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NAVAL AEROSPACE MEDICAL RESEARCH LABORATORY
PENSACOLA FLORIDA

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SUMMARY PAGE

THE PROBLEM

The perceptual and motor reactions of pilots to vestibular stimuli in aircraft are often analyzed as though the stimuli were delivered to a passenger or subject riding passively in a motion device. One means of gaining insight in the laboratory into potential effects of voluntary motor control on reactions to motion is to compare responses to similar motions experienced in different ways, e.g., passively, in a remotely controlled motion device, versus actively, by voluntary motor activity of the individual whose reactions are being observed. The present study follows this paradigm.

FINDINGS

1) Cessation of sustained passive rotation by voluntary motor actions of the limbs yields substantial suppression of the postrotational illusion of turning, but does not alter the vestibulo-ocular reflex (VOR) which decays at its normal rate. 2) Rotation produced by action of the arms augments the perrotatory VOR and suppresses the postrotatory VOR as well as the postrotatory illusion of turning. 3) Head movements made immediately after an active turn and an active stop do not produce the disorienting nauseogenic disturbance (Purkinje effect) that accompanies head movements following a comparable passive turn and passive stop.

Admittedly, the motor activity in the present studies was considerably different from the kinds of motor responses exercised by pilots. Nevertheless, the alteration of sensorimotor, perceptual, and nauseogenic consequences of motions by voluntary motor action in the present studies may involve mechanisms comparable to those that account for several frequent observations: a) Some pilots experience airsickness as passengers but are relatively immune from airsickness when they are piloting the aircraft, and b) it is the experienced pilot as opposed to the novice who is more likely to suffer simulator sickness and to be disturbed by 'the feel of' fixed-base flight simulators. The results lend credence to the possibility that the reactions of highly experienced pilots to the motions they initiate in aircraft are modulated by feedforward mechanisms which alter sensory feedback and sensorimotor consequences of the motions which must remain under the pilot's active control and emphasize the importance of developing prototype procedures for elucidating how the effects of experience in the control of motion influence the reactions to the motion.

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INTRODUCTION

The perceptual and motor reactions of pilots to vestibular stimuli in aircraft are often analyzed as though the stimuli were delivered to a passenger or subject riding passively in a motion device. Because experienced pilots must develop high levels of skill in control of aircraft motion, there are reasons to believe that their control actions alter their responses to motion relative to responses that would be predicted from passive motion studies. This is based upon the assumption that development of skills in the control of movement involves a process in which feedforward signals accompanying intentional motor acts alter perceptual and sensorimotor consequences of sensory feedback signals set off by the motion itself. One means of gaining insight in the laboratory into potential effects of voluntary motor control on reactions to motion is to compare responses to similar motions experienced in different ways, e.g., passively, in a remotely controlled motion device, versus actively, by voluntary motor activity of the individual whose reactions are being observed.

The effects of voluntary initiation of movements on motion sensed during eye movements have received a great deal of attention (16), but relatively little attention has been paid to the effects of voluntary action on vestibular responses. The dynamic response of the cupula-endolymph system to deceleration following prolonged passive whole-body rotation is such that it yields a false sensation of turning in the direction opposite to that of the preceding rotation. However, it has recently been reported that, contrary to traditional findings, the postrotatory sensation was frequently in the same direction as the preceding rotation when the rotation was actively produced by locomotor activity of the subject (9). Moreover, during active turning and stopping, the perrotatory vestibulo-ocular response (nystagmus) was augmented, whereas postrotatory nystagmus was suppressed relative to the responses produced by passive rotation and stopping (5,6,12).

It is well established that vestibular stimulation influences, either directly or indirectly, motor responses of the neck, torso, and limbs. But there is also good evidence that voluntary movements of the limbs can induce characteristic 'vestibular' sensations of turning and oculomotor responses in the absence of any angular motion of the head, and hence, any mechanical stimulation of semicircular canal receptors. For example, Bles (6) has shown that the sensation of body rotation ("circularvection"), evoked by active stepping on a small circular treadmill, was almost as potent as the sensation produced by active or passive rotation of the subject at an equivalent angular velocity. This "apparent stepping around" also induced nystagmus, though it was substantially weaker than the response obtained from adequate stimulation of the semicircular canals by rotation of the subject. Movement of just the upper limbs is also sufficient to produce circularvection and nystagmus. Brandt et al. (7) reported that stationary subjects, seated in darkness inside a rotatable cylinder, experienced an illusion of turning when they tracked the rotation of the cylinder by placing their hands on the inner wall of the cylinder. The 'walking' action of the extended arms also induced a sustained nystagmus ("arthrokinetic nystagmus") which tended to persist after the cylinder was stopped ("arthrokinetic after-nystagmus").

Efforts to understand these curious results involve several lines of speculation. The unexpected results may be a manifestation of somatosensory afferent signals initiated by vestibulospinal reflexes during rotational activity, but the data are not sufficient to establish that voluntary action during rotation and deceleration is a necessary condition for augmenting the influence of these spinal messages. It is possible that stimulus artifacts, such as head-axis wobble during active turning and head tilts on stopping, may have partially contributed to aspects of some (12) of these findings. The present report describes several experiments designed to further explore potential interactive effects of voluntarily generated vestibular stimuli. The experiments attempted to simplify the conditions of observation by using more controlled, whole-body, rotational stimuli, thereby permitting highly comparable mechanical stimuli to be produced by several conditions of active and passive rotation and deceleration.

PROCEDURE

APPARATUS

The apparatus consisted of a lightweight rotating chair with a servo-controlled drive system which could be uncoupled from the chair by an electromagnetic clutch. The chair was also fitted with an electromagnetic brake. A head holder on the chair was adjusted to provide light pressure on the back and sides of the head in order to maintain head stability. An Earth-fixed metal cylinder, internal radius of 0.52 m, surrounded the chair concentrically. The height of the cylinder was 0.6 m, with its midpoint at about eye level of the erectly seated subjects. Subjects, seated in the chair, could easily generate sufficient torque to rotate the chair and, hence, themselves, by using a hand-over-hand 'walking' action on the inner surface of the cylinder. They could arrest rotation when the chair was uncoupled from its drive system by stopping the 'walking' action and pressing their hands against the cylinder wall. Also surrounding, but not touching, the base of the rotating chair was an Earth-fixed circular platform. During chair rotation the subject's feet were positioned on a small footrest on the chair close to its rotation axis. This arrangement permitted subjects to arrest rotation by foot-and-leg action in which the feet were lifted from the footrest and placed on the concentric platform just after the chair was uncoupled from the drive system.

Horizontal components of eye movements were recorded, using silver silver-chloride electrodes and direct-coupled amplification of corneoretinal potential with electronic circuitry that provided automatic recentering for any excessive d-c drift in the recording. During rotation and for 55 seconds after rotation, the experimental room was very dimly illuminated by green light. Vision was excluded by having the subject wear goggles passing only red light. This also served to stabilize the corneoretinal potential. Before and after each rotation trial, illumination of the room with white light allowed eye movements to be calibrated without the subject having to remove the goggles. Additional eye movement calibration before the first trial and after the last trial was obtained by rotating the subject at 20 deg/sec with the white-light room illumination. Vertical black and white stripes, each subtending approximately 8-deg visual angle, on the internal surface of the cylindrical Earth-fixed surrounds provided an optokinetic stimulus generating a nominal 20 deg/sec eye velocity calibration.

Experiment I

Method. Subjects were given brief practice to learn the task of arresting rotation by use of the hands and the feet, and one familiarization trial of 6-8 turns at 60 deg/sec with a rapid passive stop. Subjects were asked to signal the end of turning sensation, if such sensation had occurred, and to remember the direction of apparent rotation produced by the deceleration. Eye movement recording was continued for 55 seconds after each deceleration. Trials were terminated by turning on the room lights, at which time subjects reported the direction of the apparent rotation sensation produced by the deceleration. The subjects also estimated the intensity of the aftersensation in a four-category scale: none, weak, medium, or strong. In practice, most subjects expanded upon this simple four-category response. For example, having categorized two responses as very strong, some subjects would say that one of the two responses was definitely stronger than all others. Included among descriptions rendered were "weak to medium," "medium to strong," "strong," "very strong," "weak," "very weak," etc. These amplifying comments were used to convert the four-point categorization into a ten-point scale, wherein simple responses of none, weak, medium, or strong were given magnitude scores, respectively, of 0, 2, 5, or 8.

In each experimental rotation period, the drive system was used to accelerate the chair at 15 deg/sec^2 to a velocity of 60 deg/sec which was maintained for 60 seconds. Stopping was then accomplished in one of four modes:

I) Passive stop. The chair was decelerated by the electromagnetic brake at approximately 100 deg/sec^2.
II) Active stop - hands. The palms of the hands were placed against the internal wall of the Earth-fixed cylinder.
III) Active stop - feet. The feet were placed on the Earth-fixed concentric platform.
IV) Active stop - hands and feet. The hands were placed on the interior cylinder surface, and simultaneously the feet were placed on the concentric platform.

In each of the active stopping trials, at the same time as the drive system was uncoupled from the chair, the subject was told to initiate the stop.

Subjects. Eight subjects, four men and four women, participated in the experiment. Subjects were within the age range 20-40 years with a mean age of 27 years. All were in normal health and without neuro-otological defect.

Experiment II

Method. Subjects were given a brief opportunity to practice the task of rotating themselves by action of the hands and of stopping by simultaneous action of the hands and feet. In order to enable subjects to attain and sustain the rotation speed desired, the frequency of an audio-oscillator was controlled by the voltage from the tachogenerator of the rotating chair.* The absence of audio beats from speakers directly over the subject's head served as a cue to the subject that the desired speed had been attained. With this audio cue, many subjects were able to maintain the average desired speed of 60 deg/sec quite well. However, preliminary trials indicated that some individuals occasionally erred in determining the proper direction of speed correction. Therefore, subjects were additionally assisted by verbal instruction over the chair intercom system from the experimenter who, whenever he deemed it necessary, indicated the direction of desired speed correction by saying, "faster," "slower," or "good," as appropriate.

In addition, subjects received one brief passive rotation trial of 6-8 turns at 60 deg/sec, which served to illustrate rotation aftereffects. Subjects then received a brief description of the three different kinds of rotation trials that would be employed in the experiment. They were told that they might experience an aftereffect of apparent rotation following each stopping stimulus, and were asked to signal the termination of any such sensation as soon as it occurred. They were also told that they would be required to describe the direction and to assess the intensity of their aftersensations.

Three conditions of rotation and stopping were used:

> Condition I) Active turn, active stop: Subjects rotated themselves in darkness at a nominal speed of 60 deg/sec for 60 seconds. Rotation was accomplished by hand-and-arm action of the subjects, as described above, and stopping was accomplished by application of the hands and feet to the fixed drum and platform.
>
> Condition II) Active turn, passive stop: Subjects rotated themselves by hand-and-arm action for 60 seconds at a nominal speed of 60 deg/sec. When 60 seconds had elapsed, they were told to cease active turning (subjects retracted their arms to their sides) and a moment later the chair was stopped by the electromagnetic brake.

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*Another oscillator operated at a fixed frequency corresponding to a rotational speed of 60 deg/sec.

Condition III) Passive turn, passive stop: Subjects were rotated and stopped passively. The experimenter used the servo-controlled drive of the rotating chair to accelerate the subject at 15 deg/sec^2 to a speed of 60 deg/sec; this speed was maintained for 60 seconds before the chair was stopped by the electromagnetic brake.

Each subject experienced each of the above conditions twice, with one clockwise and one counterclockwise trial in each condition. Five subjects had clockwise trials first, and four subjects had counterclockwise trials first. Orders of presentation of the three conditions were randomly assigned to the nine subjects.

After the procedure described above was completed, each subject experienced two additional trials, one consisting of an active turn and active stop (Condition IV), the other a passive turn and passive stop (Condition V). These trials differed from the previous trials in that, immediately after deceleration to a stop, subjects rotated their heads forward (i.e., in pitch) through an angle of about 90 degrees. The head movement was completed within 2 seconds. The primary purpose of these additional trials was to determine whether the change in the plane of the illusory sensation of turning (the Purkinje effect) induced by the head movement was equally disturbing in the two experimental conditions.

Subjects. Nine subjects, five men and four women, participated in the experiment; the mean age was 29 years with a range of 19 to 48 years. All were in normal health without neuro-otological defects. One of the nine subjects had also participated in Experiment I approximately one week earlier.

RESULTS

Experiment I

The slow phase velocity of the nystagmus during the first 45 seconds after stopping was computed from the analogue EOG recording, using the technique developed by Barnes (3). A simple decaying exponential was fitted to each postrotational response, and from this the peak slow phase velocity, the time constant of decay, and the nystagmus output (i.e., the cumulative eye displacement from $t = 0$ to $t = 45$ seconds) were calculated. Analysis of variance of these measures showed that there was no significant effect attributable to the direction of rotation, so in the preparation of Table I the responses following clockwise and counterclockwise rotation were combined. On inspection of the three measures (peak nystagmus velocity, time constant of decay, and nystagmus output), it was apparent that the postrotational nystagmus responses were remarkably similar in the four stopping modes, a feature that was confirmed by the absence of F values having even marginal statistical significance in the analysis of variance.

In contrast, there were highly significant ($P < .001$) differences in the duration and magnitude of the aftersensations according to the way in which the turntable was decelerated. As shown in Table I, the greatest duration and subjective magnitude occurred with the passive stop (Mode I), while with active stops, the duration of the aftersensations was approximately halved. The greatest reduction was achieved in Mode IV (stop with hands and feet), with somewhat less suppression when only the hands were used (Mode II), and suppression was least in the 'feet only' mode.

In the passive stop condition all subjects reported aftersensations in the traditional direction (i.e., opposite to that of the preceding rotation). In only one of the 48 trials with active stops (Modes II -IV) did a subject report an aftersensation in the same direction as the preceding turn (an antisomatogyral illusion [9]), though in eight of these trials subjects were uncertain about the direction of their aftersensation. Thus the active stopping conditions yielded aftersensations having a lesser duration, magnitude, and clarity than those evoked by passive deceleration.

Table I

Mean measures of postrotational nystagmus and sensation in the four stopping modes of Experiment I

	Stopping Mode			
	I Passive	II Hands	III Feet	IV Hands and Feet
Postrotational Nystagmus				
Peak slow phase velocity (deg/sec)	35.1	35.1	37.6	33.3
Time constant of decay (sec)	16.3	15.8	15.1	16.0
Nystagmus output (deg)	554	529	539	521
Postrotational Sensation				
Duration (sec)	28.0	13.1	16.3	12.3
Magnitude estimate	7.5	3.9	4.9	3.2

Experiment II

Summarized nystagmus and subjective data from Conditions I, II, and III are presented, respectively, in Tables II and III; summaries of both nystagmus and subjective data from Conditions IV and V are presented in Table IV. The slow phase of the nystagmus recorded during the per- and postrotational phases of each trial was extracted from the analogue EOG recording by digital computer; and, as in Experiment I, a simple decaying exponential was fitted to the individual plots of slow phase velocity against time. From this the peak slow phase velocity, the time constant of decay, and a measure of nystagmus output were determined.

Analysis of variance showed that there was no significant effect attributable to the direction of rotation, so in the preparation of Figure 1 and Tables II and IV, measures obtained for clockwise and counterclockwise stimuli were combined. Figure 1 illustrates the mean slow phase velocity of the per-and postrotational nystagmus and the mean speed of rotation of the chair in the three main conditions of stimulation. The ordinates are modulus values and hence do not show that the direction of the postrotational nystagmus was always in the opposite direction to that of the perrotational response.

Table II

Mean measures of per and postrotational nystagmus in Experiment II, Conditions I-III

	Experimental Condition					
	I		II		III	
	Active/Active		Active/Passive		Passive/Passive	
	Turn	Stop	Turn	Stop	Turn	Stop
Peak slow phase velocity (deg/sec)	39.83	21.18	40.53	23.32	33.7	29.17
Time constant of decay (sec)	29.07	22.44	28.57	20.47	14.82	29.97
Nystagmus output (deg)	1061	441	1062	479	558	605

Inspection of Figure 1 and Table II reveals the appreciable augmentation of the perrotational nystagmus during active turn, in comparison with the responses obtained during passive rotation. Despite subjects taking, on average, some 10 seconds or more to actively attain the desired rotational speed in Conditions I and II, the peak slow phase velocity was significantly ($P < .01$) greater than when the turntable was driven electrically and accelerated to constant speed in 4 seconds. There was also a notable increase in the time constant of decay of the perrotational nystagmus in the active turn conditions. This was due, in part, to a modification of the exponential decay, which differed from the typical perrotational response to passive rotation; the active perrotational response had a more linear decay trajectory (vide Figure 1). The combination of a higher initial response velocity and prolongation of the perrotational response yielded nystagmus output measures which, on average, were about twice as great as those obtained during passive turn, a difference which is highly significant ($P < .001$) in the analysis of variance. The perrotational nystagmus responses during active turn (Conditions I and II) were, as might be expected, very similar, and none of the measures differed significantly ($P > .05$) between the two conditions.

Differences in the postrotational responses were less dramatic than those associated with the perrotational phases. In both Conditions I and II the peak eye velocity, immediately after deceleration, was sig-

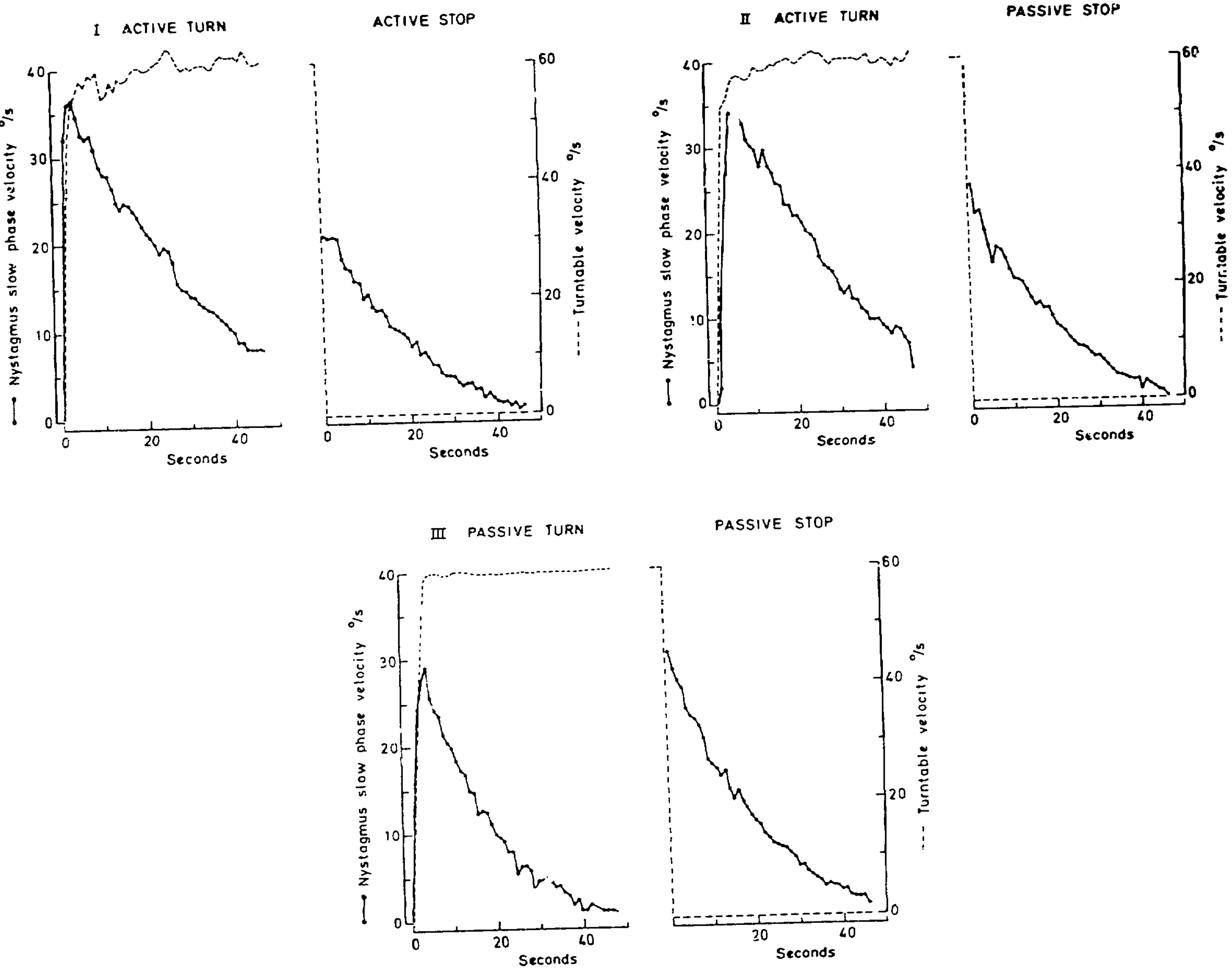

Figure 1

Mean Slow Phase Velocity of Per- and Postrotational nystagmus in Conditions I, II, and III of Experiment II nificantly (P <.01 >.001) lower than in the Condition III, and the nystagmus output was also somewhat less ($P < .05$); the time constant of decay, however, was similar in all conditions. On average, the weakest postrotational response occurred in the active turn/active stop condition, though none of the measures discriminated between Condition I and Condition II at the $P = .05$ level of significance.

The mean durations and subjective magnitude estimates of the postrotational sensation of turning are assembled in Table III. Responses following clockwise and counterclockwise rotation have been combined, as direction of rotation was again not a significant treatment when tested by analysis of variance. In contrast to the postrotational nystagmus, the aftersensations differed appreciably among the three experimental conditions. The sensations following a passive stop from passive rotation (Condition III) had, on average, almost twice the duration and twice the subjective intensity of those following an active turn with passive stop (Condition II). These, in turn, had approximately twice the magnitude of the aftersensations evoked by an active stop from active turn (Condition I). Indeed, in this experimental condition two of the nine subjects were unable to detect any sensation of turning following the active stop maneuver. Analysis of variance showed that both the aftersensation durations and the magnitude estimates differed significantly between experimental conditions with Condition I < Condition II ($P < .01$), and Condition II < Condition III ($P < .001$).

The two additional conditions (IV and V) involving head movement immediately after stopping yielded postrotational nystagmus that was appreciably suppressed ($P < .001$) relative to the responses obtained in the preceding trials in which there was no head movement in the postrotational period. On comparison of the measures of the postrotational nystagmus obtained in these experimental conditions (Table IV) with those of Conditions I and II (Table II), it is apparent that the reduction in the response is attributable, principally, to the accelerated decay (i.e., shorter time constant) of the postrotational nystagmus ($P < .001$), though there is also a significant ($P < .01$) reduction in the peak slow phase velocity. As when no head movement was made on stopping, the response following the passive stop was somewhat larger than that following the active stop, though the difference in the nystagmus output is not highly significant ($P < .05$).

The main purpose of the trials involving head movement, however, was to determine if there would be a difference in the subjective responses according to whether the provocative stimulus was achieved by active or passive rotation. In particular, an attempt was made to assess whether there was a difference in the unpleasant, disturbing, or nauseogenic quality of the vertigo that accompanies a head movement after a stopping stimulus (the Purkinje effect [18]). Measures of the duration of the aftersensation showed the expected reduction ($P < .01$) when a head movement was made in the passive turn/passive stop trials (cf. Conditions III and V), and there was a slight, but not significant, decrement of the mean aftersensation in the active turn/active stop condition (cf. Conditions I and IV). Subjects' reports of the unpleasant or disturbing quality of the sensation induced by the postrotational head movement are summarized in Table IV. It may be seen that in the active turn/active stop condition the majority of subjects experienced no disturbance, while in the passive turn/passive stop condition all but two subjects found the sensations unpleasant to a greater or lesser degree. Comparison of the frequencies of 'no' and 'slight' disturbance with those of 'mild' and 'strong' disturbance in the two conditions (IV and V) yielded a significant difference at the P = .01 level (Sign Test).

Table III

Mean durations and magnitude estimates of postrotational sensations of turning in Experimental Conditions I-III, Experiment II

Experimental Condition	Mean Duration of Aftersensation Seconds	Mean Magnitude Estimate
I. Active Turn/Active Stop	7.4	2.0
II. Active Turn/Passive Stop	14.6	4.6
III. Passive Turn/Passive Stop	24.9	8.3

Table IV

Mean measures of per- and postrotational nystagmus and of the aftersensations in Experimental Conditions IV and V, Experiment II, in which a head movement through 90 deg in pitch was made immediately after stopping

	Experimental Condition			
	IV		V	
	Active/Active		Passive/Passive	
	Turn	Stop	Turn	Stop
Peak slow phase velocity (deg/sec)	49.3	15.6	41.7	21.3
Time constant of decay (sec)	24.6	7.7	17.2	9.4
Nystagmus output (deg)	1211	164	740	229
Duration of aftersensation (sec)		6.2		13.9
Subjective assessment of aftereffect				
Number of subjects reporting:				
No disturbance	6		2	
Slight disturbance	3		2	
Mild disturbance	0		2	
Strong disturbance	0		3	

DISCUSSION

Because the head is the uppermost motion platform of the body, vestibular messages must be integrated with visual and proprioceptor inputs in order to set off reflexes that adequately compensate for independent but coordinated movements of the head and body relative to the Earth. It is clear that intricate interactions between the visual and vestibular systems influence oculomotor control, visual performance, and perceived states of motion (2,11,13,14). Nystagmus elicited by semicircular canal stimulation in darkness is augmented during rotation and suppressed after rotation by the introduction of visual Earth-fixed targets. Similarly, interactions between the two classes of vestibular endorgans influence perceptual and sensorimotor responses. With a tilted axis, perrotational nystagmus from semicircular canal stimulation is augmented, and postrotational nystagmus is suppressed, in that it decays more rapidly, presumably as a result of interactions with otolithic and/or somesthetic gravitational cues (4).

The present results indicate that sensory feedback from motor activity also enters into those interactions during active control of motion and suggest that the presetting of central neural processing by active (voluntary) initiation of motion sequences can alter the perceptual, nauseogenic, and sensorimotor consequences of a given motion.

The results demonstrate, without ambiguity, that volitional movements of the upper and lower limbs can modify per- and postrotational vestibular responses. Previous studies (5,6,9,12) have shown that active voluntary movement of the whole body, producing angular motion about the longitudinal (Z) body axis, augmented perrotational nystagmus and sensations of turning, and suppressed postrotational responses. There was a significant reduction of postrotational nystagmus, but the alteration of the aftersensations was even more profound. In many subjects the illusory sensation of turn (the somatogyral illusion) was not in the expected direction (i.e., opposite to that of the preceding turn) but in the same direction as the antecedent rotation. The results of the present experiments, in general, accord with those findings, insofar as they demonstrate that voluntary movement of only the upper and lower limbs is sufficient to modify per- and postrotational vestibular responses, though without the reversal of the somatogyral illusion that occurs following ambulatory self motion.

Experiment I

The least pronounced alteration of postrotational responses by active control actions was observed in Experiment I in which the voluntary arm-and-leg action to accomplish a stop from sustained passive rotation reduced the duration and magnitude of the aftersensation but was without any discernible effect on the postrotational nystagmus. At the outset, it should be recognized that the attentional demands on the subject were greater in the active than in the passive stop mode, and it is possible that the shortened aftersensation was due in part to a shift in attention in the active stops. However, in the following discussion it is also important to bear in mind that purely intellectual information concerning the true state of motion has little effect on sensation of turning during a strong semicircular canal response. For example, subjects who are, intellectually, fully aware that they are not turning still perceive vestibular postrotational turning sensations if other sensory indicants of the state of motion are absent. Moreover, a dissociation of subjective and objective indicants of vestibular activity comparable to that observed in Experiment I has been observed in a number of other experimental situations in which signals from the semicircular canals do not accord with information from another group of sensory receptors, suggesting that false turning sensations are more effectively altered by sensory vis á vis intellectual information. For example, a brief view of a veridical fixed surround during postrotational nystagmus suppresses both the sensation of turning and nystagmus, but with removal of visual suppression, nystagmus recovers almost to the level of its unsuppressed trajectory of exponential decay, whereas the sensation remains substantially suppressed (8,10). Similarly, following rotation about an Earth-vertical axis, tilting to a horizontal position increases the rate of decay of postrotatory nystagmus and quickly suppresses the turning sensation, but upon return to vertical, nystagmus returns almost to its normal rate of decay (4) and persists long after the turning sensation subsides. However, in these other examples of dissociation between oculomotor and subjective aspects of the vestibular reaction, one involving a 'corrective' visual input and the other involving 'corrective' otolithic (and somatosensory) inputs, both vestibular nystagmus and sensation were altered during the introduction of the 'corrective' orientation cues. The results of Experiment I are curious because the postrotatory sensation was clearly altered by the voluntary muscle torque that arrested the turn, while postrotatory vestibular nystagmus was remarkably unaffected.

Possibly the explanation of this finding can be found by considering the subject's ongoing vestibular response at the time that he initiated his stopping action; viz., there was no sensation of turn and no primary vestibular nystagmus at this time. Therefore, when the subject arrested his turn, he did not receive sensory inputs discordant with ongoing vestibular signals, but, rather, generated a vestibular stimulus by voluntary arm and leg actions. During the course of the deceleration, the torques applied by the musculature of the arms and legs to arrest rotation were in the same direction as the torques necessary to start rotation in opposite direction; i.e., the actively applied torques to arrest the body turn were concordant with the vestibular stimulus from the deceleration. From this point of view, absence of suppression of vestibular nystagmus is not surprising, but, rather, the selective attenuation of the turning sensation by the voluntary stopping action is to be resolved. Here we must consider differences in angular motion of the limbs relative to the trunk as, for example, when a clockwise (CW) body turn is arrested by limb actions and when counterclockwise (CCW) body turn is commenced by limb action. The angular momentum of the body during CW rotation will drive the limbs CCW relative to the body when the hands and feet are extended to the Earth-fixed external surface to serve as brakes in stopping the body turn, and so, while the muscular torque (relative to the body) reacts to this external force with an opposed CW torque, the initial angular movement of the limbs relative to the body is in a CCW direction (which is contradirectional to the vestibular past-point reflex). In contrast, if CCW body rotation from rest is initiated by action of the hands on an external surface, then the limbs move in a CW direction relative to the body; the direction of both the muscular torque and the arm rotation relative to the body is the same (and concordant with the vestibular past-point reflex). Differences in directions of applied muscle torques and limb movements are apparently discriminated at a level of the nervous system which results in a suppression of the turning sensation but does not influence the vestibulo-ocular reflex when the body is actively stopped after sustained passive rotation.

This interpretation derives in part from some observations of Brandt et al. (7) which bear upon the possible contributions of 'palmar slip' (friction) and palmar contact cues. They reported both arthrokinetic nystagmus and sensation of turning (arthrokinetic circularvection) when horizontally extended arms of a stationary subject were passively rotated in the horizontal plane at the shoulder joint by palmar contact against a moving surface. However, by pressing the hands against the internal surface of a concentric rotating cylinder, the subjects of Brandt et al. did not apply opposing muscle torque, but to some degree applied active smooth concordant torques in keeping the hands stationary on the rotating surface. Thus the findings of Brandt et al. (7) are not inconsistent with our interpretations. They also reported that two other conditions failed to induce either arthrokinetic nystagmus or circularvection effects: 1) voluntary torsional arm movements in the horizontal plane made without hand contact against the rotating surrounding cylinder, and 2) placing the palmar surface against the surface of the rotating cylinder with the arms held stationary so as to yield 'palmar slip' signals. Apparently neither 'palmar slip' without torsional arm movements nor voluntary torsional arm movement without palmar contact against a moving surface is sufficient to generate circularvection or arthrokinetic nystagmus. It would appear that feedback concerning the consequences of voluntary torsional limb movement is critical to the determination of the perceptual and oculomotor responses, and that the palmar contact 'closes the loop' in which feedforward signals released with voluntary motor actions are compared with feedback resulting from the motor response. Here we are suggesting that voluntary action was involved in the "passive condition" of Brandt et al. In our Experiment I, palmar contact and some torsional arm movement (albeit slight) occurred in the active stop mode. The subject's intention was to arrest rotation. The vestibular feedback as a consequence of this voluntary action was a signal of rotation in opposite direction, and the muscle torque required to arrest rotation was directionally the same as that required to commence rotation in the opposite direction; but the direction of torsional limb movement was opposite in direction to the a) applied muscle torque, b) the vestibular signal, and c) the vestibular past-point reflex. This set of consequences of the voluntary effort to arrest rotation yielded a greatly suppressed sensation of rotation but had no effect on the vestibulo-ocular reflex.

Experiment II (Conditions I, II, and III)

The salient findings of Experiment II were the augmentation of perrotational nystagmus and the suppression of postrotational responses when subjects rotated themselves by voluntary arm movements. The difference in the mean nystagmus slow phase velocity in active turn/active stop condition with that recorded during passive turn and passive stop is plotted in Figure 2. This shows that, on average, the voluntary arm movement increased slow phase velocity by approximately 9.8 deg/sec throughout the period of rotation at near constant velocity. This, more or less, sustained increment in nystagmus velocity accounts for the increase in nystagmus output and apparent increase in the time constant of the perrotational response found in the active turn condition.

The magnitude of the augmentation of the perrotational nystagmus is similar to that found when whole-body rotation was produced by ambulatory movements of the lower limbs of standing subjects (9,12). It is also remarkably similar in magnitude to the nystagmus induced by tracking movements of the outstretched arms, in the absence of any direct vestibular stimulation, for Brandt et al. (7) reported that at a drum velocity of 60 deg/sec the average nystagmus velocity was 10 deg/sec and that the latency of the "arthrokinetic" nystagmus was "between one and several seconds." Those authors also described an "arthrokinetic after-nystagmus" which persisted for "several seconds" following the cessation of drum rotation. As may be seen from Figure 2, the disparity between the nystagmus slow phase velocity recorded in Conditions I and III persisted into the postrotational period, and, immediately after stopping had a magnitude similar to that which occurred during the perrotational phase. However, the difference in slow phase velocity was not dissipated within a few seconds, but decayed in an approximately exponential manner over the 45 seconds for which the postrotational nystagmus was analyzed.

The parsimonious explanation of the enhanced nystagmus found during rotation in Conditions I and II is that the augmentation was due solely to the presence of an arthrokinetic nystagmus which summated, in an essentially algebraic manner, with the perrotational vestibular nystagmus. Likewise, the reduction in the peak slow phase velocity immediately after stopping can be attributed to the presence of an arthrokinetic afternystagmus which, being in the same direction as the perrotational nystagmus, opposed the postrotational response -- a feature that is reminiscent of the effect of optokinetic afternystagmus on postrotational vestibular nystagmus (8,17,19). However, it seems unlikely that the arthrokinetic nystagmus decays as slowly as is depicted in Figure 2, so it may be that there is some central reduction of the vestibularly driven response, perhaps a "dump" in "velocity storage" as Raphan et al. (19,20) have suggested to account for other observations.

The reduction in the duration of the aftersensations that characterize both conditions involving active or passive stop from active turning is explicable in terms of the mechanisms discussed above; namely,

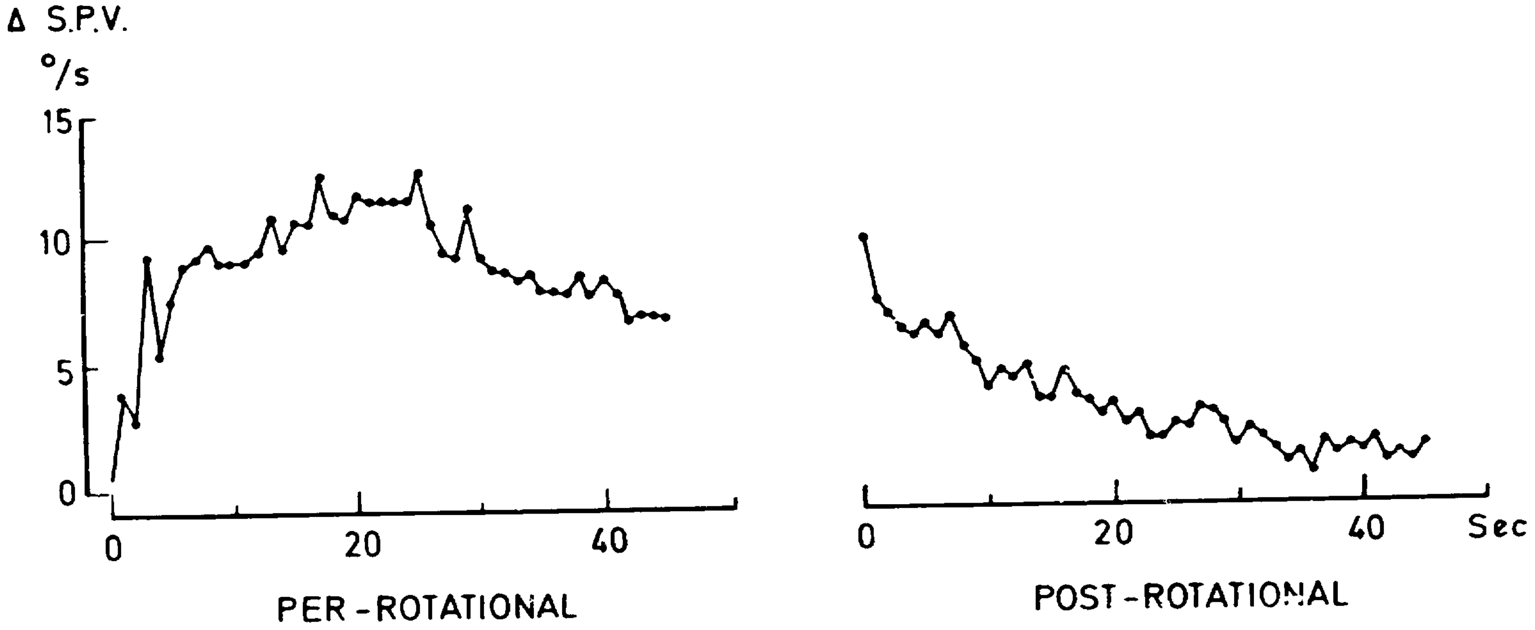

Figure 2

Difference in Slow Phase Velocity (Δ SPV) of Nystagmus during Active and Passive Turning and Stopping Conditions of Experiment II a reduction in the intensity of the resultant "central vestibular" signal and somatosensory suppression. Following active turn (Conditions I and II) the effective vestibular signal, as manifest by the oculomotor response, is reduced because of an arthrokinetic aftereffect. Accordingly, the associated sensation of turning is also attenuated, though the magnitude of the suppression is greater than would be predicted solely from the measures of slow phase velocity. In the passive turn/passive stop condition, the mean nystagmus slow phase velocity at the mean time of disappearance of the aftersensation was 8.0 deg/sec, but the corresponding velocities following active turn were 11.6 deg/sec with the passive stop and 15.5 deg/sec with the active stop. Thus the interruption of a sequential turning action by a voluntary stopping action (Condition I) reduced the postrotational turning sensation more effectively than did the arthrokinetic aftereffect of Condition II, but the voluntary stop did not alter postrotational nystagmus beyond the reduction produced by the arthrokinetic aftereffect, a result which is consistent with Experiment I.E

Experiment II (Conditions IV and V) - The Purkinje Effect

The fast forward head tilt immediately after stopping reduced the magnitude and rate of decay of postrotational nystagmus relative to simple postrotational responses uninterrupted by head tilts. The dynamic response of the semicircular canals is such that the rapid forward head tilt would generate a cupula deflection in the vertical canals during the head tilt but no residual deflection when the head tilt was completed. Therefore, upon completion of the head tilt, the deflection of the cupula in the horizontal canals (which had been produced by the stop) would be the only residual response in the semicircular canals. In the passive turn and stop condition the residual nystagmus response is suppressed because the plane of the responding canal is in a tilted position relative to gravity (cf. Benson, 4, p. 297) which the otolithic receptors signal, and it is probably this otolithic position signal <u>in combination with absence of change-in-position</u> otolithic signals that suppresses the nystagmus from the continuing semicircular canal input. Alternatively, the changed head position yields a "dump in velocity storage" (cf. 19,20). In the active turn and stop condition, the residual nystagmus response is even more suppressed due to arthrokinetic aftereffect as well as the canal tilt relative to gravity. Associated with the fast forward head tilt immediately after stopping rotation is the Purkinje effect. This effect was significantly less disturbing in the active turn and stop condition than in the passive turn and stop condition. Because the angular impulses delivered to the semicircular canals by the active and the passive stops were equivalent when the forward head tilts in the two situations were executed, equivalent inputs from the horizontal semicircular canals were in progress, neglecting the possibility of efferent suppression of the peripheral afferent inflow. In any event, the results indicate significantly less disturbance from an equivalent mechanical stimulus to the semicircular canals under the active turn and stop condition, and this suggests that the introduction of voluntary motor control actions may alter the processing of complex inputs from the semicircular canal and otolithic receptors at a level of the nervous system that can alter the nauseogenic propensities of this particular combination of physical stimuli to the two classes of vestibular receptors.

These modifications of per- and postrotational vestibular responses by concurrent volitional motor activity, and the evocation of vestibular-like responses by volitional limb movements in the absence of any rotational stimulus to the vestibular apparatus, have a number of potentially important theoretical and practical implications. If voluntary control of the whole-body motions that elicit vestibular stimuli can substantially alter the form of the perceptual and reflexive responses relative to the responses that would be produced by comparable passive vestibular stimuli, then patients undergoing an episodic vestibular disorder may have different vertiginous experiences, depending upon their efforts at voluntary control of body movements. Thus, potential application of these findings relates to neuro-otology. They may indicate means of clarifying and interpreting the patients' reports of vertiginous episodes, and if simple procedures can be found that measure the alteration of vestibular responses by voluntary motor activity, then such procedures may prove to be of diagnostic value comparable to the current use of the visual suppression index (1,15). The results also lend credence to the possibility that the reactions of highly experienced pilots to the motions they initiate in aircraft are modulated by feedforward mechanisms which alter sensory feedback and sensorimotor consequences of the motions which must remain under the pilot's active control. Admittedly, the motor activity in the present studies was considerably different from the kinds of motor responses exercised by the pilot. Nevertheless, the alteration of sensorimotor, perceptual, and nauseogenic consequences of motions by voluntary motor action in the present studies may involve mechanisms comparable to those that account for several frequent observations; viz., a) some pilots experience airsickness as passengers, but are relatively immune from airsickness when they are piloting the aircraft (21), and b) it is the experienced pilot as opposed to the novice who is most likely to suffer simulator sickness and to be disturbed by 'the feel of' fixed-base flight simulators (21).

SUMMARIZING INFERENCES

1. Limb movements that are directionally concordant with muscle torque in generating body rotation yield arthrokinetic effects that augment perrotational nystagmus and sustain perrotational turning sensations.
2. Prolonged active turning yields arthrokinetic aftereffects that reduce postrotational nystagmus and postrotational turning sensation produced by a passive stop.
3. An active stop following a passive turn introduces a complicated interaction between the direction of muscle torque exerted and the direction of limb motion. Limb motion resulting from the force required to overcome the angular momentum of the rotating body is in a direction to suppress the decceleratory nystagmus, but the voluntary active muscle torque applied is opposed in direction to the brief limb movement. In this circumstance, vestibular nystagmus is unaltered by the active stop, but the turning sensation is substantially suppressed.

4. An active stop following prolonged active turning also introduces a conflict between the directions of muscle torque and limb movement. The direction of limb movement during the stop is again dictated by the angular momentum of the body and is directionally opposite the volitionally applied muscle torque. The postrotational vestibular nystagmus is reduced by the arthrokinetic afternystagmus but is unaffected by the voluntary stopping conditions, and so it is indistinguishable from the postrotational nystagmus produced by an active turn with a passive stop. However, the postrotational sensation is reduced both by the arthrokinetic aftereffect and the active stop condition, and so this condition yielded postrotational sensations that were substantially less in magnitude and duration than those in any other stopping condition of the two experiments in which equivalent angular impulses were delivered to the semicircular canals by the stop.

5. From these findings it is inferred that the directional discordance between the muscle torque and limb movement that occurs in actively arresting whole-body rotation is processed at a level of the nervous system that alters the vestibular turning sensation but does not alter the vestibulo-ocular reflex.

6. Active turn and stop conditions which suppress the postrotational sensation of turning also suppress the nauseotypic disturbance (the Purkinje effect) that usually accompanies head movements immediately following sustained rotation.

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18. SUPPLEMENTARY NOTES

Dr. Benson is Head of the Behavioral Sciences Division, RAF Institute of Aviation Medicine, Farnborough, Hants, England, where these experiments were conducted.

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

Active and passive motion and turning sensation; Active and passive motion and nystagmus; Voluntary motor control and vestibular responses; Postural-vestibular interactions; Vestibulo-ocular reflex; Nystagmus; Turning sensations

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

The reactions of pilots to vestibular stimuli in aircraft are often analyzed as though the pilot were a passive rider. A means of gaining insight into effects of voluntary motor control on reactions to motion is to compare responses to similar motions experienced in different ways. The present study indicates that cessation of sustained passive rotation by voluntary limb actions strongly suppresses the postrotational turning sensation, but does not alter the vestibulo-ocular reflex; rotation produced by arm action augments

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