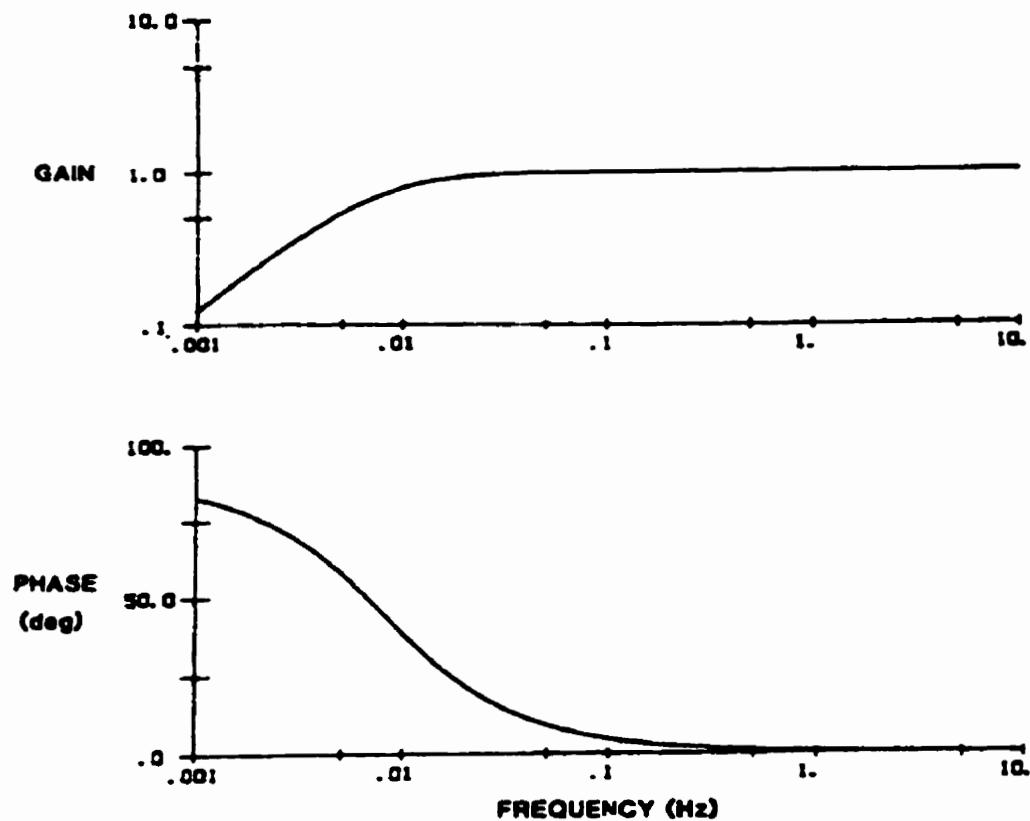


Fig. 1.4 Bode plot of the frequency response representing the dynamic semicircular canal response. Gain and phase are expressed with respect to head angular velocity. In the low frequency range, the vestibular signal is unreliable. Reproduced from: Leigh RJ, Zee DS, 1991, The Neurology of Eye Movements, Contemporary Neurology Series, Editor-in-chief Fred Plum, F.A. Davies Co, Philadelphia.

Chapter 2 : CHARACTERISATION OF THE PODOKINETIC ADAPTIVE SYSTEM

Introduction

During normal locomotion one encounters two quite different ranges of angular movement, one associated with the high frequency jolts of stepping (Grossman et al 1989; Bloomberg, 1991) and the other with slow, low frequency, directional changes in the course of forward progression (Gordon et al, 1995; Takei et al, 1996). Although the vestibular canal system is well matched to the jolts of stepping (Melvill Jones & Milsum, 1971; Wilson & Melvill Jones, 1979), its high pass filtering characteristic renders it inappropriate for the low frequency changes of directional control (see Chapter one). Vision provides an obvious source of low frequency information, but there must also be a non-visual source since locomotor trajectory can be controlled quite accurately in the absence of vision (Hollands & Marple-Horvat, 1996; Takei et al, 1996; Glasauer et al, 1994).

When on solid ground the stance foot is stable relative to space. Therefore trunk rotation relative to the stance foot is equivalent to trunk rotation relative to space. Mergner et al (1993) showed that somatosensory signals of trunk rotation relative to the feet are perceived consciously and that such perception remains veridical at low frequencies and velocities. Thus the “bottom-up” somatosensory signal generated by rotation of the trunk-re-foot is well suited to provide non-visual input for spatial orientation and control of trajectory curvature during natural locomotion.

In a previous study, Gordon et al, (1995) adaptively remodeled the relation between trunk rotation relative to the stance foot and the perception of trunk rotation

relative to space by having subjects walk-in-place for two hours on the periphery of a horizontally rotating platform. Vision provided a veridical percept of trunk stationarity while the feet walked round a curved trajectory on the rotating disc. Following this adaptive stimulus, subjects were blindfolded and asked to walk straight ahead on solid ground. Instead, they consistently walked around nearly circular trajectories at starting angular velocities ranging between 10 and 20 °/s. Although these values are an order of magnitude above vestibular sensory threshold (Guedry, 1974; Mergner et al, 1991, 1993), no subject experienced any sensation of turning, indicating that the adaptive stimulus had rearranged the relationship between the rotation of the trunk relative to the foot and both the perception and the control of trunk position in space and. From these results Gordon et al (1995) inferred that sensory/motor signals of trunk-re-foot rotation are primarily responsible for low frequency spatial orientation and directional control during locomotion in the absence of vision.

The present study set out to investigate further the adaptive characteristics of this somatic sensory/motor system. Since path curvature for a given forward speed is defined by the angular velocity of trunk rotation relative to the foot-on-the-ground, we employed a paradigm that invokes this rotation without linear motion. Instead of walking on the periphery of a rotating treadmill, subjects stepped-in-place on the axis of a small rotating disc without themselves turning relative to space (see Fig 2.1). After adaptation to this stimulus the blindfolded subjects were asked to step-in-place on the floor without turning. An advantage of this procedure was that it allowed prolonged periods of post-adaptive body rotation without forward locomotion in a confined area of laboratory space.

Analogous with arthrokinetic and optokinetic terminology (Bles & de Wit, 1978; Bles & de Jong 1982; Bles & Kotaka, 1986; Brandt et al, 1977; Guedry, 1974; Lackner & DiZio, 1993) we now introduce the terms “Podokinetic” (PK) to describe the system responsible for this form of “bottom-up” sensory/motor control and “Podokinetic After Rotation” (PKAR) to describe the post-adaptive rotation observed during walking or stepping-in-place in darkness. In this study we specifically investigated the velocity and time course of the PKAR as a function of the velocity and duration of the adaptive podokinetic stimulus.

Methods

Control tests

Six normal volunteers, five male and one female, whose ages ranged from 27 to 72 years, participated in the study after giving informed consent. Experimental sessions began with five pre-adaptation control tests to determine any inherent tendency to turn while attempting to step-in-place without vision. In each test, the blindfolded subject was asked to step up and down on the spot without turning for one minute at a constant stepping frequency of 2 Hz (i.e. one second for a complete stepping cycle). One minute rest periods separated each control test. Rotational velocities were estimated from the total angle of turn during a one minute test using a simple compass rose and a rectangular grid on the laboratory floor, after the manner of Fukuda (1959) and Pietersen (1967).

Adaptive stimulus

Following the control trials subjects removed their blindfolds and mounted a 76 cm diameter circular disc, which could be rotated by a high-torque, velocity-controlled servo motor (Neurokinetics, model 80-RP). Subjects stepped-in-place on the axis of the disc at a frequency of 2 Hz as it rotated horizontally beneath their feet. The disc gradually accelerated to a pre-determined angular velocity and remained at that rate for a set duration. During the first few minutes of rotation they grasped a pair of safety handles hanging from the ceiling, but then they were able to release the handles and comfortably step-in place while maintaining a stationary trunk position using visual cues. While the subject's veridical percept was of no trunk rotation relative to space, the stance foot was always actively rotating relative to the trunk at the same angular velocity as the disc turned relative to space.

In the main experiment, each of the six subjects was exposed to seven different adaptive stimulus conditions in separate trials. These comprised rotations at four different angular velocities maintained for a duration of 30 minutes, and for three additional durations at an angular velocity of $45^\circ/\text{s}$, as shown in Table 2.1. In order to avoid potential cumulative adaptive effects, the intervals between trials were at least two days (average interval for all trials was 7 days) and the direction of disc rotation was alternated between trials.

Post-adaptive response

When the disc was stopped, a blindfold and ear-plugs were applied to the subjects to deny the use of visual or auditory cues for spatial orientation. They were transported in a wheel

chair to an adjacent laboratory floor space, where the subsequent stepping maneuver could be performed in a safe and natural manner. They were instructed to stand up and step-in-place without turning until told to stop. Stepping frequency was maintained at 2Hz with periodic reinforcement from a metronome. Since all subjects rotated relative to space with initial rates of rotation much higher than those during the control trials, angular position was initially measured at 20 second intervals. When the angular velocity of stepping fell to around 6°/s, usually after two to five minutes, measurements were then taken at one minute intervals until the rate of turn showed no apparent change over several minutes. The total recording period of post-adaptive stepping ranged from 25 to 40 minutes. All measurements were referred in time to the moment of stopping the turntable, which was approximately 45 seconds before beginning to step-in-place on the floor. Occasionally during attempted stepping-in-place on the floor, subjects had to be passively moved away from impending obstructions due to inadvertent translational movement. Data samples spanning such events were excluded from the results.

Additional long term experiments

All subjects showed a residual steady rotational velocity at the end of the recording period. Therefore two additional experiments were performed to investigate the implied longer term PKAR. In the first of these a single subject was exposed to a podokinetic stimulus of 45 °/s for 60 minutes. Immediately following this adaptive stimulus, PKAR was measured for 40 minutes continuously in the manner previously described. On each of the subsequent four days, five standard control trials were recorded. Normal daily activities were permitted during the intervening days.

In the second experiment, two subjects were each exposed to this same adaptive stimulus and their tendency to turn while stepping on the floor was measured over the ensuing eight hours. Initial post-adaptation stepping and recording were performed as in the main experiment. After the initial post-adaptive recording period of 40 minutes the response was sampled for 6 minutes every half hour until completion of the eight hour trial. For analysis, the first minute of each such sample was discarded in order to exclude the potential influence of transient vestibular stimuli. The average angular velocities during each of the remaining five minutes were plotted for each 30 minute test series as in Figure 2.7. Between successive samples the subject remained quietly seated, with eyes open but refraining from any locomotor activity.

Data analysis

Average angular velocities of control stepping were derived from the change of angular position during each of the five one minute pre-adaptation control tests. Velocities of post-adaptation rotation were similarly derived from the change in angular position measured over 20 second intervals during the initial few minutes and over 60 second intervals thereafter. For each subject PKAR velocities were corrected by subtraction of the average control velocity. When plotted against time, the decaying velocities so obtained were fitted by least squares regression to a first order exponential curve, as exemplified in Fig 2.2. Data points occurring within two minutes of stopping the turntable were excluded from this analysis to avoid possible interaction with vestibular input. These calculated curves were extrapolated to intersect the ordinate at time zero and used to estimate

adaptive response gain, time constant of response decay and a final asymptote for the first order response.

To obtain the cumulative data of Figs 2.3 and 2.5, results such as those in Fig 2.2 were pooled for all six subjects in each of the conditions shown in Table 2.1. Individual estimates were binned in each of the 20 second or 60 second sample durations noted above and the summed value for each bin divided by the number of subjects (6) to obtain an average response expressed in degrees per second ($^{\circ}/s$). On occasion, due to non-coincidence of absolute times of individual samples across the six subjects, as well as sample exclusions incurred by repositioning subjects on the floor, bin width had to be extended until at least one valid estimate was obtained from each subject. When other subjects contributed several estimates within such an extended time slot, their values were averaged before committing that subject's value to the bin. Bin width extensions appear in Figs 2.3 & 2.5 as regions of reduced data point frequency. The average binned data were plotted against time and fitted with a first order exponential curve as described for the individual data. As with the individual data, the fitted curves reached final asymptotic values that were significantly greater than zero. Therefore, to obtain an estimate of the initial first order response velocity the asymptotic value was subtracted from that of the ordinate intersect. The resulting first order response velocities were plotted against stimulus velocities and stimulus durations as in Figs 2.4 & 2.6.

In the longer term experiment individual data were fitted to a second order equation in order to distinguish the short and long term characteristics of the response, as in Fig. 2.7.

Results

Control trials

Mean angular velocities for each subject during control trials ($N= 42$) ranged from $0.6^\circ/\text{s}$ clockwise to $0.7^\circ/\text{s}$ counterclockwise, with an almost even proportion of clockwise (41%) and counterclockwise (59 %) turns. The mean angular velocity for all subjects and all trials was $0.25^\circ/\text{s}$ ($S.E.= 0.08$, $N=210$) to the left, which was not significantly different from zero. The possibility of long-term adaptive effects carrying over from one experiment to the next was examined by comparing successive mean control values for each subject throughout the whole experimental series. No evidence of carry-over emerged, indicating that the minimum inter-experiment period of two days sufficed to prevent any measurable effects between trials. This conclusion was supported by the fact that there were no residual effects after the first day when one subject performed the standard control test on four successive days following a one hour adaptive stimulus of $45^\circ/\text{s}$.

Podokinetic adaptation

General observations

When stepping on the rotating disc all subjects initially felt somewhat unstable and used the suspended hand-grips for support. After a few minutes they became sufficiently comfortable to release the hand-grips and the stepping pattern became remarkably steady. However, as has been noted before in somewhat similar circumstances (Bles & de Wit, 1978), head tilting tended to produce imbalance and to trigger a return to the hand-grip

support at any stage of the adaptive stimulus. A noteworthy feature is the fact that when comfortably stepping on the turntable there was no sensation of jolt during the transition from the swing to the stance phase. The significance of this observation is discussed below.

On stopping the turntable at the end of an adaptive session there was no sensation of movement as long as both feet remained firmly on the stationary platform. At the moment of initiating a stepping movement in order to dismount the turntable, all subjects experienced a strong illusion of turntable rotation in the direction of its previous movement. In a similar study with linear treadmill adaptation, Anstis (1995) also noted no after-effects until subjects attempted locomotion, at which time the illusion of apparent forward motion occurred.

Podokinetic after-rotation (PKAR)

When starting to step-in-place on solid ground without vision, all subjects turned relative to space in the same direction as the previous trunk rotation relative to the turntable. The subsequent course of events is exemplified in Fig 2.2, which shows corrected post-adaptation angular velocities obtained from one individual after an adaptive stimulus of $45^\circ/\text{s}$ for 60 minutes. The subject's angular velocity relative to space is plotted against time elapsed after cessation of turntable rotation. Typically the first data points lay below the main curve, but thereafter the response rather closely followed an exponential decay towards a positive asymptotic value (abscissa). After excluding data points in the first two minutes, the fitted curve yielded a decay time constant (τ) of 6.7 min and a final

asymptote of 5.7 °/s. Extrapolation of this curve to intersect the ordinate at time zero yielded an estimated initial PKAR value of 19.7 °/s.

Figures 2.3 and 2.5 show the cumulative results obtained in a similar way for all subjects and all conditions. The plotted points represent binned averages calculated as described in Methods. Figure 2.3 illustrates the effect of adaptive stimulus *magnitude* (turntable angular velocity) on the subsequent pattern of PKAR for a constant stimulus duration of 30 min on the turntable. As in Fig 2.2 these averaged data points closely fit exponentially decaying curves, with the added feature that they demonstrate a marked dependence of the amplitude of the first order response on that of the adaptive stimulus. Figure 2.4 illustrates the characteristic of this feature by plotting the amplitude of PKAR against stimulus amplitude, both expressed as angular velocities. Since the relevant feature here is the response of the first order system implied by the fitted curve, the response values on the ordinate of Fig 2.4 are expressed as the difference between the values of the extrapolated ordinate intersect and the corresponding asymptote of each curve of Fig 2.3. Expressed in this way the PKAR velocity was related almost linearly to stimulus angular velocity up to the 45 °/s condition. However at 90 °/s there appears to be a degree of saturation. From the slope of the curve up to 45 °/s a response gain of 0.27 ($r^2 = .99$) emerges for the first order component of the adaptive system.

Figure 2.5 shows corresponding data relating response characteristics to the *duration* of the adaptive stimulus, with stimulus magnitude maintained constant at 45 °/s. As before the averaged data points closely fit calculated exponential curves of signal decay. However as shown in Fig 2.6, the response amplitude of the first order system tended to plateau at about 12 °/s after an initial rise compatible with an adaptive

"charging" time constant of between 5 - 10 minutes, similar to the average "discharging" time constant of about 7 minutes noted below.

Tables 2.2 and 2.3 show for each stimulus condition the calculated values of the y-intercept, the asymptote, the estimated first order response magnitude and the time constant of response for each of the curves in Figs 2.3 and 2.5. The mean time constants from these two tables emerge as 7.5 and 7.1 min respectively with an overall mean of 7.3 minutes.

Long-term experiments

As shown in Figs 2.3 and 2.5, and Tables 2.2 and 2.3, subjects consistently rotated at significant angular velocities after reaching an approximately steady state at the end of an experiment. Thus the adaptive phenomenon appeared to cause longer term effects. Consequently we undertook to examine the adapted response over an extended time course of 8 hr in two of the six subjects as described in Methods.

Figure 2.7 shows the results from each subject plotted on an extended time base and fitted with a second order equation. The values of the ordinate intersects (average 21 °/s) were on the same order of magnitude as those produced by the same magnitude of stimulus of the main experiment, as were the values of the "short" time constants of the fitted curves (average 5.6 min). In contrast the "long" time constants were greatly extended, emerging as 120.5 min and 71.4 min for subjects A and B respectively. The final asymptotic values of both curves were close to zero, indicating effective loss of the adapted condition after 6 hours.

In a separate experiment, subject A was exposed to the same adaptive stimulus (45 °/s for 60 minutes), followed by daily recordings of five one-minute stepping trials on each of four consecutive days. No residual PKAR was found at one or more days after adaptation, consistent with the long time constant of 120 minutes estimated from the eight hour trial.

Discussion

The findings of Gordon et al (1995) demonstrated an adaptive somatosensory/motor control system capable of remodeling the relation between trunk rotation relative to the space stable stance foot, and the perception of trunk rotation relative to space. It was found that walking-in-place on the periphery of a rotating disc systematically altered spatial orientation and trajectory during walking. In the present study, we show that stepping-in-place over the axis of a rotating disc caused an analogous adaptation in the perception and control of angular trunk position during stepping. The results of both studies support the existence of an adaptive system that uses information about trunk rotation relative to the feet to control spatial orientation and the trajectory of locomotion.

Podokinetic stimulation is analogous to optokinetic stimulation

To stabilize the trunk relative to space while stepping on the rotating platform, the stance foot rotates relative to the trunk at the same rate as the platform rotates relative to space. Similarly, to stabilize the eyes during optokinetic stimulation, optokinetic ocular nystagmus generates slow phase eye movement compensatory to the velocity of the

optokinetic stimulus. By analogy, we term the rotating disc used in the present study a podokinetic (PK) stimulus. The control of trajectory during walking in the experiments of Gordon et al (1995) and spatial orientation during stepping in the present experiments were adaptively remodeled by this podokinetic stimulus. Exposure to this stimulus caused a podokinetic after-effect in which the stance foot continued to rotate on the trunk during stepping. Similarly, exposure to optokinetic stimuli, such as a rotating drum, causes an optokinetic after-effect in which the eyes continue to rotate relative to the head. This is called optokinetic aternystagmus (OKAN). Again by analogy, we term the after-rotation of the foot relative to the trunk podokinetic after-rotation (PKAR). Like OKAN, PKAR exhibits an initial velocity that is related to preceding stimulus velocity and that subsequently shows an exponential decay. Thus, both the optokinetic and podokinetic systems may be said to show “velocity storage”.

“Short” and “long” term components of “velocity storage” in the PK system

Extrapolating the curves of Fig 2.3 to intersect the ordinate, a closely linear relation emerges between stimulus angular velocity and initial response amplitude over the range of 11.25 - 45°/s. In Fig 2.4 we see that linear regression over this range yields the equation:

$$Y = 0.27X + 0.54 \quad (r^2 = 0.99).$$

In this equation Y gives the initial response velocity of the stepping subject and X the corresponding podokinetic stimulus velocity. From this the gain (slope) of the first order adapted system emerges as 0.27. At the maximum stimulus of 90°/s the response lies below this line, suggesting the intrusion of some form of saturation. Possibly this

saturation arises from mechanical constraints imposed by the relatively large angles of trunk rotation relative to the foot which are necessary for maintenance of a space-stable trunk during stepping on the rotating platform.

Consider next the consistently positive values of the abscissa noted in Table 2.2. This feature demonstrates that there is a longer term component of the adaptive effect than implied by the above equation. Plotting these values against stimulus amplitude also reveals a linear relationship, over the first three data points, in this case with the slope (gain) of 0.08. Summation of these “short” term and “long” term gains indicates an overall gain of the adaptive system of 0.35.

The above findings, together with those of the supplementary long term study of Fig 2.7, indicate that the “storage” mechanism invoked by the adaptive stimulus comprises at least two different components, both of which discharge with closely exponential profiles, but with quite different time constants of around 5 - 10 minutes and 1 - 2 hours respectively. Furthermore they both prove to be roughly linear in their response, at least up to $45^\circ/\text{s}$.

The effect of stimulus duration, seen in Figs 2.5, 2.6 and Table 2.3 is clearly different from that of stimulus velocity. Recall that the response of the first order, or short term component of the adaptive system was defined as the initial response (y-intercept) minus the value of the final asymptote. Figure 2.6 plots the dependence of this response component on stimulus duration. In contrast to the effect of stimulus amplitude, we see an initial rapid rise of the curve followed by an almost flat response. Indeed this is to be expected in view of the shortest stimulus duration being roughly the same duration as the time constant of the first order system.

The consistent nature of both curves of Fig 2.7 clearly implies the combined activity of two sub systems having time constants separated by at least an order of magnitude. It is true that conditions of the first 40 minutes of these records (continuous stepping) were different from the later time period (intermittent test with rest periods). Nonetheless, the persistent rotations noted as positive asymptote values in the short term studies demonstrate retained rotation after "run out" of the first order system. In fact, consistent with a long time constant sub system, the residual asymptotic values progressively increase with stimulus duration. Taken together we conclude that both short and long term effects are indeed at play in this form of adaptation.

The fact that both curves of Fig 2.7 produce asymptotes close to zero indicates that all podokinetic after-effects from a 60 minute exposure were lost within 6 hours of the adaptive stimulus. Thus, the absence of residual PKAR in the subject tested at 24 hours after adaptation was not surprising. But would this be true for longer periods of stimulus exposure? Certainly in an analogous adaptive manipulation of vestibulo-ocular reflex gain, longer term retention on the order of days (Miles & Eighmy, 1980) and even weeks (Gonshor & Melvill Jones, 1976b) expressed itself when subjects were exposed to the adaptive condition for comparable durations. The magnitude of the time constants of these longer term effects were dependent on the duration of the adaptive VOR stimulus. Perhaps in the continuous exposure to natural circumstances, longer term effects could occur than have been demonstrated in the present study. In this connection one could ask, why do we not see more than 1/3 gain in our overall responses? Possibly the much longer term influences encountered in everyday life might account for the remainder. Alternately, the low gain may indicate that the podokinetic system normally acts in conjunction with

other neural systems in the manner of the optokinetic and vestibular systems to produce velocity storage of the relevant neural signal.

“Charging” and “discharging” characteristics of the PK system

Do the “discharge” characteristics arrived at above reflect the “charging” pattern during the course of a continuous stimulus? Theoretically the question could be addressed by examining the relation between the amplitude of the first order response and the duration of the stimulus (Fig 2.6). The choice of stimulus durations denies this option however, except that the system appeared to be nearly fully “charged” after 7.5 minutes of stepping on the disc. There was a trend for progressive increase of the overall response (Y intercept values in Table 2.3) and asymptote beyond this duration, presumably reflecting the ongoing charging of the second order system noted above.

Evidence of interaction between the vestibular and podokinetic systems

An interesting feature of the first minute or so of post-adaptation stepping was the consistent suppression of rotational velocities below the extrapolated line fitted to the rest of the data as exemplified by Fig 2.2 ($p < .001$). Since the onset of PKAR would likely stimulate the semicircular canals, this suppression may represent transient vestibular opposition to the PKAR. Such suppression would presumably be reduced to an insignificant level over the first minute, owing to the short time constant of the central canal response (around 20 seconds; Wilson & Melvill Jones, 1979) relative to that of PKAR (5 - 10 min). Due to this large difference between time constants of the vestibular and podokinetic systems, the PKAR after the first minute would presumably be relatively

free of vestibular influences. Nonetheless, it is likely that interactions of these two systems would occur over the range of velocities and duration encountered in natural locomotion.

In the “top-down” vestibulo-spinal system, the vestibular canal’s response to rotation acts as a high pass filter and as such, loses its veracity rather quickly during the relatively prolonged duration of turn incurred with continued locomotion around a curved path. In contrast the sensory perception of trunk rotational velocity relative to the feet exhibits no such dynamic filtering (Mergner et al, 1993). Furthermore, Mergner and colleagues (1993) showed that this form of somatosensory derived perception has a roughly five fold lower angular velocity threshold than that of vestibular sensation. Perception of self-motion has been modeled by linear summation of the high-pass vestibular signal and a “bottom-up” proprioceptive signal with low-pass characteristics (Mergner et al, 1991, 1993). Given the time course of the vestibular signal, the bottom-up PK pathway would likely be a better candidate for controlling the angular velocity profiles expected during normal locomotion.

Central processes

In a study by Anstis (1995) perception and motor output of locomotion were remodeled by adaptive conditioning on a linear treadmill. Compared to subjects who jogged in place or ran around the block, subjects who jogged in place on a straight treadmill for 60 seconds could not thereafter jog in place on the ground without vision. Instead, they advanced linearly. Despite altered perceptual after-effects, Anstis (1995) ruled out central components such as vestibular adaptation by a hopping test in which his subjects hopped in place with a single leg on a moving treadmill, and afterward attempted

hopping in place on the ground without vision. The subjects then unconsciously traveled forward when hopping on the same (adapted) leg but not when the contralateral leg was used to hop. The fact that no inter-limb transfer occurred suggested to the authors that the adaptation occurred within neural pathways that control each leg independently during locomotion (i.e. the spinal level of control). Alternately, this may demonstrate a dependence of the adaptive manifestation on the action of locomotion, i.e. on the context of the adaptation.

Indeed, Brandt et al (1977) have demonstrated illusory ego-motion and nystagmus in a stationary subject during passively generated movement of the arm in contact with a rotating drum in the dark. Bles & Kotaka (1986) also recorded nystagmus during *apparent* locomotion in the dark on the periphery of a rotating treadmill. These results indicate that arthrokinetic and podokinetic information arriving via somatosensory inputs reaches at least the level of the brainstem.

Podokinetic information may be provided via feed forward mechanisms related to locomotion. The fact that there was no "jolt" during initial foot contact with the rotating disc during adaptive conditioning suggests that information about the appropriate angular position and velocity of the foot is available prior to foot contact.

The adaptive characteristics of the podokinetic system observed in the present study indicate that it is capable of using somatosensory information for spatial orientation and maintaining calibrated motor output during slow, prolonged locomotion. Given a space stable environment, rotation of the body in space can be accurately measured via the relative movement between feet and trunk. This source of proprioceptive information has been shown to interact with vestibularly derived information to give accurate perception of

spatial orientation (Mergner, 1993). The above results suggest that the podokinetic system is well suited for control of spatial orientation during locomotion.

min °/sec	11.3	23	45	90
60				
30				
15				
7.5				

Table 2.1 Podokinetic Adaptive Conditions. Six subjects each completed seven experimental conditions in which the adaptive stimulus velocity and duration were varied. The conditions used in the present study are hatched in gray.

Stimulus Amplitude (°/s)	Response characteristics (°/s)			
	y-intercept (col 1)	asymptote (col 2)	1 st order resp (col 1) - (col 2)	time constant (min)
11.25	5.6	1.9	3.7	9.1
22.5	9.3	2.8	6.5	8.3
45	17.3	4.4	12.9	8.0
90	24.6	5.0	19.6	4.5

Table 2.2 Stimulus Magnitude. Calculated values of y-intercept, the asymptote, the estimated first order response magnitude and the time constant of response for each of the curves in Fig 2.3. The estimated first order response magnitude is calculated by subtracting the value of the asymptote from that of the y-intercept for each stimulus amplitude. Note the increasing value of the estimated first order response with increasing stimulus amplitude.

Stimulus Duration (min)	Response characteristics (°/s)			
	y-intercept (col 1)	asymptote (col 2)	1 st order resp (col 1) - (col 2)	time constant (min)
7.5	10.7	1.9	8.8	4.2
15	13.2	2.2	11.0	5.9
30	17.3	4.4	12.9	8.0
60	15.2	4.2	11.0	10.3

Table 2.3 Stimulus Duration. Calculated values of y-intercept, the asymptote, the estimated first order response and the time constant of response for each of the curves in Fig 2.5. The estimated first order response is calculated by subtracting the value of the asymptote from that of the y-intercept for each stimulus duration. Note the relatively consistent value of the estimated first order response with increasing stimulus duration after 7.5 minutes.



Fig. 2.1 Podokinetic Adaptive Stimulus. Subjects stepped in place around the axis of the horizontally rotating treadmill in the light during all adaptive conditioning. Vision and overhead safety handles maintained trunk stationarity while the stance foot was required to turn with the treadmill. During swing phase the foot angle reset relative to the trunk.

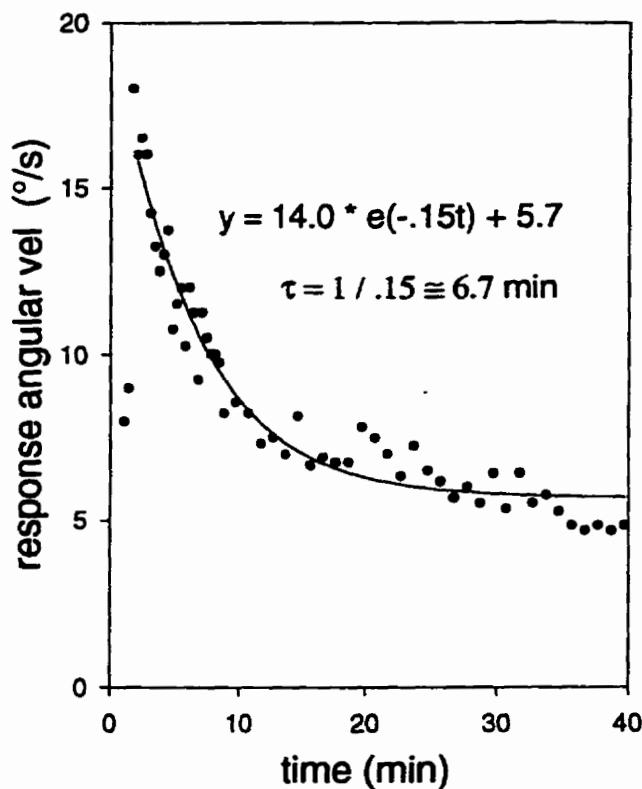


Fig. 2.2 Individual Podokinetic after rotation (PKAR). Example of data obtained from one blindfolded subject attempting to step-in-place without turning after podokinetic adaptation of 45°/s for 60 min. The subject's angular velocity relative to space is plotted against duration after cessation of the adaptive stimulus. Each point shows the subject's average angular velocity of rotation relative to space during 20 or 60 sec sampling intervals. Angular velocity of trunk rotation relative to the ground measured over 40 min shows an exponentially decaying response and a continued tendency to turn at the end of 40 min. Note that responses obtained within the first minute are significantly lower than subsequent measurements and are excluded from fitted curve.

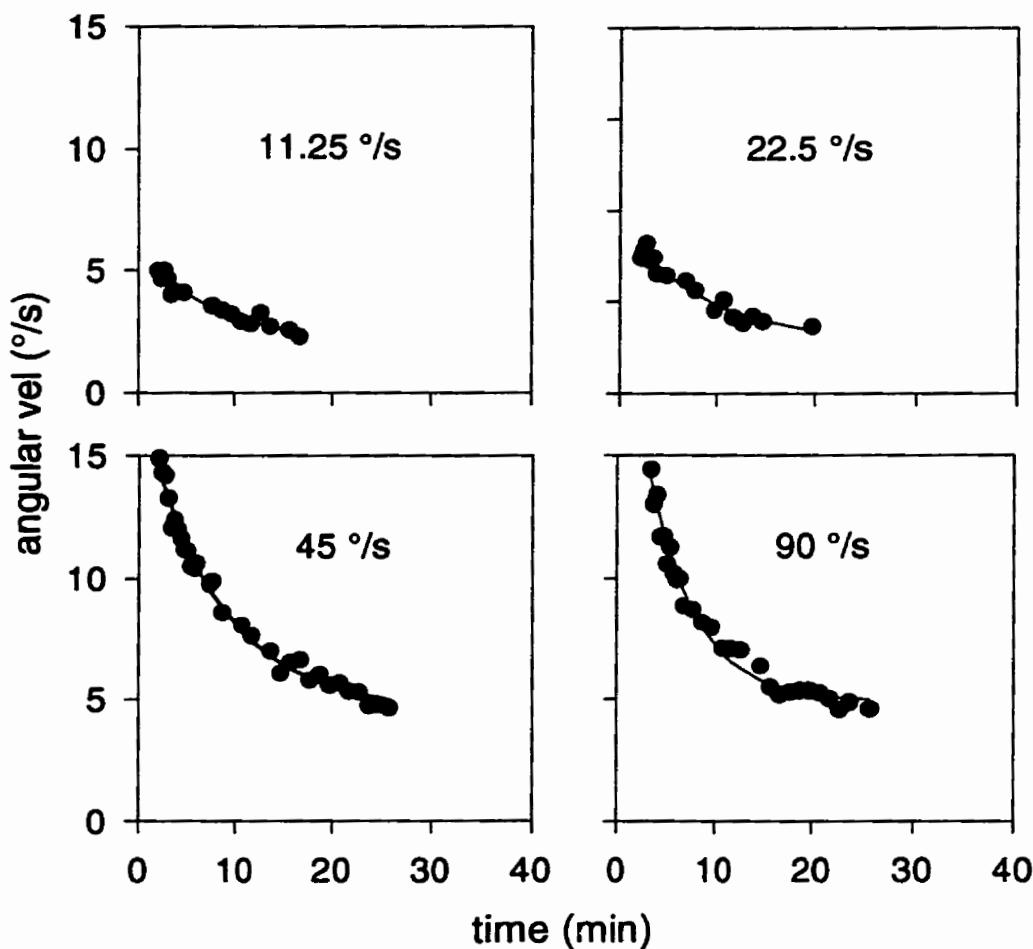


Fig. 2.3 Effect of Stimulus Magnitude. Average data from six subjects following adaptive conditioning at stimulus velocities of 11.25, 22.5, 45 & 90 deg/sec, each maintained for 30 min. ($N = 6$ for each data point plotted) Each data point represents the average value obtained from six subjects within a given time slot (bin) after cessation of the adaptive stimulus. Bin duration is adjusted to include at least one estimate from each subject (see Methods); hence the apparent paucity of points in some regions of the curves. The difference between the extrapolated ordinate intersect and the corresponding asymptote of each curve is defined as the response amplitude of the first order system. Averaged PKAR demonstrates a marked dependence of response amplitude on the amplitude of the adaptive stimulus (see text).

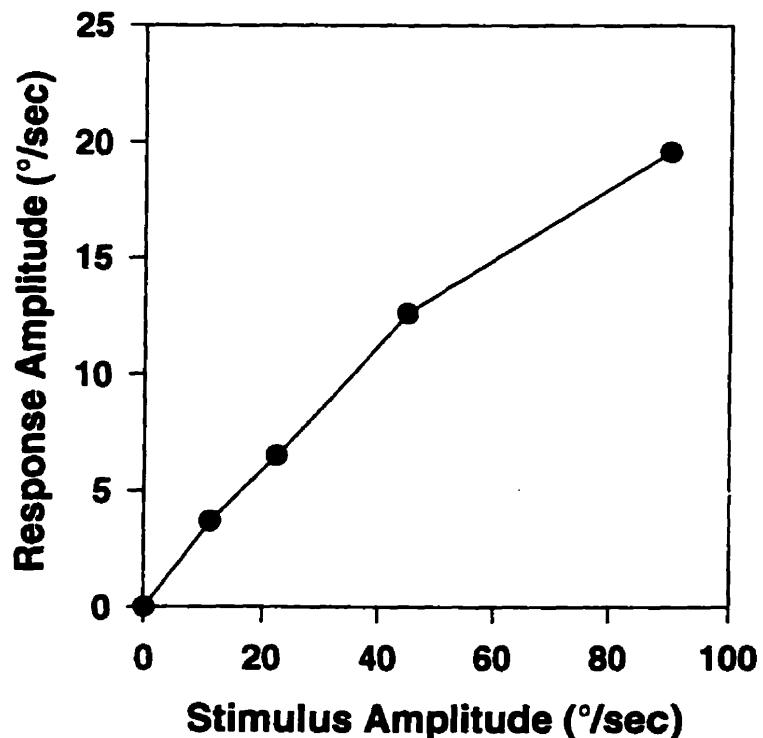


Fig. 2.4 Relationship of PKAR velocity to stimulus velocity. The response amplitude of the first order system is plotted against stimulus velocity ($^{\circ}/s$). The response amplitude is estimated by calculating the difference between the extrapolated ordinate intersect and the corresponding asymptote of each curve of Fig 2.3. Each data point represents the average response amplitude of six subjects ($N = 6$). Linear regression of the plot of the response velocity vs. stimulus velocity up to $45 ^{\circ}/s$ produces a response gain of 0.26 ($r^2 = .99$) for the first order component of the locomotor output of the adapted podokinetic system.

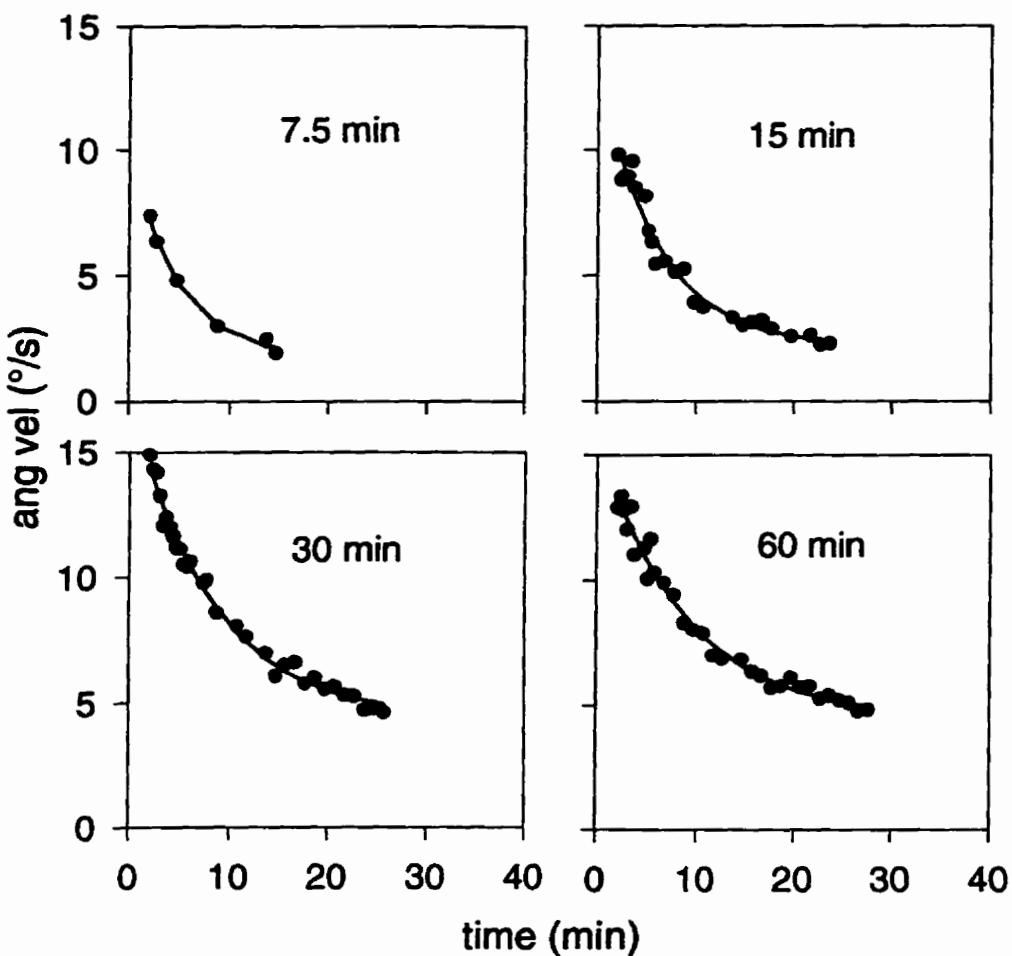


Fig. 2.5 Effect of Stimulus Duration. Average data from six subjects following adaptive conditioning at a stimulus velocity of 45 °/s and maintained for each of 7.5, 15, 30 & 60 minute durations. Each data point represents the average value obtained from six subjects within a given time slot (bin) ($N = 6$). Bin duration is adjusted to include at least one estimate from each subject (see Methods); hence the apparent paucity of points in some regions of the curves. Averaged PKAR demonstrates little dependence of the first order response amplitude (calculated as the difference between the extrapolated ordinate intersect and the corresponding value of the asymptote) on stimulus duration after 7.5 minutes.

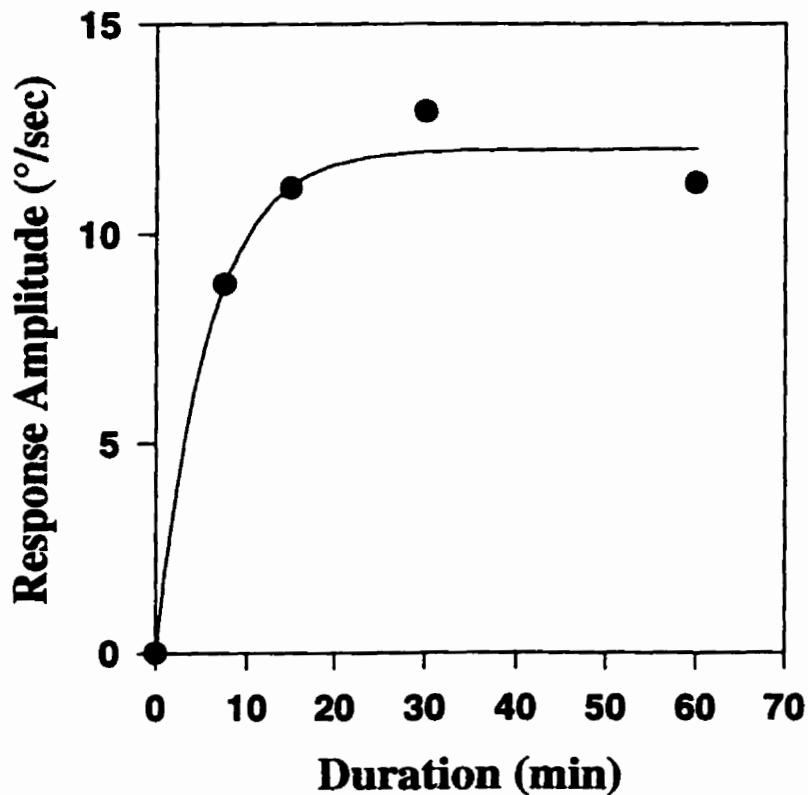


Fig. 2.6 Relationship of PKAR velocity to stimulus duration. The response amplitude of the first order system is plotted against stimulus duration (min). The response amplitude is estimated by calculating the difference between the extrapolated ordinate intersect and the corresponding asymptote of each curve of Fig 2.5. Each data point represents the average response amplitude of six subjects ($N = 6$). The response amplitude tends to plateau at about 12 °/s after an initial rise compatible with an adaptive “charging” time constant of between 5 - 10 minutes, consistent with the average “discharging” time constant of 6.3 ± 0.05 S.E minutes.

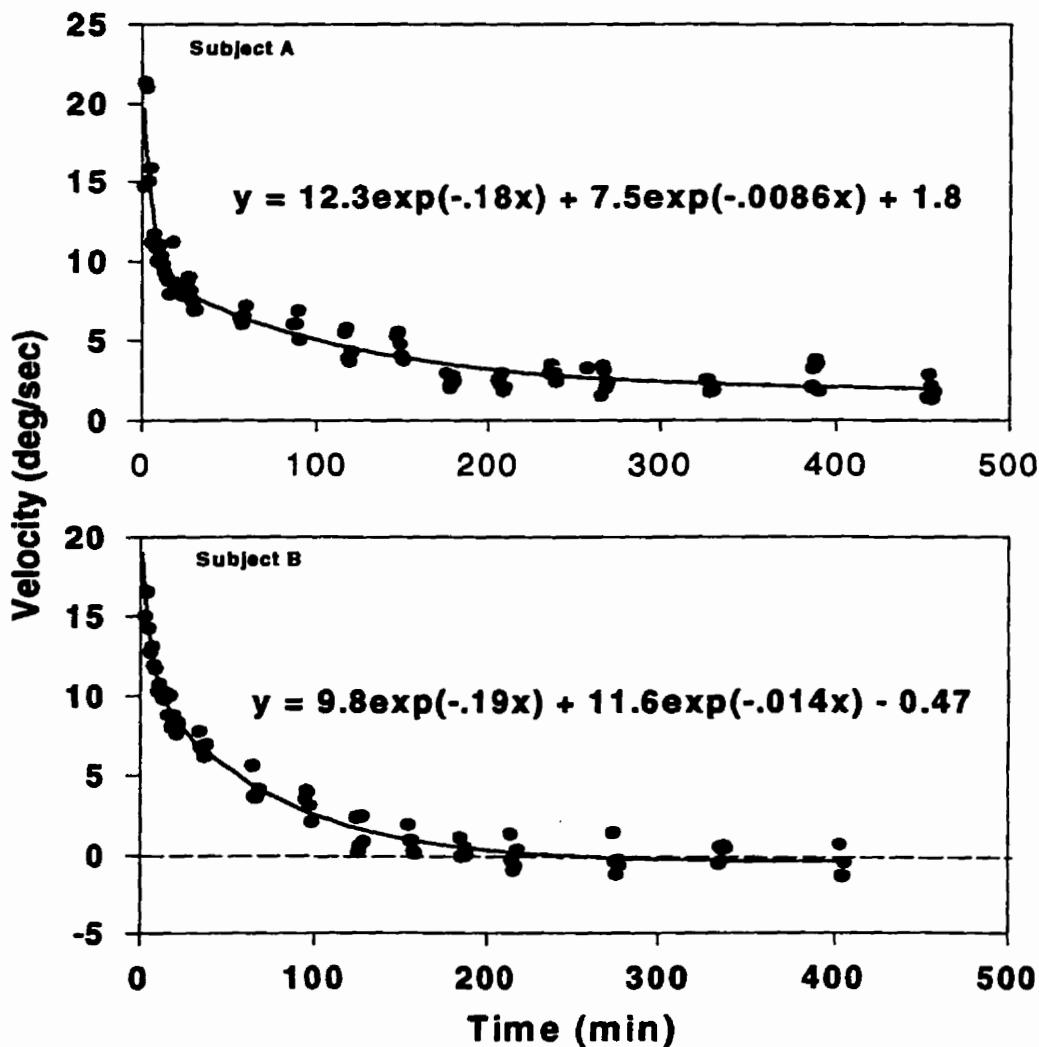


Fig. 2.7 Long Term PKAR. Results of long-term experiments conducted on two subjects. The adaptive stimulus was 45 °/sec maintained for 1hr. Results are plotted on an extended time base and fitted with second order curves defined by the insert equations. The values of the ordinate intersects (average 21 °/s) were similar to those produced in the main experiment, as were the “short” time constants of the fitted curves (average 5.6 min). In contrast the “long” time constants were greatly extended, emerging as 120.5 min and 71.4 min for subjects A and B respectively. The final asymptotic values of both curves were close to zero, indicating effective loss of the adapted condition by 8 hours.

Chapter 3 : PODOKINETIC AND VESTIBULAR INTERACTION

Introduction

Spatial orientation during locomotion is thought to be orchestrated by the visual, vestibular and somatosensory systems. Due to its high-pass characteristics the vestibular system is inappropriate for the control of slow, low frequency changes of direction during normal walking. In the study described in Chapter Two, we demonstrated that an alternative means of control is available through Podokinetic (PK) reference of body orientation to the space-stable foot on the ground.

In the study described in this chapter we asked two questions: 1) How does concurrent vestibular stimulation interact with the PK signal generated by stepping around in the dark?; and 2) What is the effect of PK adaptation on this interaction?

Important in the context of the present study is evidence from several studies that both self-motion perception and nystagmus can be generated in the absence of vestibular canal input by either arthrokinetic or optokinetic stimulation (Brandt et al, 1977; Bles et al, 1983; Bles & Kotaka, 1986; Guedry & Benson, 1983; Solomon & Cohen, 1992). Furthermore, there is compelling evidence for *interaction* between vestibular and arthrokinetic oculomotor influences. Guedry and Benson (1983) found that per-rotational nystagmus and self-motion perception were augmented during rotation generated by active lower limb movement when compared to similar passively induced rotation. Bles & Kotaka (1986) demonstrated that compensatory nystagmus occurred in human subjects while they walked at a constant angular velocity for a prolonged period inside a darkened

circular drum. Although actual head-re-space movement occurred, the relevant vestibular signal quickly decayed due to the constant angular velocity of the head in space. They also showed that the post-rotational nystagmus that is normally associated with stopping rotation exhibited reduced velocity, suggesting that central information from a source other than vestibular stimulation was available to counter the post-rotational input from the semicircular canals. They concluded that somatosensory input or an efferent copy of motor output related to angular walking had activated velocity storage in the vestibular system, and that velocity storage had produced the continuing nystagmus during locomotion and caused reduction in the post-rotational response.

What purpose would such velocity storage serve in spatial orientation? Solomon & Cohen (1992) suggested that velocity storage might support ocular nystagmus during natural locomotion and minimize inappropriate post-rotational nystagmus with stopping. Thus the first phase of the study described in this chapter examined the oculomotor response in human subjects to active stepping around in the dark at 15 °/s (combined podokinetic and vestibular stimulation) and compared it to the response produced by passive rotation at 15 °/s (vestibular stimulation alone). In addition, we examined the effect of these stimuli on post-rotational nystagmus.

An interesting feature of the podokinetic after-rotation (PKAR) in the study described in Chapter Two, was that although blindfolded subjects turned relative to space at angular velocities above vestibular threshold, no subject perceived self-motion. Perception of self-motion is generally reflected in the magnitude of the “compensatory” oculomotor response. Given the lack of perceived rotation during PKAR, one might expect the oculomotor response to be similarly attenuated. Furthermore, PKAR is a

similar stimulus to self-propelled stepping around in the unadapted state, except that the movement, albeit active, is not consciously generated. Thus the second phase of the current study examined the oculomotor response during stepping around in the unadapted state and compared it to the response after adaptation (PKAR).

Perception of self-motion during passive horizontal sinusoidal rotation ranging from 0.025 - 0.4 Hz frequency has been extensively investigated by Mergner and co-workers (1983, 1991, 1993; Hlavacka et al, 1992). They developed a psychophysical model of perception of self-motion during combined vestibular and proprioceptive stimulation. The model predicts that during low frequency, low velocity rotational movement, such as stepping slowly around on solid ground, low threshold proprioceptive stimuli derived from the "bottom-up" along the body axis (i.e. foot, trunk, neck), will sum linearly with the high threshold vestibular response of head-in-space rotation (Mergner et al, 1991, 1993; Hlavacka et al, 1992). By doing so, low frequency information needed for spatial orientation is retained, and self-motion perception is veridical even at low frequency and velocity. The present studies extend the range of the psychophysical model and examine its application to ocular-motor control.

In view of the above observations, the aim of the present study is to employ reflexly induced compensatory eye movement as a quantitative index of interaction between the vestibular and podokinetic systems in the normal and PK-adapted states. First we compare the normal passively induced VOR with the compensatory oculomotor response obtained in the dark when the unadapted subject *consciously* steps around over the axis of the stationary turntable. This self-propelled rotation generates simultaneous vestibular and PK stimuli. How does the vestibular signal, generated by the semicircular

canals, interact with the podokinetic signal generated by stepping around? Next, bearing in mind the results reported in Chapter Two, we asked how the vestibular-PK interaction would be modified by similar active rotation induced *subconsciously* by post-adaptive podokinetic after rotation (PKAR)? Would the resulting loss of rotational perception be associated with an altered oculomotor response?

Methods

Five healthy subjects between the ages of 20 - 72 years participated in this study after providing informed consent. Three of the subjects were experimenters, and participated in the previous studies described in Chapter Two. Each subject performed a total of four experimental sessions; two "passive" and two "active" sessions as detailed below.

Subjects wore a snug-fitting adjustable head-band. An infrared transducer (Skalar IRIS , Model 6500, Netherlands) was attached to the head-band in front of the right eye, and recorded changes in the horizontal position of the eye relative to the head. The transducer was able to record $\pm 30^\circ$ of horizontal eye movements with a resolution of < 1.5° of arc and a bandwidth of 200 Hz. A Watson single axis rate sensor (Model Vorteq 100, $\pm 100^\circ/\text{s}$) was clipped to the head band and recorded horizontal angular velocity of the head relative to space. The data was collected on-line by a PDP11/73 computer and REX system (Hayes et al, 1982). The sampling rate of the recorded signals was 200 Hz.

The leads from the IRIS and the Watson were positioned to ascend axially above the subject's head allowing 10 - 15 rotations in the horizontal plane. Subjects stood over the axis of a rotating platform mounted on the same rate controlled turntable system

(Neurokinetics Model 80R) as was used in the previous studies (see Chapter Two Methods). The room was made light-tight and inappropriate auditory cues were eliminated. On the head-band were four small luminescent stickers located at 90° intervals. These were not visible to the subject, but used by an observer in an otherwise dark room in the active conditions as outlined below.

Each subject was asked to stabilize his/her head relative to the trunk as shown in Fig 3.1, and to maintain that position throughout all experiments. Inspection of records of head position relative to space showed no head nystagmus during trunk rotation suggesting that this method of head-re-trunk stabilization was effective. Eye blinking occasionally obscured eye movement records and were excluded from analysis.

Calibration routines

For calibration, the subjects stood over the axis of the turntable and stabilized their head relative to their trunk as described above (Fig 3.1). Next, by adjusting their horizontal angular position on the turntable, they subjectively centered their eyes with respect to their head using a central target for reference. This established a baseline for the IRIS system. The measurement of horizontal eye position (re head) was calibrated by having subjects make saccades between targets at +20° and - 20° located three meters from the subject (Fig 3.2a). The measurement of head position was calibrated by having the subject fix their eyes on the central target and rotate their head and trunk together through approximately 20° to the right and left as in Fig 3.2b. With the eyes fixed on the central target, the change in head position was equal and opposite to the recorded change in calibrated eye position. The calibration routines were performed several times

throughout the experiment. No subject demonstrated spontaneous nystagmus in the dark prior to experimentation.

Overview of experimental paradigms

Each subject performed four separate experimental sessions. Each of the four sessions comprised a combination of two fundamental conditions, namely the type of stimulus (active or passive) and the state of adaptation (unadapted or adapted). Firstly, in two of the four sessions the stimulus was passively induced rotation of the subject while he/she stood on the axis of the turntable. In the other two sessions the stimulus was active rotation generated by the subject stepping round the axis of the stationary turntable. These stimulus conditions allowed comparison of the oculomotor response during purely vestibular stimulation (passive rotation) to the response during concurrent podokinetic and vestibular stimulation (active rotation). Secondly, the response in each experimental session was recorded first while the subject was in the “unadapted” state and again (after standard podokinetic adaptation) in the “adapted” state. These conditions allowed examination of the effect of podokinetic adaptation on the responses to both passive and active rotation. Thus, each experimental session began by recording the “unadapted” response to either passive or active rotation. Next, subjects underwent standard podokinetic adaptation, followed immediately by recording the “adapted” responses to either passively induced rotation or to PKAR. For each experimental session, the type of rotational stimulus (i.e., passive or active) in the adapted state was the same as that in the unadapted state. Each paradigm is described in detail below.

In the two experimental sessions in which the rotational stimulus was passive, the direction of turntable rotation during adaptation (the adaptive stimulus) was the same in both sessions. The difference between the two "passive" sessions was that the direction of the rotational stimulus in the adapted state was clockwise in one session and counterclockwise in the other. Thus, the two sessions together examined the effect of podokinetic adaptation in one direction on the vestibular response in both directions. Note that the direction of the adaptive stimulus was counterclockwise for three subjects and clockwise for two subjects.

In the two sessions in which the rotational stimulus was active, the direction of the adaptive stimulus was clockwise in one session and counterclockwise in the other. Thus, the resulting PKAR (i.e., the rotational stimulus in the adapted state) was counterclockwise in one session and clockwise in the other, respectively.

The adaptive podokinetic stimulus in all experimental sessions was $45^{\circ}/s$ for 30 minutes. Recall from Chapter Two that following such a podokinetic adaptation subjects rotated at approximately $15^{\circ}/s$ while attempting to step-in-place in the dark. Therefore, a velocity of $15^{\circ}/s$ was used for passive rotational stimuli and for active rotational stimuli in the unadapted state, in order to compare the resulting oculomotor responses. All measurements in the adapted state were completed within the "short" time constant of the podokinetic system (5 - 10 minutes).

During all paradigms, subjects were asked to attempt to "look" at a mental image of the outside world. Barr et al (1976) found that subjects were able to achieve a VOR gain of close to unity when asked to fixate imaginary targets in the dark that were

stationary in space, compared to a VOR gain of around 0.65 when doing mental arithmetic during sinusoidal rotation.

Measurement of the VOR response to passively induced rotation

Unadapted State

After performing the calibration routines, the lights were extinguished and subjects were exposed to a step of turntable velocity of 15°/s in the clockwise direction (see Fig 3.3) while compensatory per-rotational eye movements were recorded for two minutes (Fig 3.4). At this point the turntable was stopped instantaneously (i.e. with a step change to zero velocity) and the resulting post-rotational VOR was recorded for two minutes while subjects stood still. The light was then switched on and the calibration routines were repeated. The lights were again extinguished and the procedure was repeated in the opposite direction. The calibration routines were repeated again.

Adapted State

Immediately upon cessation of podokinetic adaptation, the calibration routines were performed quickly. The lights were extinguished and subjects were exposed to the first half of the step velocity paradigm used in the unadapted state (i.e., the first four minutes of the stimulus profile in Fig 3.3). In another otherwise identical experimental session, after adaptation, the subjects were exposed to the other half of the paradigm (for further explanation see “Overview of experimental paradigms” above).

Measurement of the oculomotor response to actively induced rotation (combined vestibular and podokinetic stimulation)

Unadapted State

In order to generate simultaneous vestibular and podokinetic stimulation subjects were required to actively "step around" the axis of the stationary turntable at 15°/s for 2 minutes in the dark. To retain centrality on the platform they maintained periodic foot contact with a smooth nylon cylinder of eight centimeters diameter rising from the center of the turntable. This prevented linear movement of the subject but did not provide an angular space reference. Attempting to maintain a prescribed angular velocity of stepping for two minutes in the dark proved difficult and required practice. To this end an experimenter observed luminescent markers on the subject's headband and verbally indicated 90° of the subject's rotation. This permitted the subject to maintain a relatively constant angular velocity by reference to the time base of 2 Hz stepping frequency and without absolute directional references. Care was taken to avoid generating a vestibular bias during practice.

After sufficient practice, the measurements of eye and head position were calibrated as described above. Subjects then propelled themselves around the axis of the turntable at approximately 15 °/s in the clockwise direction for two minutes in darkness while the eye position and head angular velocity were recorded. At the end of two minutes subjects stopped stepping and the post-rotational response was recorded for a further two minutes. The lights were then switched on and the calibration was repeated. The active

stepping routine was then repeated in the counterclockwise direction. Thus, the stimulus velocity profile simulated that of passive rotation (see Fig 3.3). After the second trial, the calibration routines were repeated.

Adapted State (PKAR)

Immediately following the podokinetic adaptation the calibration routines were performed quickly. Subjects then attempted to step-in-place in the dark on the disc (but in fact turned at angular velocities of close to $15^{\circ}/s$) for a duration of two minutes while eye position and head angular velocity were recorded. The subjects then stopped and stood still in the dark for another 2 minutes, after which the lights were switched on and the calibration routines repeated.

Data analysis

Analogue signals from the Iris (eye position-re-head), the Watson (head velocity-re-space) and the turntable tachometer (turntable-re-space) transducers were digitized and recorded by the PDP 11/73 computer system noted above. PC software programs were developed to calibrate these digitized records prior to interactive analysis of the data. After transfer to a PC system the eye position signal gain was adjusted according to the $\pm 20^{\circ}$ calibration (Fig 3.2a). To obtain a record of head position the Watson signal of head velocity was integrated. To calibrate the derived head position signal, the gain was adjusted to match the amplitude of head position with that of eye position (in the opposite direction) for the calibration routine shown Fig 3.2b. To minimise cyclical perturbations of

head velocity caused by the physical action of stepping at 2Hz, the change of head position was averaged over consecutive 10 s periods. Figure 3.4 illustrates the traces of eye and head positions obtained from one subject during a passively imposed rotational stimulus of 15 °/s, maintained constantly for 60 seconds. The head position trace has been offset in Figs 3.4, 3.7 & 3.14, for illustrative purposes.

To obtain plots of eye velocity with respect to time consecutive selected segments of slow phase eye movement were marked by cursor on the computer screen. Eye velocities were then calculated from the slopes of each trace within each segment and, together with head velocities (estimated as described above), were plotted against time, as exemplified by Figs 3.5 , 3.8, and 3.15.

To obtain the averaged response of the group of five subjects, individual eye and head mean velocities were binned for every one second interval and the summed value for each bin was divided by five. After binning, averaged head velocities obtained for the active paradigms were smoothed by a 7 point running average. Averaged eye and head velocities were then plotted against time at the mid-point time of each bin. When subjects contributed several estimates within a time bin, their values were averaged before committing that subject's value to that bin. When subjects did not contribute to a time bin because there were no slow phase eye movements observed a zero value was assigned and included in the average value. The group data shown in Figs 3.6, 3.9, 3.11, 3.12.,3.13.,3.16, and 3.18 were obtained in this way. As shown in those figures, the resulting average responses obtained for each of the four paradigms were plotted against time and fitted by least squares regression to a first order exponential curve. These calculated curves were extrapolated to intersect the ordinate and used

to estimate the response velocity (y-intercept), the time constant of response decay, and the asymptote (abscissa).

Results

Although subjects attempted during rotations in darkness to imagine and "look" at the surrounding room, most reported great difficulty in doing so while stepping around. Perception of rotation relative to the environment varied between subjects; one experienced subject was able to detect post-rotatory sensations, while the naive subjects had less clear perceptions of turning.

Oculomotor responses in the unadapted state

VOR response to passively induced rotation

Fig 3.4 shows an example of eye and head movements obtained from one subject in response to a step velocity stimulus of 15 °/s of passively induced clockwise rotation. The slope of the trace of head position indicates a constant head velocity of 15 °/s. The eye position trace shows the resultant ocular response (nystagmus) relative to the head, in which compensatory slow phase segments are interspersed with quick repositioning quick phases. The velocity (slopes) of the slow phases reflect the initial vestibular response and its subsequent exponential decay, as described in Chapter One. This feature is more clearly evident in Fig 3.5 which plots the calculated eye angular velocity of each slow phase segment against time for one subject. The upper set of open data points shows the

constant servo-driven turntable angular head velocity of 15 °/s. The lower, filled points, show the progressively declining slow phase eye velocity, fitted with a first order exponential curve, and yielding a classical VOR response with a gain (ordinate intersect/stimulus velocity) of 0.60 and a time constant of 12.5 seconds.

Fig 3.6 shows the averaged response of all subjects to a step velocity stimulus of 15 °/s of passive rotation, fitted to a first order exponential curve. The equation that emerges from the fitted curve shows an initial response of approximately 10 °/s, indicating a VOR gain of approximately 0.67. The calculated time constant of the equation is 20 seconds (see left panel of Table 3.1).

The average post-rotational VOR response of all subjects was indistinguishable from the average per-rotational VOR response and was thus grouped together as a baseline measure of VOR response to passively induced rotation in the unadapted state.

Oculomotor response to actively induced rotation

Fig 3.7 shows an example of eye and head movements obtained from one subject during active self-propelled stepping around in the dark. Evident in the trace of head position re space is the “noise” originating from the 2 Hz stepping frequency. The trace of eye position re head shows the resultant ocular response. Here too, considerable “noise” is introduced compared with the traces of Fig 3.4, due to the irregularities of active stepping and the resultant compensatory eye movements.

Calculated head and slow phase eye velocities for this record are shown in Fig 3.8. Recall that each data point of eye movement is derived from a single slow phase segment.

Although these points are more widely scattered than in the passive condition, there is a trend for a vestibular-like decay during the first 60 seconds. However, unlike the responses to passively induced rotation, as exemplified in Fig 3.5, there remains a distinct average positive bias of slow phase eye velocity during the second half of the response. These features are more clearly evident in Fig 3.9, which shows the corresponding averaged responses from all subjects. As suggested in Fig 3.8, there is clearly a vestibular-like decay during the first half of the record and a positively maintained response during the second half of the record. This latter feature is in marked contrast to the purely vestibular response to passive rotation, as shown in Fig 3.6. Taken together these two features suggest the combination of two response components, one vestibular and one due to podokinetic stimulation incurred by the actively generated rotation. Fig 3.10 shows the result of subtracting the purely vestibular response to passive stimulation (Fig 3.6) from the response to combined stimulation (Fig 3.9). The outcome is a rather constant ocular slow phase response which has a mean value of 5.5°/s (+/-0.2 SE), which presumably represents the ocular response to the actively generated PK stimulation. Linear regression of the eye movement yields the equation:

$$y = 6.2 - 0.01t,$$

indicating virtually no slope to the described data. The amplitude ratio of eye to head velocity reveals a PK-generated oculomotor gain of approximately 0.37 (5.5/15).

Post-rotational oculomotor response on stopping “active” stepping around

When subjects stop active self-propelled stepping round and stand still, a reversed vestibular signal is generated. Fig 3.11 shows the averaged response from all subjects to cessation of active stepping round in the dark following an average angular head velocity of 15.0°/s ($\pm 0.2\text{SE}$) during the second minute of the stimulus profile of Fig 3.3. The data in Fig 3.11, when fitted with a first order exponential curve, shows an average initial velocity of 6.4 °/s (see Table 3.1). Although clearly showing a vestibulo-ocular response, the initial VOR gain is 0.43 (6.4/15.0), which is reduced when compared to the averaged passive VOR gain of 0.64 (9.6/15.0) (see Table 3.1). Similarly, the fitted curve in Fig 3.11 reveals a calculated time constant of 10s, compared to 20s for the equivalent value representing the average passively induced per-rotational VOR response.

Oculomotor responses in the adapted state

VOR response to passively induced rotation

Following PK adaptation, the VOR responses to passively induced rotation of 15 °/s for 2 minutes duration in the dark were divided into two groups according to the direction of passive rotation as related to the direction of the preceding adaptive stimulus (see Methods). The first per-rotational post-adaptation trials, which were in the *same* direction as the adaptive stimulus were grouped together, as were the second trials, which were in the *opposite* direction. The per-rotation ocular responses in the adapted state were averaged and plotted against time as described in Methods (data analysis). Figs 3.12 & 3.13, show the averaged per-rotation adapted VOR responses to passive rotation in the

“same” and the “opposite” directions respectively. The calculated time constants of the averaged “same” and “opposite” adapted VOR responses are 14.3 and 25 seconds respectively; and the corresponding gains are 0.77 and 0.57 (see Table 3.1).

Oculomotor response to actively induced rotation

As expected, in response to attempted stepping-in-place in the dark immediately after PK adaptation, all subjects showed robust podokinetic after-rotation (PKAR), which was neither consciously generated nor self-perceived. Fig 3.14 shows an example of the PKAR and oculomotor response of one subject. When compared to Fig 3.7, the eye trace shows an apparent absence of identifiable slow phases in the second minute of the recording.

The slope of the PKAR head position trace in this individual record was calculated and plotted against time, and shown as the open circles in Fig 3.15. The observed pattern of decay is consistent with the pattern of PKAR shown in Figs 2.3 and 2.5 of Chapter Two. The filled circles of Fig 3.15 show the slow phase eye velocities derived from the eye position trace of Fig 3.14. The ocular motor output observed in the first minute presumably reflects the vestibular response to the recorded head movement. In the second minute there is no detectable slow phase oculomotor response despite continued active rotation. This is clearly different from the response to consciously generated self-propelled stepping around, as seen in Fig 3.9. Also note that during the time period of approximately 25 - 55 seconds in the middle panel of Fig 3.14, no slow phase eye movements could be detected, and therefore no data points are generated. When the data from all subjects are

averaged and plotted over two minutes, as shown in Fig 3.16, these points are recorded as zero values, as described above in Data analysis.

As with the unadapted active per-rotation response, (see Fig 3.9) the data of Fig 3.16 represents the average response of all subjects to concurrent vestibular and PK stimulation, but now in the adapted state. As before, it should be possible to algebraically identify the PK contribution to the observed ocular-motor response by subtracting the presumed purely vestibular response of Fig 3.6. However, the initial velocity of head rotation was constantly changing during the first minute of PKAR (Fig 3.16). Therefore, we used the data during the second minute of the response when PKAR was relatively constant and when the vestibular contribution presumably was insignificant. Fig 3.17 shows the averaged and subtracted values during the second minute of recording, and reveals the effective disappearance of the oculomotor response compared with the corresponding response prior to adaptation (see Fig 3.10).

Post-rotational oculomotor response on stopping PKAR

When asked to stop after two minutes of attempted stepping-in-place, a reversed vestibular signal was once again generated due to cessation of the actual head rotation incurred during PKAR. Fig 3.17 shows that the average head velocity during the second minute of PKAR was approximately $12^{\circ}/s$, representing the amplitude of the peripheral vestibular stimulus incurred upon sudden cessation of stepping. Fig 3.18 shows the averaged post-rotational response of all subjects to that stimulus, fitted with a first order

exponential curve, revealing a gain of 0.79, and a time constant of approximately 10 seconds (Table 3.1).

Discussion

The results reported in Chapter Two demonstrated a robust adaptive component in a somatosensory/motor system, which we have termed "Podokinetic" (PK) on account of its presumed function of controlling spatial orientation during locomotion by referencing trunk angular position relative to the space-stable stance foot. In the present chapter the following two questions are addressed. First, how does the response of this presumed PK system interact with the concurrent vestibular stimulation of most natural movements? Secondly, given such interaction, how would it be modified by adaptive remodeling in the PK system as defined in the preceding chapter?

The compensatory oculomotor response to rotational stimulation was chosen for these investigations because of the extensive background knowledge of the vestibulo-ocular reflex (VOR), and because of evidence in the literature that appropriate arthrokinetic stimuli can generate "compensatory" nystagmus (Bles et al, 1983; Bles & Kotaka, 1986; Guedry & Benson, 1986; Solomon & Cohen, 1992).

VOR response to passively imposed rotation

A standard stimulus of 15 °/s was used throughout this study to allow comparison with the PKAR, which was predicted to have a velocity of about 15°/s from the results of Chapter Two. First the normal VOR was tested using conventional methods, both to

ensure the normality of our subjects in this respect and to provide a base reference against which to compare the response to combined vestibular and PK stimulation. The results summarized in Fig 3.6, indicate that the dynamics of the averaged VOR response of our subjects are consistent with the theoretical response of the vestibular system. Recall from Fig 1.3, that while the initial response to a step change in head angular velocity is a proportionate cupular deflection, during subsequent constant velocity rotation, the elastic restoring force of the cupula causes an exponential decay of the vestibular signal. The peripheral vestibular time constant has been shown to be extended by brainstem mechanisms to a value of 15 - 20 seconds. This value is consistent with the results of the present study, which found an average passively induced VOR time constant of 20 seconds.

The rather low VOR gain of about 0.67, shown in Fig 3.6 indicates that our subjects may have experienced difficulty in maintaining continuity of mental imagery of the external environment, as indeed was reported subjectively. Barr et al (1976) reported VOR gains in a similar range when subjects performed non-relevant tasks, such as arithmetic.

Oculomotor response to voluntary stepping around in the unadapted state

Next the combined vestibular and PK-oculomotor response was measured during self-generated rotation of approximately the same angular velocity profile in the expectation that any PK response component would be revealed by subtraction of the previously defined VOR. It might be argued that a more direct approach to generating a PK-oculomotor response would be to step-in-place on the rotating disc without

concurrent vestibular stimulation. This approach was discarded because it could not be achieved without external spatial reference, for example through vision, audition or tactile sensation. Also, it was intended that the PK-oculomotor response be examined under conditions likely to operate during natural locomotion, analogous to known optokinetic/vestibular interaction when one has free head movement in the light.

The results summarized in Figs 3.9 and 3.10 provide convincing evidence that under these circumstances there were indeed two components of response. During the first minute of rotation, when a transient VOR can be expected, there was an initial response of close to unity gain, which subsequently decayed in a vestibular-like manner. However, instead of decaying towards a zero asymptote, there was a steadily maintained response throughout the second minute, when the VOR would be expected to have disappeared. A primary feature of this study is that on algebraic subtraction of the average vestibulo-ocular response in Fig 3.6, there was a residual oculomotor response of about 1/3rd gain, *throughout* the 2 minute period of rotational movement.

Two important conclusions are drawn from this observation. First the constancy of the residual response during the *first* minute implies that during this period there was on average linear summation of vestibular and PK drives to the brainstem oculomotor system. Secondly, in contrast to the “high-pass” characteristic of the vestibular system (see Fig 1.4), the unchanging nature of the inferred PK response in Fig 3.10 implies a “low-pass” characteristic for the PK-oculomotor system. This feature is particularly interesting in view of the low-pass psychophysical perceptual response modeled by Mergner and colleagues (1993). They showed that with low frequency and velocity rotational movement on solid ground, low threshold proprioceptive input from the “bottom-up”

along the body axis will sum linearly with the high threshold vestibular stimulus of head-in-space rotation, thus retaining the low frequency content of the trunk-re-space signal.

The constant PK component of the oculomotor response in the present studies (see Fig 3.10), appears to sum linearly with the high threshold, high-pass vestibularly induced signal, (see Fig 3.6). Thus the results of the present studies support such a model of spatial orientation by lending oculomotor evidence for this "bottom-up" pathway used during slow, low frequency rotation with a stable spatial reference (the ground).

An interesting feature of Fig. 3.9 is the fact that the combined stimulus of actively generated rotation produced an initial response of close to unity gain, as would be predicted by the above model. And yet it is well known that with the appropriate mental set, the VOR alone can achieve this value (Barr et al, 1976). However in our experiments the average initial response gain of the passively generated VOR was in fact only about 2/3rd. One must wonder, if our subjects had been successful in attaining the intended mental set, would a greater than unity gain in combined PK/vestibular oculomotor response have been observed? Presumably, such a feature would not be biologically useful, and one may speculate that the gain of the PK generated ocular response may be adjusted according to context. Such an adjustment was shown to occur with vestibular/visual interaction at high rotational frequencies in the monkey (Keller, 1978); Keller reported that although there was an excessive VOR gain of 1.3 when rotationally oscillating in the dark at 5 Hz, this immediately reverted to the ideal value of 1.0 on switching on the light. It is important to remember that at this frequency there could have been no direct visual feedback acting on the oculomotor drive (Fuchs, 1967). It is also interesting that the inferred PK-oculomotor response of Fig 3.10 operates at approximately 1/3rd gain, in

view of the fact that this is similar to that of the “short-term” PKAR which emerged in the experiments of Chapter Two.

Oculomotor response to involuntary stepping around (PKAR) in the adapted state

The compensatory oculomotor response to passively and actively induced rotational stimulation was next examined after 30 minutes of adaptation to the podokinetic stimulus described in Methods. Recall that while the active rotation in the normal state is generated by consciously stepping around, in the adapted state it is unconsciously generated by PKAR, at an initial rate of turn approximating the passively imposed stimulus of 15 °/s.

The results shown in Figs 3.6, 3.12, and 3.13, indicate that the podokinetic adaptation had no significant effect on the VOR response to passively induced rotation. However the response to podokinetic after rotation (PKAR) demonstrated that although the VOR is preserved, the maintained PK-induced component of response seen in the unadapted state (Fig 3.10) disappeared in the adapted state. This is discussed further in “Central processes” below.

Post-rotatory (stopping) oculomotor response

A reversed vestibular signal was generated when rotation was stopped after the required two minute period, as exemplified in Fig 3.3. Bles & Kotaka (1986) in humans, and Solomon & Cohen (1992) in monkeys, reported that post-rotatory VOR was attenuated following prolonged constant velocity circular locomotion in the dark. Similarly, there appears to be a trend (see Table 3.1) for the gain of the post-rotatory

VOR to be reduced in the unadapted actively generated condition compared to the unadapted passively generated condition.

Central processes

What kind of central processes might exist to maintain podokinetic drive to the oculomotor system and to cancel it during PKAR in the adapted state? The demonstration of a specific component of oculomotor output that is induced by podokinetic stimulation, as evidenced in Fig 3.10 indicates that the PK system gains access to premotor components of the brainstem oculomotor system.

In these experiments, the physical process of actively stepping around was remarkably similar in the unadapted and adapted states; the main distinction of the adapted state was not in locomotor output nor in the peripheral afferent input but rather in the perceptual correlate. In the normal state the subjects were aware of their rotation whereas in the adapted state they were not. It was therefore functionally appropriate that in the adapted condition there should be no PK-oculomotor response. Is there a common factor responsible for the absence of these correlated psychophysical and motor responses? Both may be related to central remodeling of the relationship between podokinetic input and both oculomotor output and perception. During adaptation, constant podokinetic signals are generated in the absence of movement of the head or trunk in space. Under these conditions, PK-induced ocular movement and perception of rotation would be inappropriate. Thus, it follows that central remodeling may occur.

Alternatively, as noted in Chapter One, efferent copies of motor commands may contribute to context-appropriate changes in motor output and perception. If such efferent

copy signals are normally responsible for driving both the psychophysical (perceptual) and oculomotor response, perhaps the task of attempting to step-in-place without turning in the PKAR state (with no perception of turning) might cancel the relevant efferent copy signals.

In a similar context, in the adapted state, the perception of “no movement” may reflect “perceptual re-mapping” associated with the adapted motor output. Lackner (1993) has described similar perceptual re-mappings associated with distinct motor expressions, for instance in parabolic flight situations where body weight is altered and in optokinetic drum situations where the visual feedback associated with the stepping movements is altered. In other words, perception may be remodeled by the adaptation to match the new state of the locomotor output.

Putative role of the cerebellum

It is well established that the vestibulo-ocular reflex is susceptible to substantial adaptive remodeling when called for by behaviorally imposed demands for change (reviewed in: Melvill Jones, 1977; Miles & Eighmy, 1980; Berthoz & Melvill Jones, 1986). Moreover it is clear that the vestibular cerebellar cortex plays an essential role in this form of adaptive plasticity (Ito, 1982; Miles & Lisberger, 1981). For example Robinson and colleagues have demonstrated that both surgical (Robinson, 1976) and physiological (Luebke & Robinson, 1994) cerebellar cortical inactivation, completely abolished the ability to produce adaptive change in the reflex. The current view is that while cerebellar cortex is responsible for formulating the neural “teaching” signal calling for plastic change of synaptic efficacy in the reflex, the specific “learning” process takes place in brainstem neural relays of the vestibular nuclei targeted by cerebellar cortical Purkinje cell projections (duLac et al, 1995).

These mechanisms are likely to also be involved in motor learning in somatosensory motor systems. For instance, in experiments in which wedge prisms were worn as spectacles, a degree of gaze shift was required in order for subjects to visually fixate a target. When attempting to hit a seen target with a thrown object, these subjects initially missed the target by the amount proportionate to the diopter of the prism (Thatch et al, 1992). As it was evident to the subjects that the throw was not successful, with continued throws, subjects demonstrated motor learning by gradually becoming more accurate. In a similar task in patients with cerebellar damage such motor learning did not occur (Thatch et al, 1995). It would be particularly interesting to explore the role of the cerebellum in the podokinetic adaptation described in this thesis, recognizing the potential difficulties in establishing a patient population sufficiently proficient in walking, yet with clearly defined cerebellar deficits.

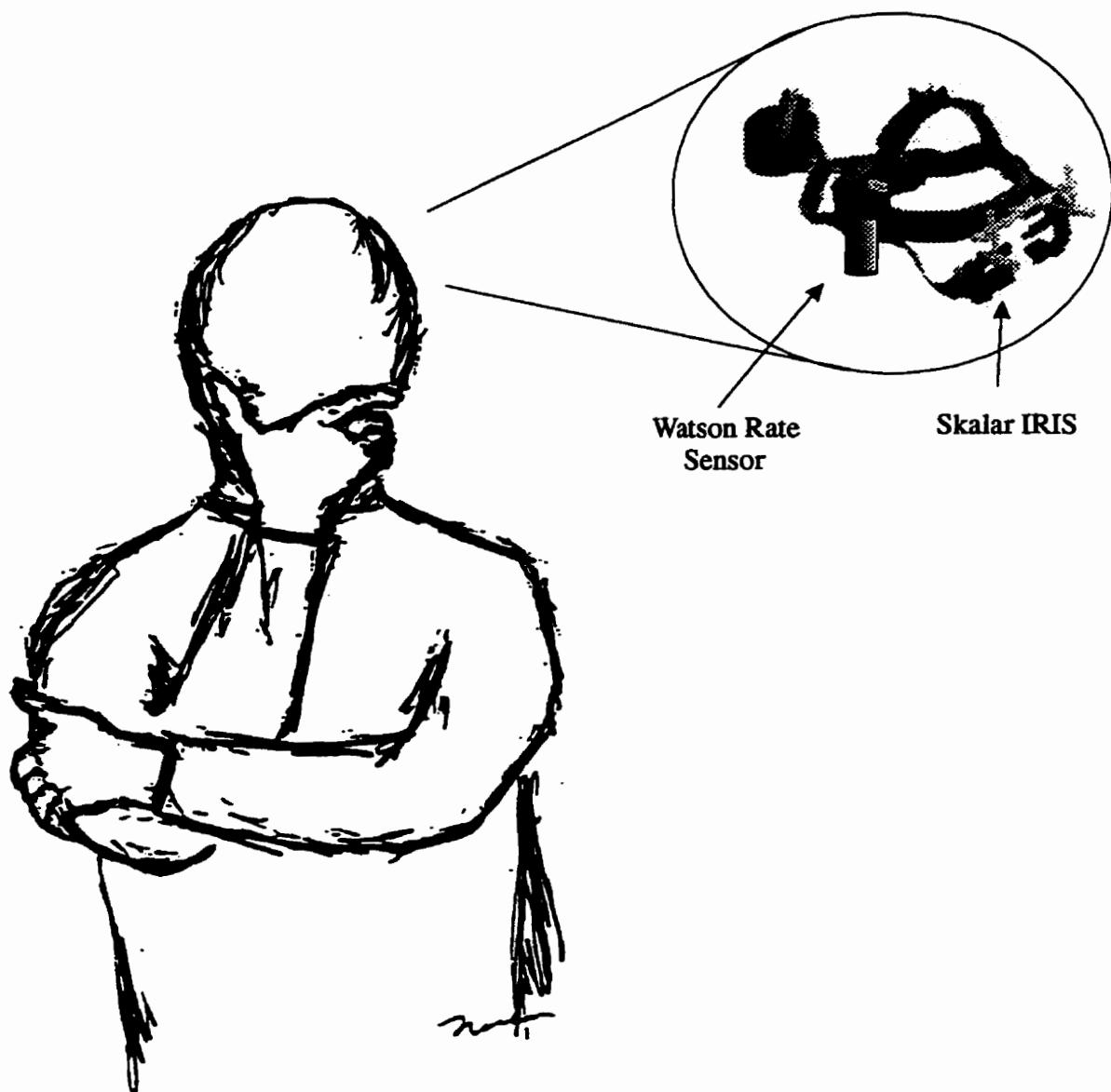


Fig 3.1 Equipment and Head Stabilization method. An infrared transducer (Skalar IRIS , Model 6500, Netherlands) attached to the headband in front of the right eye records $\pm 30^\circ$ horizontal eye in head movement. A Watson single axis rate sensor (Model Vorteq 100, $\pm 100^\circ/\text{s}$) clipped to the headband records horizontal angular velocity of the head re space. Subjects stabilized their head relative to their trunk as shown to prevent head movement on the trunk. Adapted from: Lala PK. (1996). Vestibular perception of prolonged rotational stimuli. M.Sc. Thesis Dept. of Physiology McGill University, Montreal, Canada.

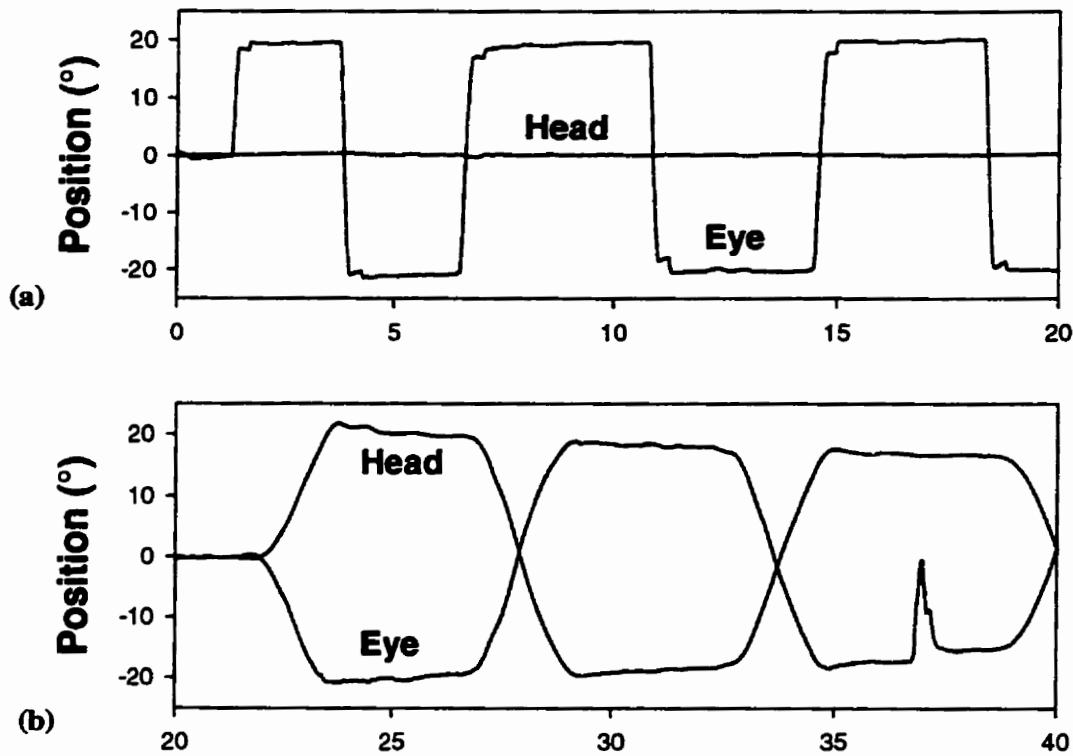


Fig 3.2 Example of calibration records. (a) Recorded angular position of eye-re-head calibrated to $\pm 20^\circ$. **(b)** Simultaneous records of angular positions of head-re-space and eye-re-head after integration of the Watson angular velocity signal. The gain of the head position trace was adjusted to match that of the eye position signal. These calibrations were applied to all subsequent data, until next re-calibrated.

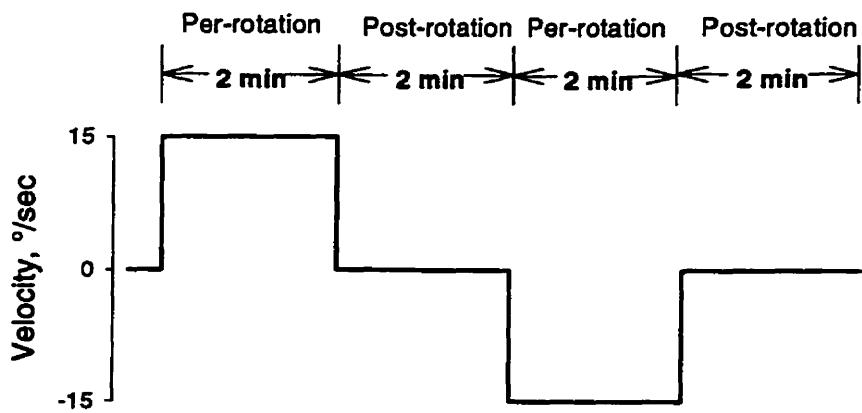


Fig 3.3 Step Velocity Paradigm in the Dark. Subjects were exposed to a clockwise step of horizontal angular velocity of $15^{\circ}/\text{s}$ for 2 minutes duration in the dark, followed by an abrupt stop for a further 2 minute period with the turntable locked and subject stationary. This procedure was then repeated in the opposite direction.

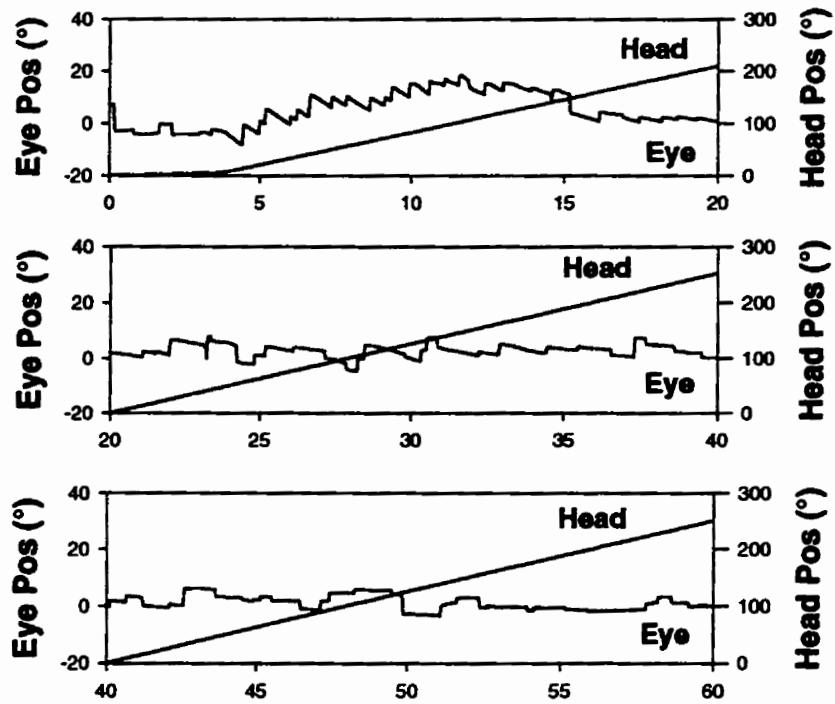


Fig 3.4 VOR response of one subject to passively induced rotation in the unadapted state in the dark. Three consecutive records show eye and head movements obtained from one subject in response to a passively induced horizontal angular step velocity stimulus of 15 °/s in the clockwise direction. Note that the time course of the decay of the slope of the slow phase eye movement (velocity) reflects the vestibular time constant.

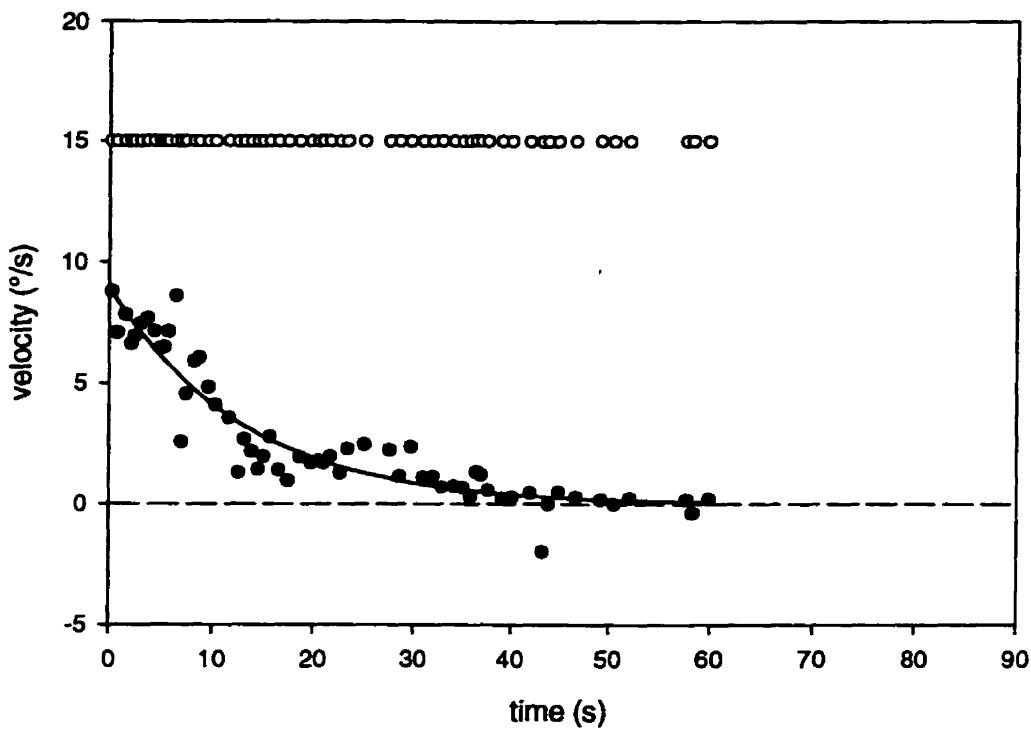


Fig 3.5 VOR response of one subject to passively induced rotation in the unadapted state. Eye angular velocities (filled circles) are calculated from consecutive selected segments of slow phase eye movement and are plotted against time (s). Open circles show the corresponding measurements of angular head velocities during constant turntable rotation at $15\text{ }^{\circ}/\text{s}$. The decay of eye velocities over time is fitted with an exponential curve, yielding an ordinate intersect at approximately $9\text{ }^{\circ}/\text{s}$, a gain of 0.6, and time constant of 12.5 seconds.

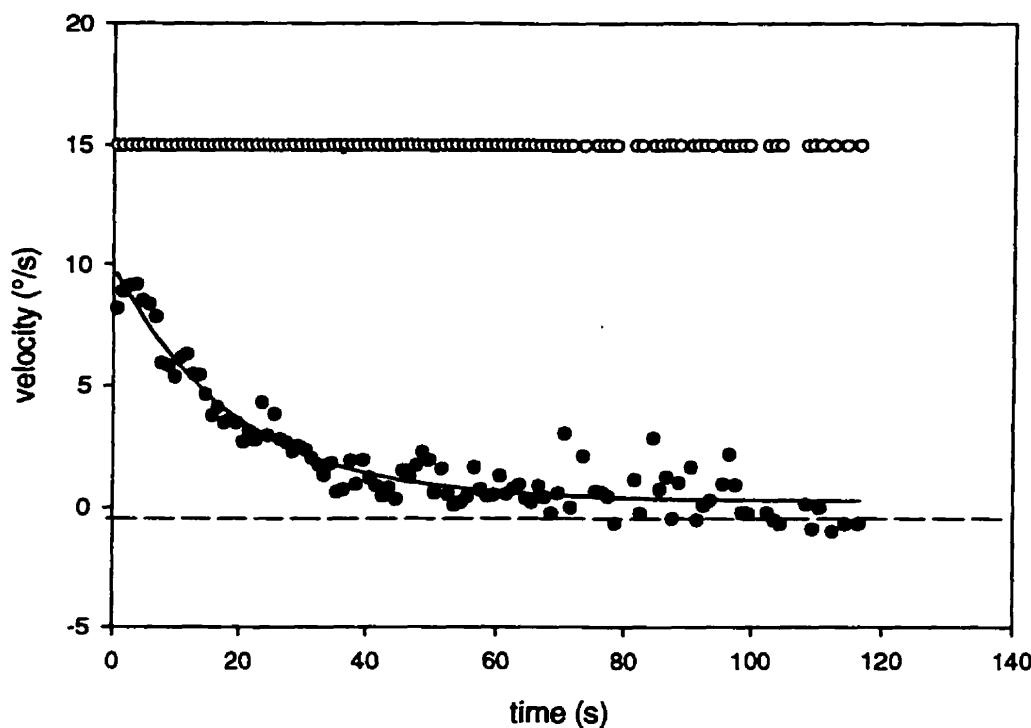


Fig. 3.6 Average VOR response of all subjects to passively induced rotation in the unadapted state. Averaged responses of all subjects (filled circles) to a passive step velocity stimulus of 15 °/s (open circles). See text for method by which average responses are calculated. The plot of eye velocity vs. time is fitted with a first order exponential curve, yielding a VOR gain of approximately 0.67, and a time constant of 20s. Note that each data point plotted represents the average of N = 40 points. (5 subjects, 2 passive trials, clockwise and counterclockwise, per and post-rotational data)

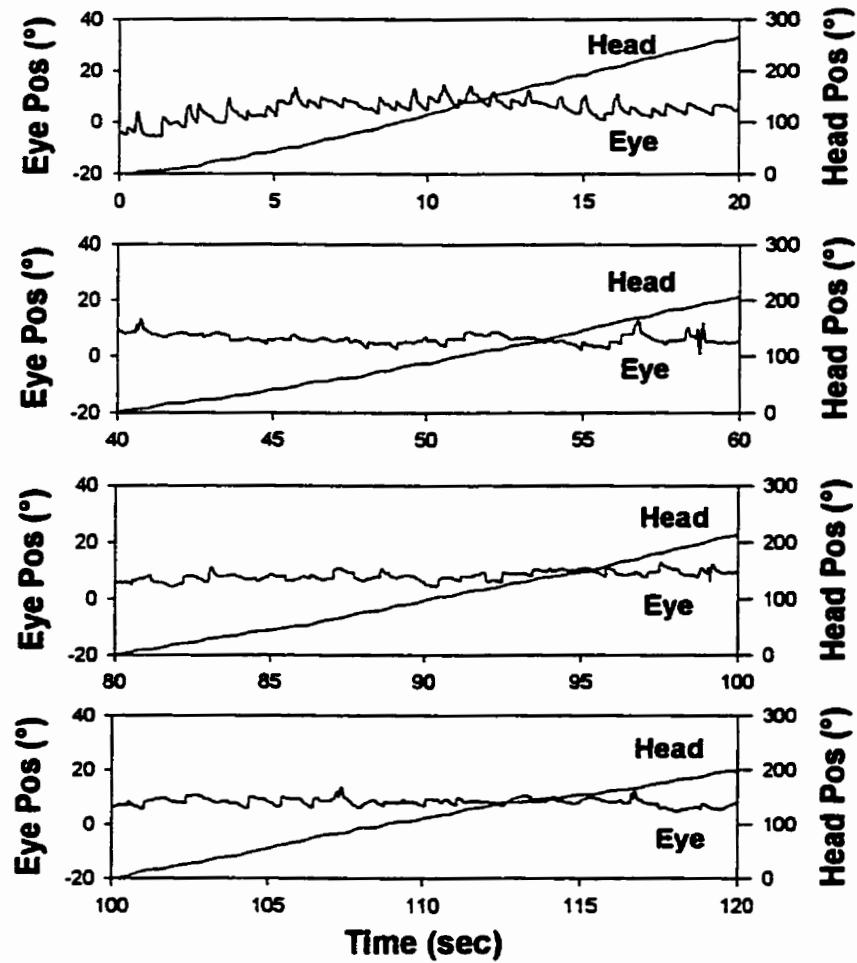


Fig. 3.7 Oculomotor response to actively induced rotation in the unadapted state. Examples of eye and head movements in response to a velocity stimulus imposed by conscious stepping around at approximately $15^{\circ}/s$ in the dark. Note how, unlike the passively generated VOR of Fig 3.4, some degree of compensatory eye movements continues to be generated for up to 2 minutes. The added noise level is due to the periodic body movement of stepping.

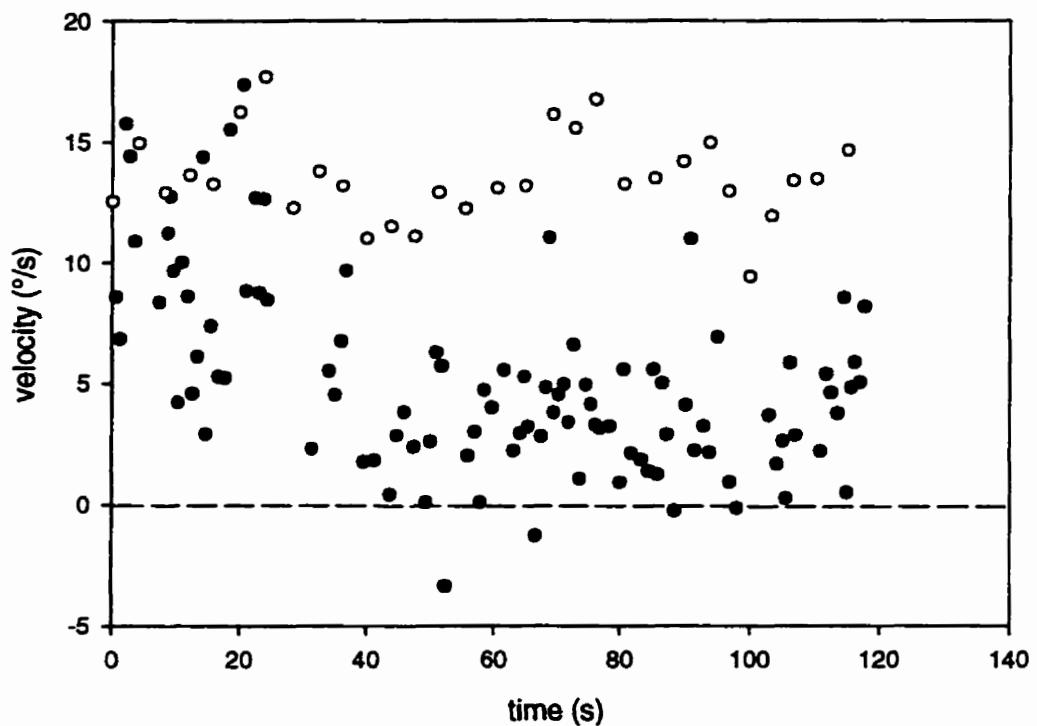


Fig. 3.8 Oculomotor response of one subject to actively induced rotation in the unadapted state. Open circles represent the head angular velocities estimated from the slope of the head position trace during stepping around. This subject achieved an average head velocity of $13.6^{\circ}/s$ (± 0.3 SE), which is close to the goal of $15^{\circ}/s$. The filled circles represent the eye velocities of consecutive selected slow phases from Fig 3.7, plotted against time (s).

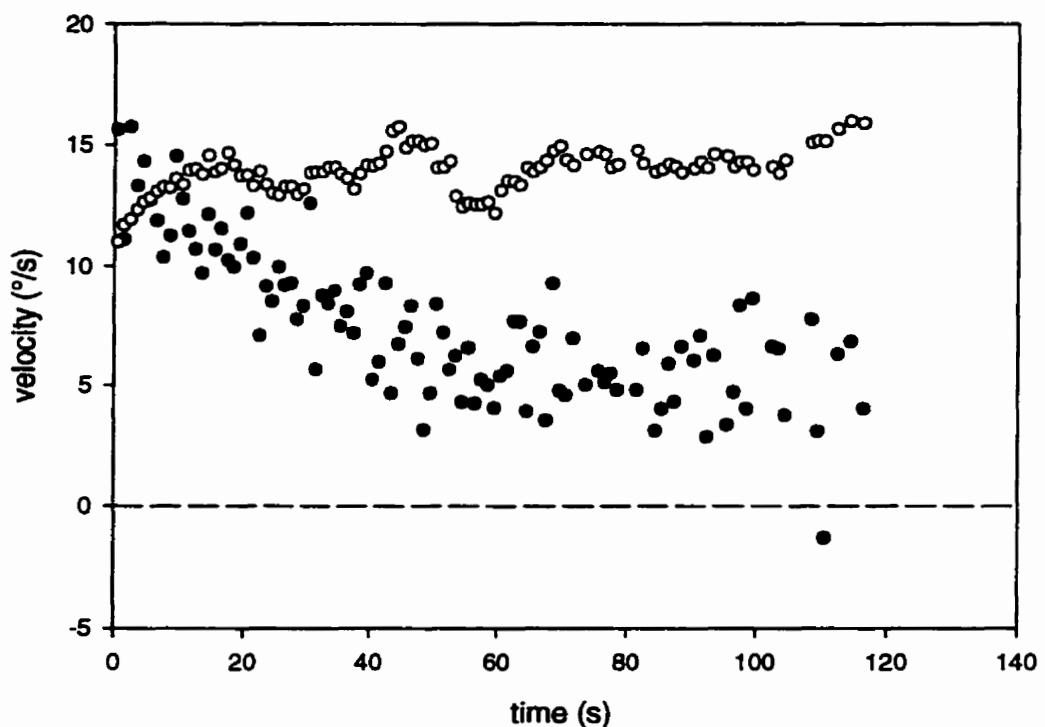


Fig. 3.9 Average oculomotor response of all subjects to actively induced rotation in the unadapted state. Open circles represent values of averaged and smoothed head angular velocities during self-propelled stepping around in the dark. The speed of turning initially tended to be lower than the required angular velocity of $15^{\circ}/s$, but thereafter remained relatively constant and close to the required value. Filled circles are values of the slow phase eye velocities, plotted against time (s). Note the vestibular-like decay of velocities during the first half of the record and the maintained eye velocities during the second half of the record. Compare to the passive VOR response shown in Fig 3.6. Note that each data point plotted represents the average of $N = 20$. (Post-rotational responses are analyzed separately).

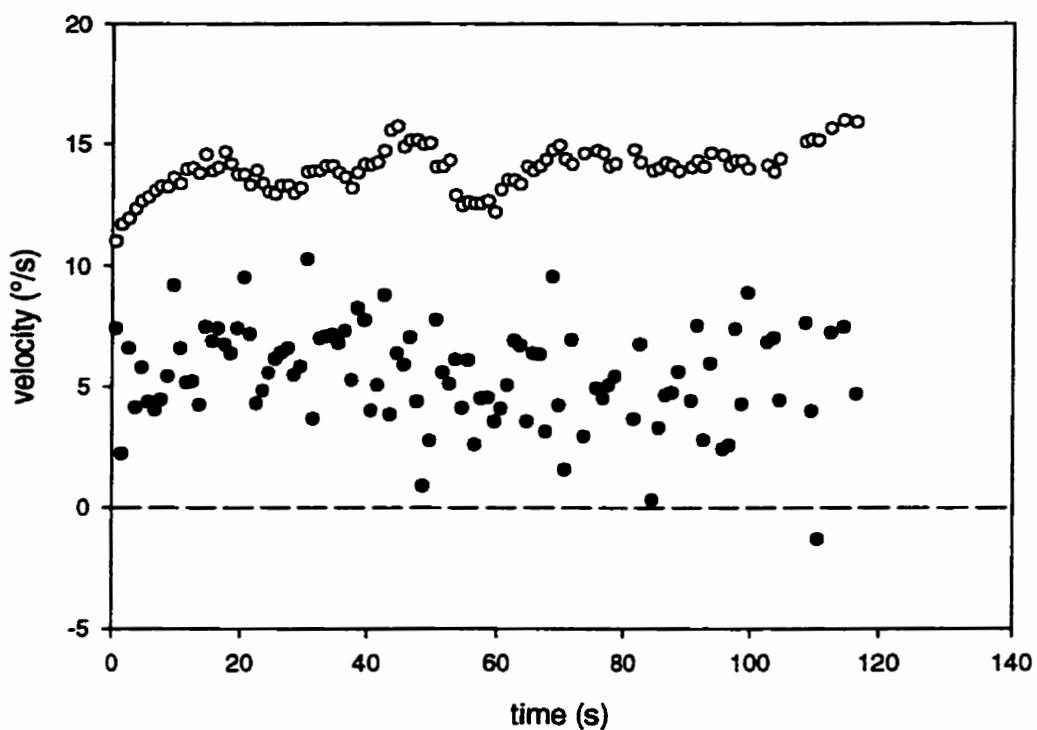


Fig. 3.10 Average PK-induced ocular response for all subjects. The open circles represent values of head velocity as in Fig 3.9. The filled circles represent the values of eye velocity that result from subtracting bin by bin, the average response to vestibular stimulation alone (data points of Fig 3.6) from the average response to combined vestibular and podokinetic stimulation (data points of Fig 3.9). The outcome is a relatively *constant* ocular slow phase response, with a mean angular velocity of $5.5^{\circ}/s$ (± 0.2 SE, $N = 20$). Presumably this represents the PK-ocular response to trunk rotation relative to the stance foot while stepping around.

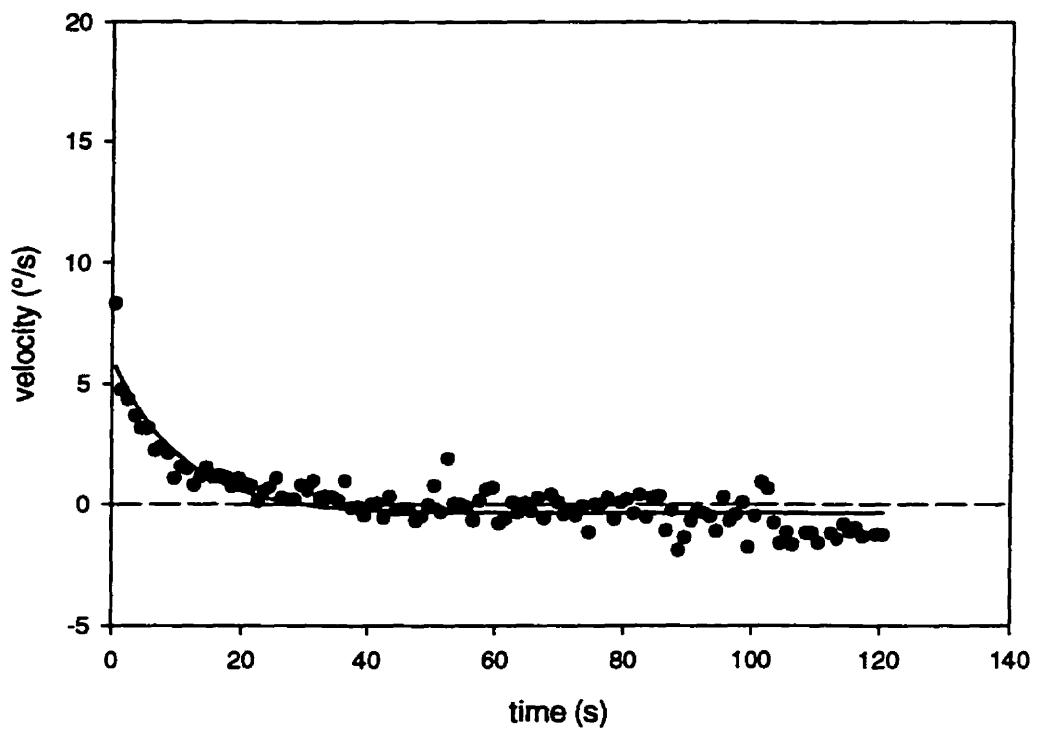


Fig.3.11 Average post-rotational oculomotor response of all subjects on stopping the “active” rotation in the unadapted state. The data points show the average oculomotor response to cessation of active stepping around in the dark ($N = 20$). The points are fitted with a first order exponential curve, yielding an initial VOR gain of 0.43 (6.4/15.0), and a calculated time constant of 10s. These values are lower than the values of the average average passively induced VOR gain and time constant (see Fig 3.6 and Table 3.1).

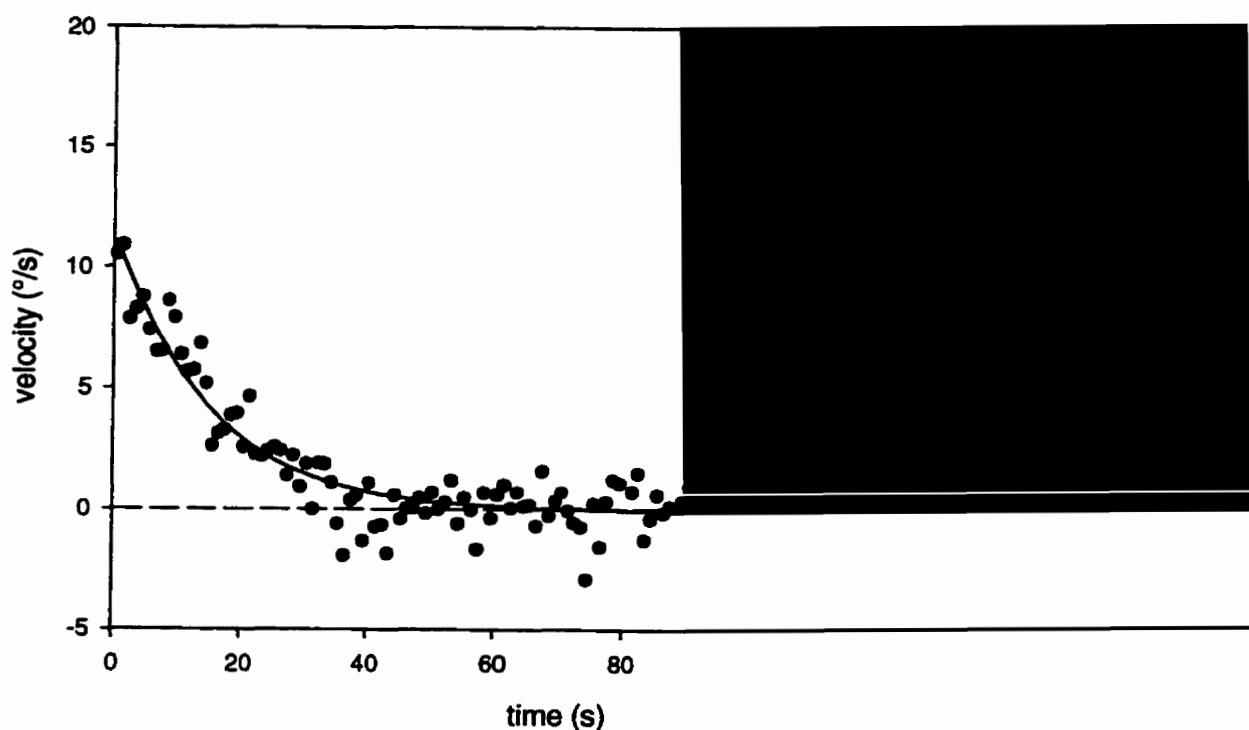


Fig. 3.12 Average VOR response of all subjects in the induced rotation in the “same” direction as that of the unadapted passive per-rotational VOR response of Fig. 3.13 (see Table 3.1). Note that each point represents the average of $N = 10$ points. (5 subjects, 2 passive trials, response)

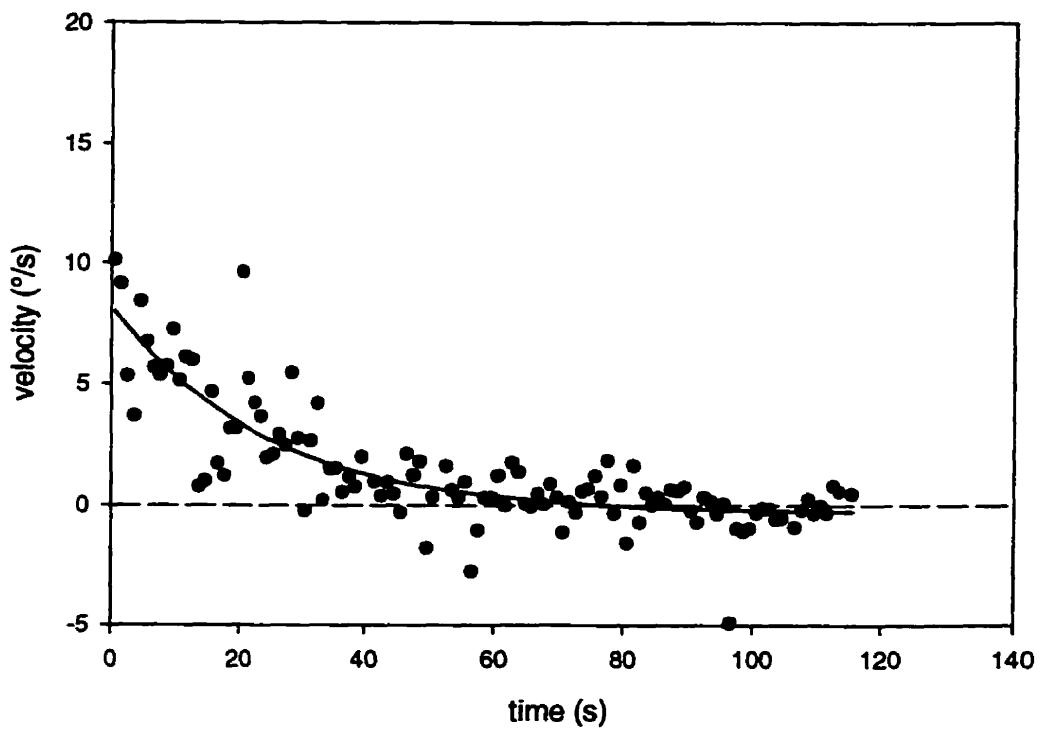


Fig. 3.13 Average VOR response of all subjects in the adapted state to passively induced rotation in the “opposite” direction to that of the preceding adaptive stimulus. Average slow phase eye velocities plotted against time (s). The fitted first order exponential curve yields a VOR gain of approximately 0.57, and a calculated time constant of 25s. Note that there is no significant difference when compared to unadapted passive per-rotational VOR response of Fig 3.6, or the “same” adapted VOR response of Fig 3.12 (see Table 3.1). Note that each data point plotted represents the average of $N = 10$ points. (5 subjects, 2 passive trials, one direction of per-rotational response)

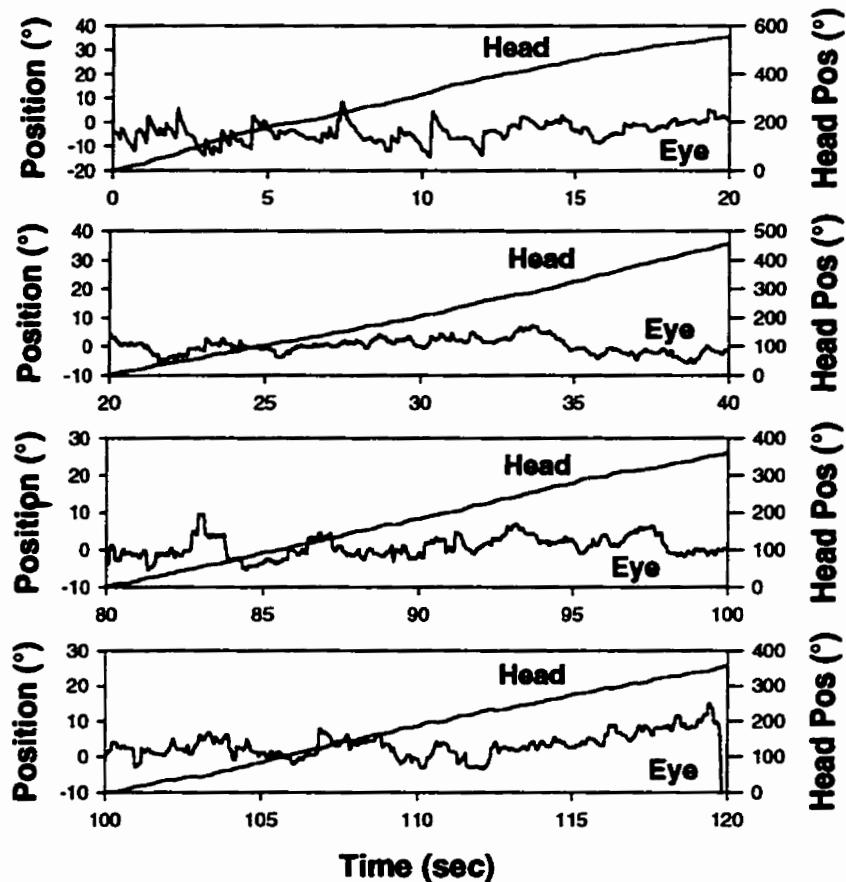


Fig. 3.14 Oculomotor response to PKAR in one subject, i.e. to actively induced, but unperceived, rotation in the adapted state. Eye and head position traces are shown over an interval of 2 minutes while the subject attempts to step-in-place following a standard PK-adaptation of $45^\circ/\text{s}$ for 30min. The change in head position over time represents the velocity of rotation during PKAR. The eye position trace shows an apparent absence of compensatory slow phase segments of eye movement in the second minute of the recording when compared to Fig 3.7.

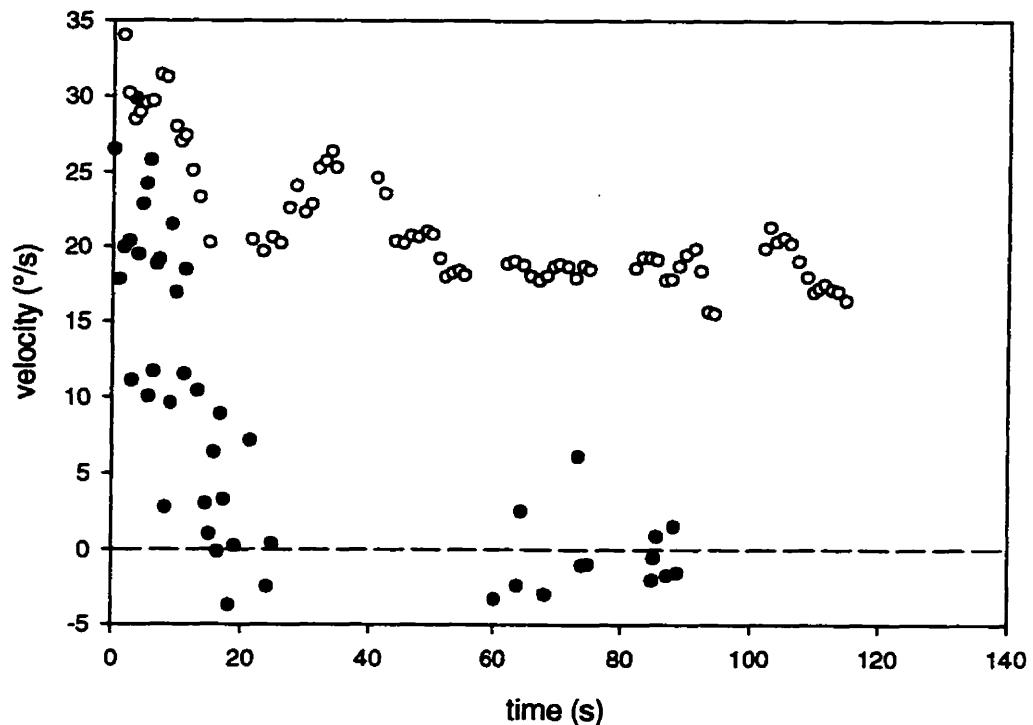


Fig. 3.15 Oculomotor response to PKAR in one subject (same subject as in Fig 3.14)

Open circles show the head velocities calculated from the slope of head position trace. Filled circles show the slow phase eye velocities estimated from the slopes of suitable slow phases in the eye position trace of Fig 3.14, and plotted against time (s). The eye velocities in the first minute presumably reflect a vestibular response, whereas during the second minute, there was an absence of compensatory eye movement (compare to Fig 3.9). Note that bins associated with periods where no slow phase eye movements could be detected, for example in this figure between 25 and 60 seconds (derived from the record shown in the middle panel of Fig 3.14) are assigned zero values during subsequent averaging, as exemplified in Fig 3.16.

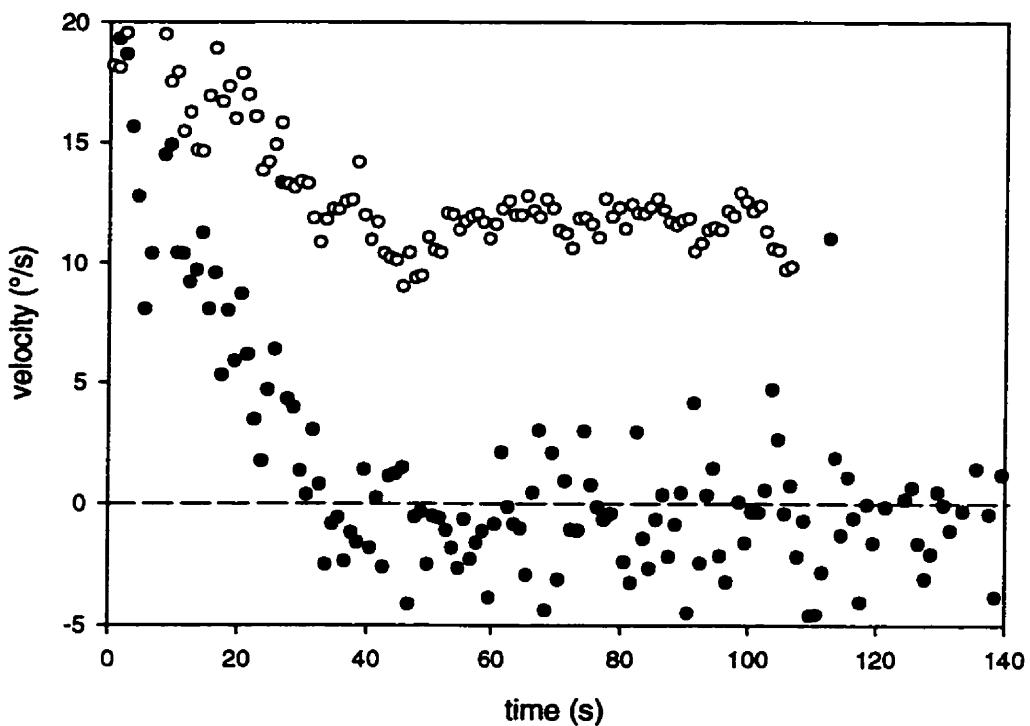


Fig. 3.16 Average oculomotor response of all subjects to PKAR-induced rotation in the adapted state. Note that each data point plotted represents the average of $N = 10$ points. (5 subjects, 2 trials, one direction of per-rotational response). Open circles signify binned and smoothed head velocities plotted against time (s). Filled circles signify the slow phase eye velocities. The pattern of decay of head angular velocity is consistent with PKAR as shown in Figs 2.3 and 2.5. As in Fig 3.15, the ocular motor output observed in the first minute presumably reflects the response to vestibular stimulation. During the second minute there was no significant compensatory response in contrast to the unadapted "active" response of Fig 3.9.

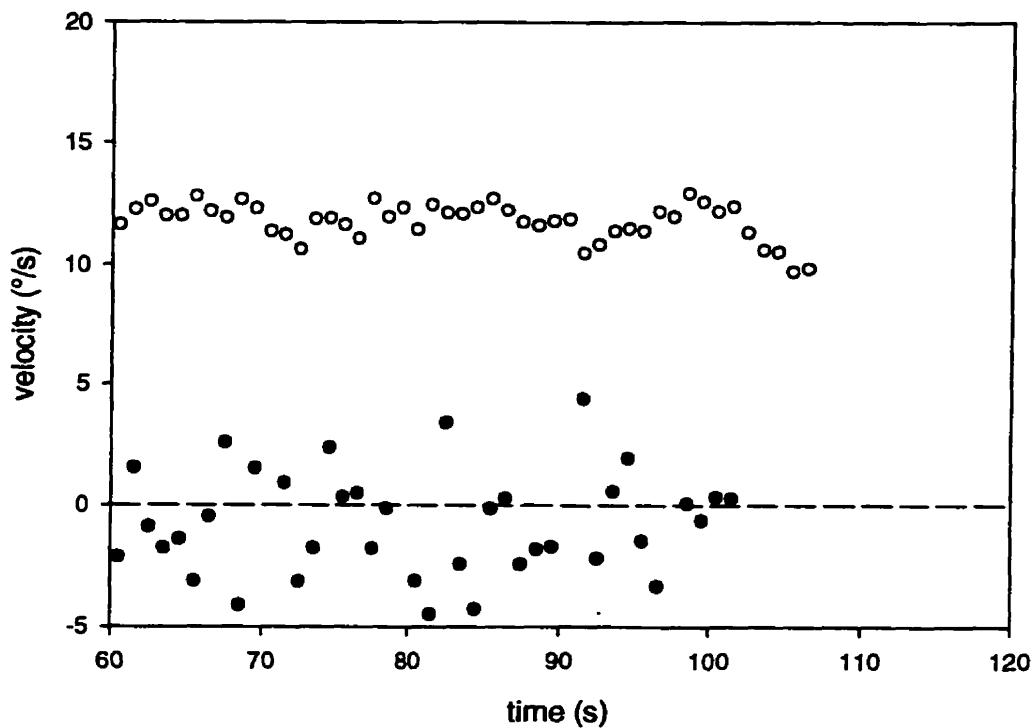


Fig. 3.17 Disappearance of the PK-induced oculomotor response during PKAR.

Similar to Fig 3.10, this figure is the outcome of subtracting relevant data of Fig 3.6 from corresponding values in Fig. 3.16. However, since the initial pattern of head rotation in Fig 3.16 was constantly changing during the first minute of PKAR, the results are confined here to the second minute of response, when PKAR was relatively constant and the vestibular contribution relatively insignificant. Note the effective disappearance of the oculomotor response compared with the corresponding data of Fig 3.10.

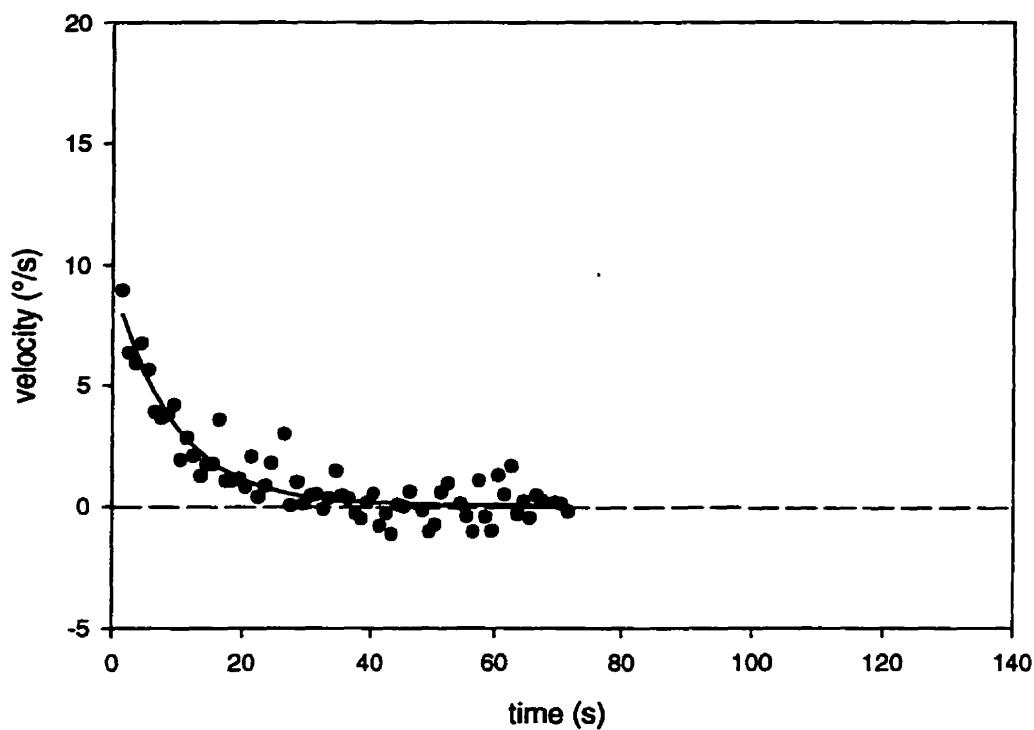


Fig. 3.18 Average post-rotational oculomotor response of all subjects on stopping PKAR. Average post-rotational oculomotor response on stopping the unconsciously generated average head velocity of $11.8^{\circ}/s$ ($\pm 0.09SE$). The fitted first order exponential curve yields an initial oculomotor gain of 0.79 ($9.3/11.8$) and time constant of 10s. Compare with the average passively induced VOR response shown in Fig 3.6 (see Table 3.1). Note that each data point plotted represents the average of $N = 10$ points. (5 subjects, 2 trials, one direction of post-rotational response)

Mean angular eye-re-head vel (°/s±SE)	VOR response to “passive” angular rotation			Ocular response to cessation of “active” angular rotation	
	Unadapted	Adapted “same”	Adapted “opposite”	Unadapted	Adapted (PKAR)
Step vel stimulus Y-intercept	15.0 9.6 ± 0.4	15.0 11.5 ± 0.5	15.0 8.5 ± 0.6	15.0 ± 0.2 6.4 ± 0.4	$11.8 \pm .09$ 9.3 ± 0.6
Gain	0.64	0.77	0.57	0.43	0.79
τ^{-1} (s ⁻¹) *	0.05 ± 0.005	0.07 ± 0.005	0.04 ± 0.006	0.1 ± 0.01	0.1 ± 0.01
τ (s)*	20.0	14.3	25.0	10.0	10.0

* τ denotes time constant

Table 1.1 Summary of average oculomotor responses to passively induced angular rotation, and to cessation of self-generated stepping around and PKAR , all in the dark.

Chapter 4 : SUMMARY AND POTENTIAL FUTURE APPLICATIONS

Summary

The studies contained within this thesis are presented in two separate experimental series in the previous two chapters, and may be summarized as follows:

1. A novel somatosensory/motor control system suitable for controlling locomotor trajectory by referencing body orientation to the stance foot on the ground, has been identified and termed the “Podokinetic” (PK) system.
2. Adaptive remodeling of the PK system by “stepping-in-place” on a rotating disc for up to an hour , reveals the presence of a Podokinetic after response (PKAR) expressed as angular rotation relative to the space-stable ground when the blindfolded subject attempts to step-in-place. Although an order of magnitude above vestibular threshold, this rotation is not associated with perception of self-motion.
3. The PKAR is linearly related to stimulus velocity, up to 45°/s, with a gain of the “short term” response of approximately 1/3; and with “charging” and “discharging” time constants of between five and ten minutes; the “discharging” time constant of the “long term” response is between one and one and a half hours.
4. Significant suppression of the locomotor response at the 20 and 40 second points of the PKAR ($p < 0.001$) was found when compared to the

corresponding extrapolated values from the fitted curves, suggesting an effect due to concurrent PK/vestibular interaction.

5. Investigation of the PK/vestibular interaction, by comparing the normal passively induced VOR with the analogous oculomotor response induced by consciously stepping around in the dark, revealed a constant PK-induced component of approximately 1/3 gain which was maintained for at least two minutes of stepping around. The PK-induced oculomotor component summed linearly with the passively induced VOR. The prolonged maintenance of the PK-generated response emulates the low-pass psychophysical perceptual response modeled by Mergner et al (1993).
6. After PK-adaptation and during PKAR, the oculomotor response reflects an intact VOR; however the PK-induced component is notably absent. The lack of change of the VOR is expected since there is neither peripheral vestibular stimulation during PK adaptation, nor behavioral impetus to modify the VOR. On the other hand, PK adaptation does provide an impetus to modify the oculomotor response to PK input. Thus, the resulting loss of the PK-induced component is also expected and may reflect central remodeling or the influence of motor efference copy.

Potential future applications

The above results have significant implications for rehabilitative therapy where such adaptation may serve a role in recovery from injury or disease. By analogy with adaptive compensation of the vestibular system through exercises designed to enhance the

VOR gain, the present studies indicate that the PK system provides auto-adaptive access to locomotor control. The application of auto-adaptation within the PK system for rehabilitation of conditions which affect balance, and in particular, control over locomotor trajectory, may prove to enhance locomotor function and reduce the level of disability in these patients.

In order to identify the patient groups most amenable to adaptive locomotor retraining, it will be necessary to examine the PK system's role in spatial orientation in several specific conditions. Particularly, it would be interesting to examine how the PK system is utilized by compensated bilaterally deficient vestibular patients to control locomotor trajectory.

Based on what is known about the role of the cerebellum in adaptation and motor learning (Melvill Jones, 1977, Thatch, 1995), it would also be most interesting to ask whether adaptation of either the oculomotor or locomotor outputs of the PK system can be induced in patients with cerebellar damage. Although this may be a difficult patient model to examine, one would ideally like to study patients who have specific cerebellar lesions, but who are able to walk in the context of the experimental paradigm.

Similarly, as the present studies demonstrate that perception of self-motion is also remodeled by PK adaptation, future investigation of the role of perception in motor learning may include examination of the effect of PK adaptation in patients with parietal lobe damage.

Chapter 5 : BIBLIOGRAPHY

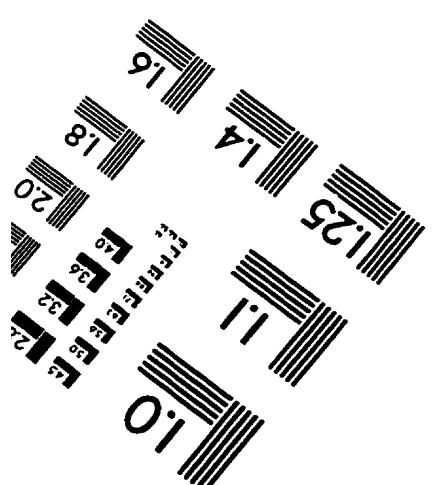
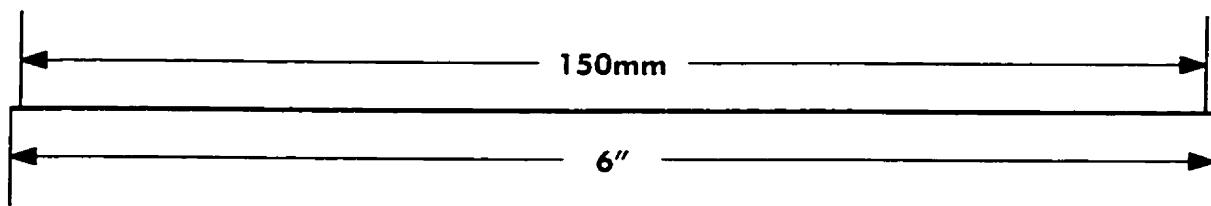
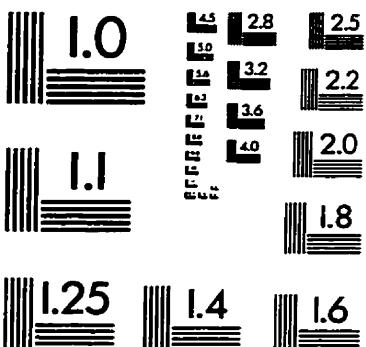
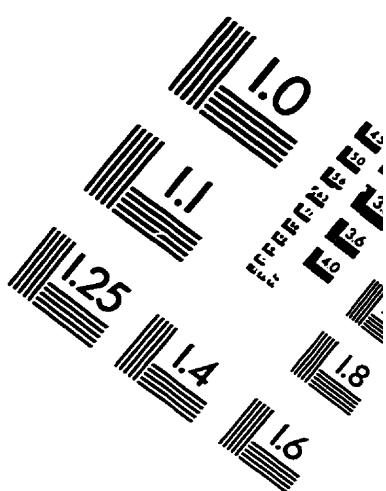
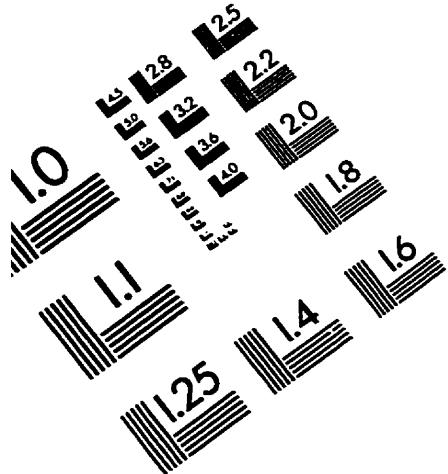
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TEST TARGET (QA-3)



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