

POST-ROTATORY NYSTAGMUS AND TURNING SENSATIONS AFTER ACTIVE AND PASSIVE TURNING

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Abstract — We measured post-rotatory nystagmus and sensations of body rotation in standing subjects brought to rest in the dark after 3 minutes of each of the following conditions: 1) passive turning about the mid-body axis, involving only vestibular stimulation, 2) active turning about the mid-body axis, involving both vestibular stimulation and motor–proprioceptive activity in the legs, and 3) stepping round while remaining facing in the same direction on the center of a rotating platform with the head held in a stationary holder (apparent turning), involving only motor–proprioceptive activity. The same acceleration–velocity profile was used in all conditions. Post-rotatory nystagmus (slow phase) occurred in the same direction to passive body turning and was reduced in velocity after active body turning. After apparent turning, nystagmus was in the opposite direction as attempted body turning. Our theoretical analysis suggests that nystagmus after active turning should conform to the mean of the responses after passive and apparent turning rather than to their sum. The results conform more closely to the mean than to the sum, but with greater weight given to vestibular inputs than to motor–proprioceptive inputs. Post-rotatory sensations of self-rotation were in the expected opposite direction after passive turning and were lower in magnitude after active turning. After apparent turning, sensations of self-rotation were in the same direction as those after attempted turning—an effect known as the antisomatogyral illusion. © 1998 Elsevier Science Inc.

Keywords — nystagmus; arthrokinetic nystagmus; turning sensations; antisomatogyral illusion.

Introduction

Passive rotation of the whole body in the dark about the vertical mid-body axis (*z* axis) produces nystagmus with slow phase in a direction opposite to body rotation and a sensation of turning in the veridical direction. During between 30 and 60 s of rotation at constant velocity, both of these effects decay exponentially to zero as the cupulas of the horizontal semicircular canals return to their resting position. When the subject is decelerated to rest, the cupulas are deflected in a direction opposite to the per-rotatory deflection. For about 30 s after the body has come to rest, nystagmus occurs with slow phase in the same direction as the previous rotation, and subjects perceive themselves rotating in the direction opposite to the original direction of turning, a sensation known as the somatogyral illusion. These post-rotatory effects also decay exponentially as the cupulas return to their resting position and the velocity-storage mechanism discharges (1).

Correia and colleagues asked subjects to step round actively for 8 turns while remaining in the same spot (2). Upon stopping, about 75% of subjects reported post-rotatory sensations of turning in the same direction as the previous turning. The investigators called this the antisomatogyral illusion. This experiment was repeated by Guedry and colleagues, who also found an antisomatogyral illusion and, in addition, found that the gain of per-rotatory nystagmus was

higher and that of post-rotatory nystagmus was lower than the gain of nystagmus after passive turning (3). Bles confirmed this finding (4). In these experiments, subjects controlled their own acceleration, deceleration, and velocity of body rotation.

Guedry and colleagues explained the antiso-matogyral illusion in terms of von Holst and Mittelstaedt's theory of reafference (5). They argued that turning movements that people execute as they move about are typically under 180°. Under these circumstances vestibular signals correctly indicate the velocity of body rotation, and there is little post-rotatory deflection of the cupulas. Hence, vestibular signals indicate the muscular effort required to bring the body to rest, and the association between efference associated with stopping the body and reafferent stimulation from proprioceptors matches normal expectations. In other words, proprioceptive signals are fully accounted for in terms of body deceleration and do not produce an illusion of self-rotation. After prolonged active self-rotation at constant velocity, the vestibular signals indicate that the body is not rotating and this leads to an underestimation of efference needed to decelerate the body. This in turn leads to a mismatch between afference and reafferent proprioception and an illusion of self-rotation. We refer to this as the reafference-mismatch theory. We do not adopt this theory of the antiso-matogyral illusion, but simply define arthrokinetic inputs as any efferent, afferent, or reafferent inputs arising from the motor and/or proprioceptive systems that generate nystagmus or sensations of self-rotation.

Guedry and Benson rotated blindfolded subjects passively at 60°/s in a rotating chair (6). After 60 s, they were stopped passively or they stopped themselves with their hands and/or feet. The gain of post-rotatory nystagmus was not affected by the manner of stopping. Post-rotatory sensations of turning were in the opposite direction to the actual turning, but were only half as strong after active stopping than after passive stopping. In a second experiment, subjects rotated themselves in the chair for 60 s by pushing with their hands against the cylinder in time to a metronome. This increased per-rotatory nystagmus and reduced post-rotatory nystagmus and

further reduced the magnitude of post-rotatory sensations of turning, especially when active turning was accompanied by active stopping. There were only a few reports of the antiso-matogyral illusion.

Bles and Kapteyn used two rotation conditions (7). In the first condition, subjects walked round the rim of a 1.5 m diameter stationary platform while holding the arm of a chair which accelerated at 20°/s², maintained a velocity of 50°/s for 30 s, and then decelerated at 20°/s². In the second condition, subjects held the arm of the stationary chair as they walked round the rim of the platform as it rotated with the same rotation profile as that used in the first condition. After actual stepping round, which generated both vestibular and proprioceptive inputs from walking, subjects experienced self-rotation in the same direction, the antiso-matogyral illusion, but the slow-phase of nystagmus was in the opposite direction—the direction corresponding to post-rotatory vestibular nystagmus. After stationary stepping, which generated only proprioceptive inputs, subjects experienced the antiso-matogyral illusion, but their nystagmus was now in the same direction. The effects produced by apparent stepping round can be due only to proprioception or motor efference associated with stepping since the vestibular system was not stimulated. Bles and Kapteyn did not provide quantitative data.

Brandt and colleagues placed a stationary seated subject in the dark at the center of a vertical cylinder rotating at 10°/s about a vertical axis (8). The subject placed a hand on the surface of the cylinder so that it rotated about the shoulder joint at the same velocity as the cylinder. This induced nystagmus with slow phase in the same direction as the arm tracking movement with a gain of 0.5 and illusory self-motion at about the same velocity as the cylinder, but in the opposite direction. Both effects continued for some time after the arm was removed from the cylinder. They referred to these effects as arthrokinetic nystagmus and arthrokinetic self-motion. De Graf and colleagues reported arthrokinetic pursuit eye movements induced by linear motion of the hand (9).

It is clear from the above evidence that arthrokinetic nystagmus is induced by motor-

proprioceptive signals associated with active body rotation in the absence of vestibular stimulation. During active rotation of the body, arthrokinetic and vestibular nystagmus operate in the same direction and produce a greater response than either stimulus alone. In the post-rotatory period after prolonged rotation, the vestibular effects of deceleration produce nystagmus opposite to the per-rotatory response, but the aftereffects of active turning produce arthrokinetic nystagmus in the same direction as the per-rotatory response. The two aftereffects are therefore opposed and partially cancel, but the net nystagmus is in the direction of vestibular nystagmus. The same is also probably true of sensations of self-rotation, but there is little quantitative data on this point.

Our purpose was to provide quantitative data on the aftereffects of passive, active, and apparent self-rotation, with greater control over the motion of the head than in previous experiments. A second purpose was to test whether arthrokinetic and vestibular nystagmus add in a linear fashion so that their combined effects can be predicted from the algebraic sum of the two effects measured separately or whether the combined effect is the mean of the separate effects. Linear addition of sensory inputs is to be expected with an in-series, or nested, sensory system (10). For instance, the position of the hand with respect to the body is indicated by the algebraic sum of inputs from the nested set of arm joints. However, in a multi-cue system, in which distinct sensory sources provide parallel information about the same judgment, one would expect signal averaging rather than addition. For example, the apparent direction of a sound source depends on the average of its position signified by interaural time differences and its position signified by interaural intensity differences. Vestibular and proprioceptive inputs are sometimes linked in series. For instance, a judgment of the velocity of passive turning of the trunk about the z axis while the head is also being rotated on the same axis relative to the trunk requires the algebraic summation of the inputs from the semicircular canals and those from proprioceptors in the neck or trunk. There is evidence that these inputs are summed linearly (11). But vestibular and proprioceptive inputs

may also be linked in parallel. For example, the velocity of active self-rotation on a stationary surface is indicated by inputs from the semicircular canals, but is also indicated by motor-proprioceptive inputs from the legs. In this case, the sensory inputs provide independent assessments of the same event, and the best estimate is a weighted mean of the two inputs, with the weights determined by the reliability of each input as a function of time.

Methods

Apparatus

The subject stood in the dark on a turntable 1 m in diameter with the head secured in a head holder. The head holder and the turntable could be rotated independently about the same vertical axis by a pair of high-torque servomotors. Optical encoders on the motor shafts registered the absolute position of the turntable and head holder with a resolution of 0.03° . The position encoders ensured that the turntable and head holder rotated in synchrony.

Three movement conditions were used to evaluate the relative contributions of the vestibular and motor-kinesthetic systems to the responses. In the passive rotation condition, the turntable and head holder rotated in phase and the subject made no voluntary effort to either help or hinder the rotation of the body. This resulted in stimulation of the semicircular canals of the vestibular system, but no efference or reafference associated with voluntary motion. In the active rotation condition the subject stepped round on the stationary platform to keep pace with rotation of the head holder. This resulted in stimulation of both the vestibular and motor-kinesthetic systems. In the apparent stepping condition, the head holder was stationary, and the subject stepped round in place to keep pace with the rotating turntable. Thus, the subject was on a rotary treadmill apparently stepping around in a direction opposite to the rotation of the turntable. The efference to the leg muscles and the associated kinesthesia were similar to those in the active condition, but the vestibular system was not stimulated. During apparent

stepping, subjects were able to keep their torsos in line with their heads, even during the deceleration phase. However, there was probably some torque in the neck during deceleration, which would add a component of proprioception from the neck muscles. For all movement conditions, the turntable and/or head holder was accelerated at a constant acceleration of $28.5^\circ/\text{s}^2$ for 2.5 s to an angular velocity of $72^\circ/\text{s}$, which was maintained for 180 s before the subject was decelerated at $28.5^\circ/\text{s}^2$ to a stop. The experimenter said "stop" just as deceleration ended.

Post-rotatory Nystagmus

Post-rotatory eye movements and sensations of self-rotation were measured on separate trials. The subject was in complete darkness with both eyes open. In eye-movement trials, post-rotatory nystagmus was measured for 3 minutes, during which time the aftereffects decayed to zero. The 3-minute period also served as an interstimulus interval. The magnetic scleral search coil technique (12) was used to record movements of one eye. The instrument was calibrated by having the subject fixate 5 points between $\pm 10^\circ$ along both horizontal and vertical axes. Positive angles refer to downward and rightward gaze relative to the gaze straight ahead position. The least squares criterion was used to find the best-fitting linear relationship between eye position and coil voltage.

Post-rotatory nystagmus was measured in one female and three male subjects, ranging in age from 25 to 67 years. Each subject participated in two eye movement sessions; one with the search coil on the right eye and one with it on the left eye. In each session, the three movement conditions (passive, active, and apparent stepping) were presented for both clockwise and counterclockwise directions. The order of presentation was randomized for each subject and counterbalanced between sessions for each subject. The head holder positioned the eyes close to the center of the magnetic field produced by the field coils. Since the sensitivity of the search coils is a nonlinear function of angular displacement, we took care to return the head to the same angular position after each ro-

tation. This was achieved by use of the encoders on the servo motors and an analogue signal from a coil mounted on the subject's head.

The horizontal and vertical eye positions and the head position were stored on digital tape. The data were digitized at 100 Hz with 12 bit accuracy for off-line analysis by computer. Eye velocity was obtained by digital differentiation of the eye position record. Saccades and blinks were removed from the record by automated filtering combined with visual inspection.

Post-rotatory Illusory Rotation

Three female and 7 male subjects participated in the trials in which post-rotatory sensations of self-turning were measured. Their ages range from 25 to 67 years. In each of two sessions, the three movement conditions (passive, active, and apparent stepping) were presented for both clockwise and counterclockwise directions. The order of presentation was randomized for each subject and counterbalanced between sessions for each subject. Following each rotation the subject called out the direction of self-rotation and numerical estimates of its magnitude, noting any changes in sensation as they occurred. Before the first trial of a session, subjects were passively rotated and instructed to assign the value of 5 to the peak velocity of the resulting sensation of post-rotatory turning. Subjects used fractional estimates of velocity when perceived velocity fell below 1. All responses were recorded on digital tape. The responses were then played back, and the sign, magnitude, and time stamp (relative to the end of the rotation) recorded.

Results

The slow-phase velocities of post-rotatory nystagmus were calculated for each subject for each condition. Since there were no significant differences between clockwise and counterclockwise directions, results for the two directions were pooled. Figure 1 shows the beat-by-beat velocity of the slow phases of post-rotatory nystagmus for one subject, as a function of time af-

ter stopping, for each type of turning. The curves of mean slow phase velocity from the four subjects as a function of time were each fitted with a double exponential function as proposed by Young and Oman (13). These curves are shown by the dotted lines in Figure 2. After passive turning of the body, the slow phase of the initial nystagmus was in the same direction as body turning and decayed exponentially to zero after about 60 s (time constant 15.5 s) and then reversed in sign to produce a weak secondary nystagmus. After active turning, the nystagmus was also in the same direction as body turning, but its velocity was less than after passive turning, and it decayed to zero in about 45 s (time constant 15.8 s). Similar values for the two types of nystagmus were reported by Guedry and colleagues (3). After apparent stepping, the slow phase of nystagmus was considerably slower than in the other two conditions and was in the opposite direction to the stepping direction, defined as the direction in which the subject would have turned if on a stationary surface. It decayed to zero in about 45 s (time constant 21.2 s), but less steeply than nystagmus in the passive and active conditions, and it showed evidence of a slight secondary nystagmus. Bles and colleagues (14) reported a time constant of 20 s for nystagmus produced by apparent stepping and of 14 s for that produced by passive rotation. The curve obtained by algebraic addition of nystagmus velocity after passive rotation and nystagmus velocity after apparent stepping is shown as a faint continuous line. The curve obtained by averaging these two velocities of nystagmus is shown as a bold continuous line. It can be seen that the velocity of nystagmus after active rotation falls between these two theoretical curves and approaches the average-velocity curve as the response continues.

The estimates of illusory body rotation that subjects experienced in the post-rotatory period were pooled into 0.5 s bins. Since there were no significant differences between clockwise and counterclockwise directions, results for the two directions were pooled. Figure 3 shows the results for one subject. We derived mean estimates of illusory body rotation for the four subjects whose eye movements were recorded and compared them with the mean estimates from

the full group of 10 subjects. Since there were no significant differences between these two estimates, we felt justified in using the results of the 10 subjects to compare with the eye movement data. Figure 4 shows the mean estimates of velocity of illusory body rotation for 10 subjects as a function of time after body rotation stopped for the 3 rotation conditions. Each curve was fitted with a double exponential function, as shown in the figure. For the passive and active turning, the illusory body rotation was in the opposite direction to body turning. The time constant for illusory self-rotation was 24.4 s after passive turning and 20.4 s after active turning. These values compare with values of 17 s and 13 s, respectively, reported by Correia and colleagues for an unspecified rate of deceleration (2). After apparent turning, illusory body turning was in the same direction as the stepping direction with a time constant of 5.3 s.

Discussion

We define the direction of nystagmus in terms of the direction of the slow phase. Passive rotation produced post-rotatory nystagmus in the direction of the previous body rotation, the direction expected from the effects of deceleration on the semicircular canals. Active rotation produced post-rotatory nystagmus in the same direction as passive rotation, but with reduced velocity. This suggests that post-rotatory vestibular nystagmus is reduced by an opposite arthrokinetic nystagmus produced by aftereffects of motor-proprioceptive stimulation. This interpretation is supported by the fact that apparent stepping produced post-rotatory nystagmus in the direction opposite to that in which the subject had been attempting to turn, but with a much lower velocity than nystagmus produced by either active or passive turning. This is pure arthrokinetic nystagmus, since the vestibular system had not been stimulated. It confirms the effect reported by Bles and Kapteyn (7).

We do not adopt Guedry and colleagues' reference-mismatch theory, described in the Introduction, since we do not see how it would account for an aftereffect of active or apparent turning that outlasts the period of deceleration.

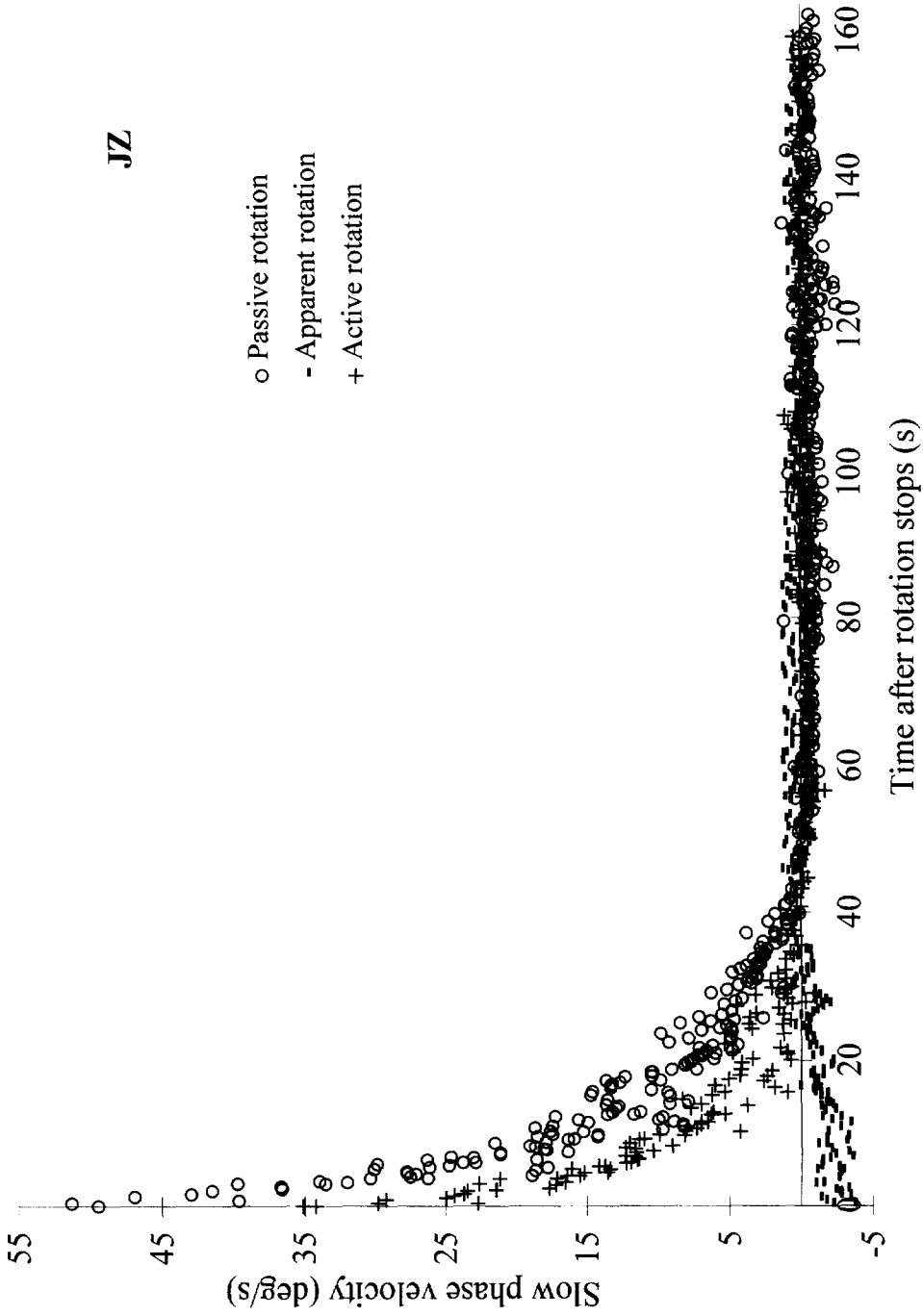


Figure 1. Beat-by-beat velocity of the slow phase of post-rotatory nystagmus of one subject as a function of time after stopping, for each of the three types of turning. Positive values indicate that the slow phase of nystagmus was in the same direction as the previous turning of the body.

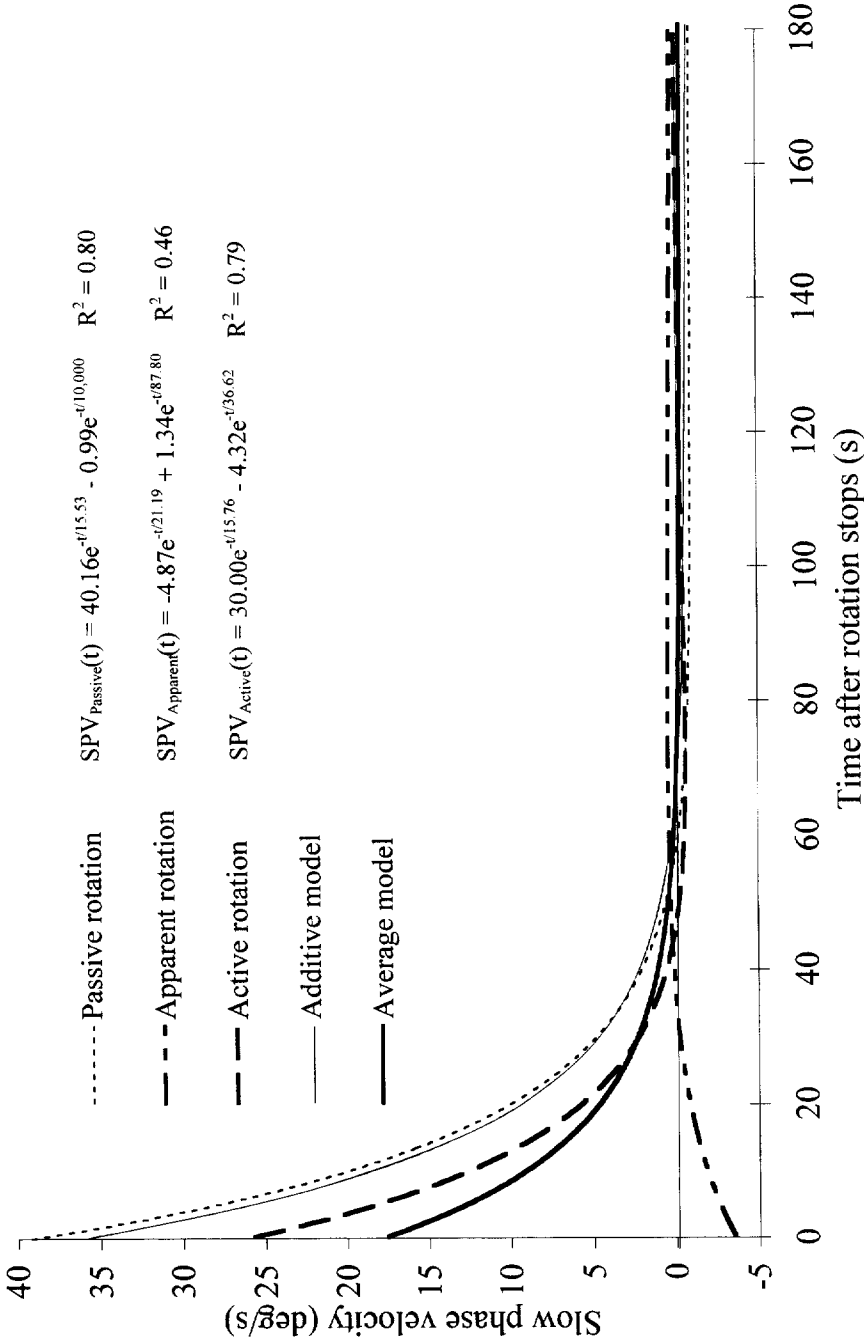


Figure 2. The dotted lines represent the best-fitting double exponentials to the mean slow-phase velocity of post-rotatory nystagmus (SPV) of four subjects, as a function of time after stopping for each of the three types of turning. The bold continuous line is the mean of the passive turning and the apparent turning curves. The faint continuous line is the algebraic sum of the passive turning and apparent turning curves. Positive values indicate that the slow phase of nystagmus was in the same direction as the previous turning of the body. R^2 represents the coefficient of determination.

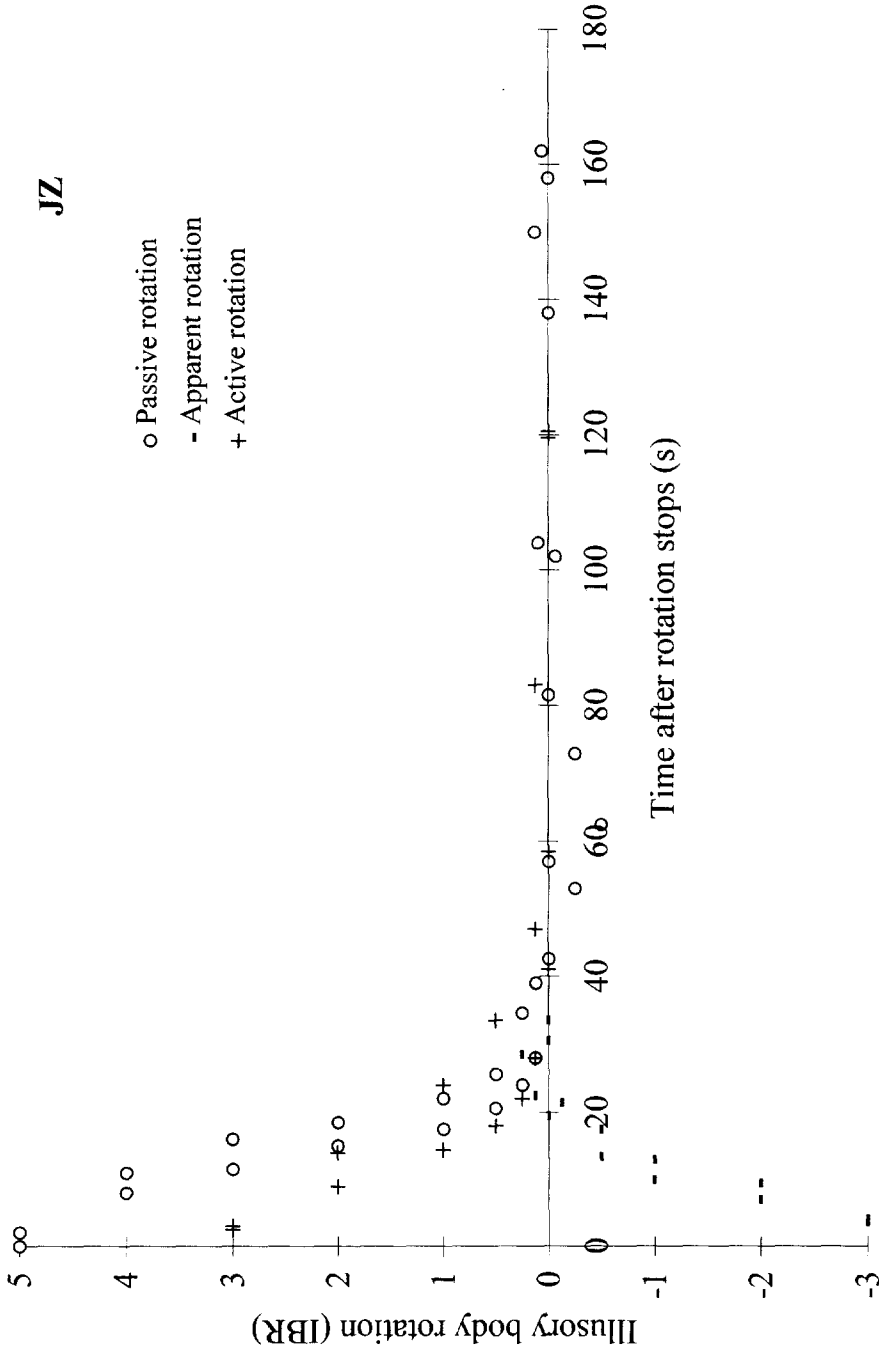


Figure 3. The magnitude of illusory body rotation of one subject, as a function of time after stopping, for each of the three types of turning. Positive values indicate that illusory body rotation was in the direction opposite to the previous turning of the body.

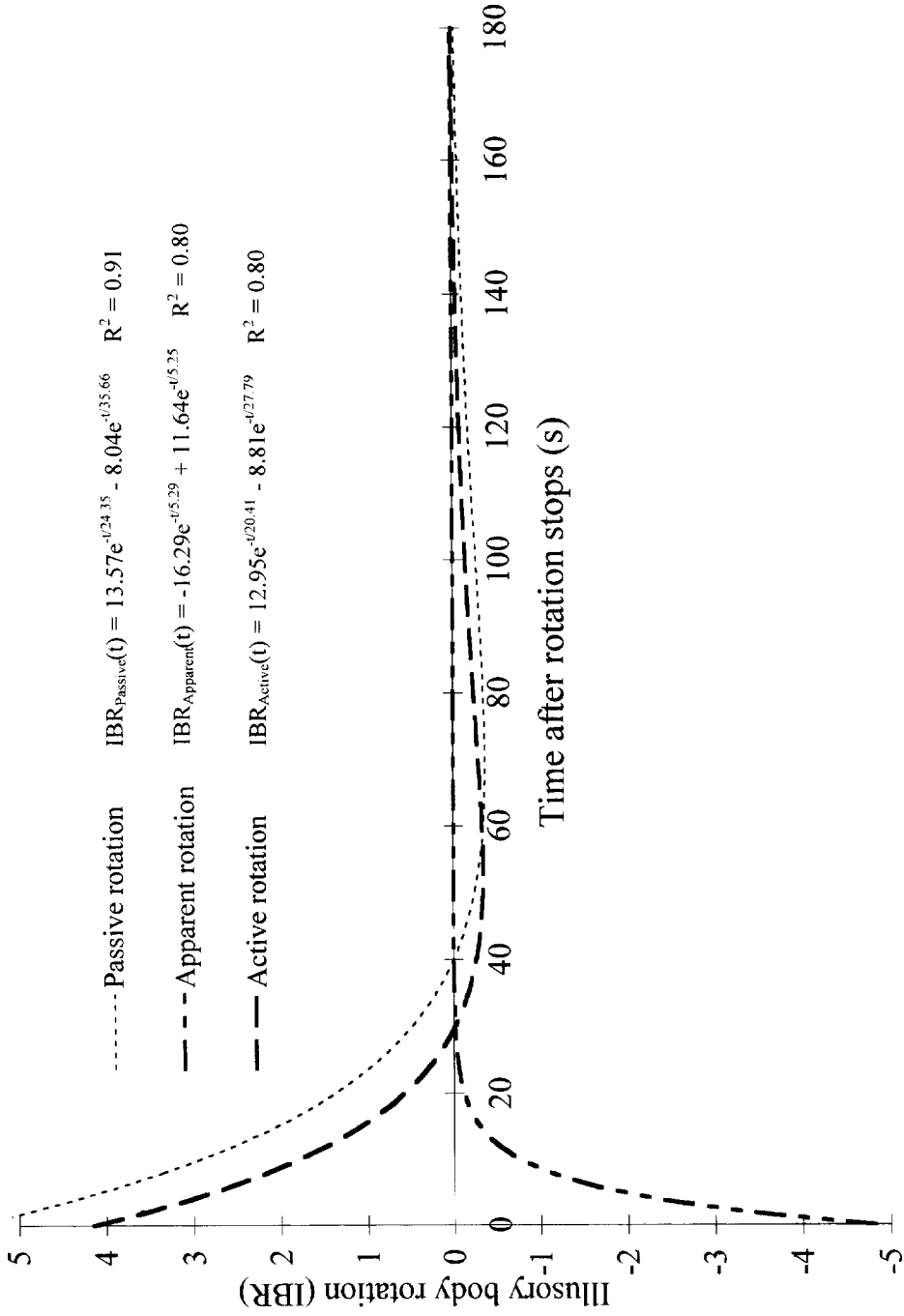


Figure 4. The mean magnitude of illusory body rotation (IBR) of 10 subjects as a function of time after stopping for each of the three types of turning. Positive values indicate that illusory body rotation was in the direction opposite to the previous turning of the body. R² represents to coefficient of determination.

Instead we adopt the simple view that the gain of vestibular nystagmus represents the outcome of combining signals arising from the vestibular system and those arising from the arthrokinetic system. In the post-rotatory period, the arthrokinetic signals are due to the aftereffects of prolonged active rotation modified by the activity associated with deceleration. We make no attempt to dissociate these signals into efference, reafference, and exafference. We only assume that they are the same after active turning as after apparent turning.

An additive model of interaction between the two types of nystagmus predicts that the velocity of nystagmus after active body rotation is the vector sum of the velocity of the pure vestibular nystagmus produced by passive body rotation and the pure arthrokinetic nystagmus produced by apparent stepping. Vector addition of distinct sensory inputs is to be expected in a nested sensory system, such as the sense organs in the joints of the arm. Thus, when we judge the position of an unseen finger with respect to a point on the body we must vectorially sum the information from each of the joint receptors in the arm (10). But when two sensory inputs provide alternative sources of information for the same judgment, it is, theoretically, best to average them, because the mean provides the best estimate when there are several independent sources of information. However, if one source of information is more reliable than another, it should be assigned a greater weight in the averaging process.

When we started this experiment we assumed that arthrokinetic and vestibular inputs arising from active self-rotation are parts of a nested sensory system, and we expected the effects of the two inputs to sum. Under some circumstances, arthrokinetic and vestibular inputs are nested. For example, if we wish to judge the motion of a seen object with respect to the torso when the head and eyes are moving, we must vectorially sum vestibular inputs which indicate the velocity of the head rotation in inertial space, motor-proprioceptive inputs which signal eye rotation in the head, and visual inputs which signal motion of the retinal image on the retina. In this situation, only the vestibular inputs signal motion with respect to the inertial

frame of space. However, when we rotate the body actively, vestibular inputs and motor-proprioceptive inputs from the legs provide alternative sources of information about the velocity of body rotation with respect to a common inertial frame. The arthrokinetic inputs provide information with respect to the inertial frame of space because the feet are on the ground, which is assumed to be stationary. Theoretically, either of these sources of information could evoke nystagmus that would fully compensate for body rotation. If their effects were summed during body acceleration, nystagmus velocity would be too high. A better strategy is to use the mean of the two signals to drive nystagmus. However, we normally rotate the head or body only through small angles so that a vestibular signal consistent with rotation is always present. Arthrokinetic inputs are present only during active motion of the whole body, or as aftereffects of active motion. Thus, it is best to give more weight to vestibular inputs than to arthrokinetic inputs, especially when these conflict, as they do after active body rotation.

During active acceleration of the body, the vestibular and arthrokinetic inputs should both produce nystagmus in the same compensatory direction. In the post-rotatory period, the vestibular signals produced by deceleration are equivalent to those produced by rotation in the opposite direction to the previous turning. However, the arthrokinetic aftereffects are equivalent to those produced by continued turning in the same direction. We will see that this is a general feature of postural aftereffects. Thus, the two signals produce the same sign of nystagmus during body rotation, but opposite signs of nystagmus in the post-rotatory period.

In conformity with the above analysis, our results show that the velocity of nystagmus in the period after active turning, during which vestibular and arthrokinetic inputs have opposite signs, falls well below that predicted from the algebraic sum of nystagmic responses evoked by vestibular and arthrokinetic inputs acting alone. However, nystagmus velocity evoked by both post-rotatory inputs is higher than predicted from the mean of the two distinct inputs. We suggest that this is because vestibular inputs are assigned more weight than arthrokinetic in-

puts, at least under the conditions of our experiment. During passive rotation, there is no nystagmus just before deceleration, but during active and apparent turning, the arthrokinetic stimuli would maintain nystagmus during the whole of the period of rotation. Our apparatus did not allow us to measure this per-rotatory nystagmus. However, after the vestibular component has faded, it should be the same in the active and in the apparent turning conditions. Bles and colleagues presented data showing that per-rotatory nystagmus for active and apparent stepping had the same velocity after 60 s of stimulation (14). The per-rotatory responses should therefore not affect the difference between the post-rotatory nystagmic responses produced by these two conditions.

Although our results for nystagmus do not conform to our initial expectation of a linear summation between vestibular and arthrokinetic inputs, they are consistent with the idea of a weighted averaging of the two inputs. Zacharias and Young (15) measured sensations of self rotation induced by vestibular, visual, and combined vestibular and visual stimulation. These stimuli, like vestibular and arthrokinetic stimuli, give independent information about self-rotation and therefore should be averaged rather than summed. Zacharias and Young concluded that the cues average when consistent, with more weight given to vestibular inputs at high frequencies of self-oscillation and more weight given to visual inputs at low frequencies. In addition, they suggested that the weighting function depends on the level of agreement between the cues. In the extreme case, when only one sensory system indicates self-rotation, it alone is used to generate a sensation of turning. They also posited an operator to allow the system to adapt to an extended period of cue conflict. Our results are consistent with this analysis.

The curves describing the decay of post-rotatory sensations of self-rotation are qualitatively similar to those describing the decay of nystagmus. For all subjects, passive rotation of the body produced a strong post-rotatory sensation of body rotation in the opposite direction. This sensation decayed exponentially to zero in about 40 s and then reversed to produce a sensation of turning in the opposite direction. This is a well

known effect and can be understood in terms of the effects of deceleration on the vestibular system—effects involving elastic decay of cupula deflection and discharge of the neural velocity integrator (1). For all subjects, active turning, also, produced post-rotatory illusory self-motion in the opposite direction, but of reduced velocity and shorter time constant. After active turning, none of our subjects experienced the antisomatogyral illusion—a sensation of turning in the same direction of previous turning. We noted in the Introduction that there are conflicting reports about the occurrence of the antisomatogyral illusion after active turning. After apparent stepping, all of our subjects experienced illusory self-rotation in the same direction as the presumed direction of body turning—the antisomatogyral illusion. This confirms the effect reported by Bles and Kapteyn (7). The reduced magnitude of illusory self-motion after active compared with passive turning must represent the conflicting effects of post-rotatory vestibular stimulation and arthrokinetic aftereffects.

After apparent turning, sensations of turning were stronger than the weak nystagmus would suggest. In all conditions, post-rotatory sensations of turning decayed to zero before nystagmus, which suggests that nystagmus is a more sensitive indicator of vestibular or proprioceptive inputs than are sensations of turning. Previous investigators have found that the first sensations of turning and the oculogyral illusion (the apparent movement of a stationary point of light) are both more sensitive indicators of body rotation than nystagmus (16, p. 367). The following are four possible reasons for this difference. First, the scleral-coil method of measuring eye movements that we used is more sensitive than methods used previously. Second, initial sensations of actual turning may be detected more easily than the tail end of post-rotatory sensations of turning because actual turning could involve spurious mechanical cues that are not present in the post-rotatory period. Third, weak stimuli are more difficult to detect after stronger stimulation than after zero stimulation. For example, the threshold for detection of luminance is higher when measured just after an afterimage has faded than after a period of complete dark adaptation. Fourth, subjects were aware

that the turntable upon which they stood could rotate, and this may have increased their criterion level for reporting self-rotation.

We do not wish to draw strong conclusions from the data on sensations of rotation since we suspect that they reflect the operation of complex assumptions that subjects make and highly nonlinear interactions between sensory signals. Mergner and colleagues (17) conducted an experiment in which subjects judged the amplitude of rotation of the head or of the torso when the whole body, only the trunk, or only the head was rotated sinusoidally and passively about a vertical axis. Passive rotation of the whole body was underestimated, especially at low frequencies, because of the low gain of vestibular inputs at low frequencies. Rotation of the torso alone induced underestimation of body rotation and an illusion of head rotation in the opposite direction, which we suspect is because rotation at the neck is usually due to head rotation in space, rather than torso rotation in space. Rotation of the head on the stationary torso was accurately perceived because the event that produced the signals from the neck and the vestibular system conformed to the normally expected event. Mergner and colleagues concluded, as we do, that the head-on-torso and torso-on-ground system provides a reliable estimate of head rotation that is independent of that provided by the vestibular system. We suspect that simple additive or averaging models cannot account satisfactorily for the complex, nonlinear sensory interactions and complex assumptions that underlie our perception of self-orientation.

Post-rotatory nystagmus and sensations of self-rotation produced by passive rotation of the body are well understood (16). The mechanisms responsible for post-rotatory arthrokinetic responses are not well understood. One possibility is that arthrokinetic activity produced by active turning charges the nystagmus velocity integrator in a manner similar to the charging of the integrator by vestibular inputs (18). We assume that arthrokinetic inputs, like visual and vestibular inputs, converge in the central mechanism controlling nystagmus, presumably the vestibular nuclei. However, central convergence does not necessarily imply that the adaptive mechanism responsible for the arthrokinetic

post-rotatory response is centrally mediated. One possibility is that arthrokinetic activity produced by active turning charges the same velocity storage integrator that is charged by vestibular inputs. Bles and colleagues (14) developed a model of this mechanism. The similarity in the time constants of all the aftereffects is consistent with this hypothesis. The postulated inputs to the integrator must interact in a nonlinear manner. In the post-rotatory period, vestibular signals are present and contribute to the response. Thus, to match the decay of the vestibular response, the parallel arthrokinetic input must be transformed to match cupular dynamics. During constant velocity rotation, the cupular response is transient and decays while the arthrokinetic response is maintained. In this sense, the arthrokinetic response is similar to the optokinetic response, which is believed to share the velocity storage mechanism with the VOR. Optokinetic afternystagmus has a similar time constant to vestibular afternystagmus. In the model of Robinson (19), this is achieved by injecting the vestibular signal at a different location in the velocity storage loop to compensate for the radically different dynamics of the sensory inputs. Unlike the arthrokinetic case, optokinetic eye movements are driven by a closed-loop feedback system, and optokinetic and vestibular inputs appear to add linearly in the combined response.

A second possibility is that post-rotatory arthrokinetic responses are an instance of a broader class of proprioceptive-motor aftereffects. For example, if a person holds one outstretched arm well above eye level and the other below eye level for about one minute and then attempts to place both arms at eye level, the arms will be displaced in the direction of their previous posture. Similarly, if the eyes and head are held in an extreme lateral position for some time and then restored to the apparent straight ahead, they deviate by several degrees in the direction of the previous position (20,21). These are aftereffects of static posture. There are also aftereffects of active movement. For example, Anstis reported that after a period of jogging in one place on a treadmill in the dark subjects move in the same direction as their attempted motion on the treadmill when asked to jog in one spot (22). More relevant to the present ex-

periment is an experiment by Gordon and colleagues (23). Subjects walked in place on the rim of a 5-ft-diameter rotating horizontal disc for 2 h. Subsequently, when asked to walk straight, the blindfolded subjects curved in the direction of the original apparent turning. The aftereffect lasted for about 40 minutes—and longer in some subjects. The following are some possible causes of proprioceptive–motor aftereffects:

1. Muscles become more responsive to a given level of innervation after a period of active contraction. This effect is known as posttetanic potentiation (24,25). Posttetanic potentiation is counterbalanced by the increase in elastic tension in the antagonist muscle produced by prestretching (26).
2. There is a persistent sensory discharge from muscle-spindle receptors after the contraction of a muscle, which is probably due to an alteration in the contractile state of extrafusal fibers (ordinary muscle fibers) and intrafusal muscle fibers (muscle fibers within sensory muscle spindles) (27,28).
3. The discharge from Golgi tendon organs and ligament receptors adapts when these structures are subjected to steady tension (29,30).
4. The above effects would not be expected to last more than a few minutes. Gordon and colleagues suggested that their long-lasting effect of apparent turning was due to recalibration of the proprioceptive–motor system

with respect to the absence of expected vestibular inputs from centripetal acceleration in the 2-h exposure period. The only way to test this theory would be to see whether subjects with bilateral vestibular loss experience the same aftereffects. Recalibration of the proprioceptive–motor system is not likely to be a factor in our experiment. Subjects rotated about the body axis, so there were no expected vestibular inputs in the exposure period.

There is abundant physiological evidence of interactions between vestibular and motor–proprioceptive inputs. Cells have been found in the suprasylvian gyrus of the cat that respond synergistically or antagonistically to vestibular inputs and to inputs from proprioceptors in the neck (31). Similar cells have been found in the parieto-insular vestibular cortex of the monkey (32), in the vestibular nuclei (33), and in the medullary reticular formation of the cat (34). Cells have been found in the lateral and medial vestibulospinal tracts of the cat that respond to vestibular inputs and to somatosensory inputs from the limbs (35). The physiology of interactions between vestibular and motor–proprioceptive inputs is discussed more fully by Howard (10).

Acknowledgments—This research was supported by a Centres of Excellence grant from the Province of Ontario to the Institute for Space and Terrestrial Science. We thank S. Glasauer and an anonymous reviewer for several helpful suggestions.

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