Modulation of vestibular sensitivity by passive motion

Master thesis in Medicine

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Photo: Frida Emilson

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Abstract

Information from the vestibular system contributes to the interpretation of how the body is oriented in space. The purpose of this study was to investigate if perception of vestibular input is affected by passive motion. We hypothesized that vestibular afference is down regulated by a period of conditioning (10 minutes of passive, stochastic, rotating movement while blindfolded) and that the perception of movement based on vestibular input, therefore, is decreased after conditioning. By using galvanic vestibular stimulation to create illusionary movements, response to vestibular signals can be investigated independently from other sensory information. We studied sway response during standing on a stable surface, perception of rotation when seated and threshold for detection of motion. All tests were performed, before as well as after motion conditioning, with either GVS or real movement as stimulus.

The results indicate that vestibular sensitivity is modulated by motion conditioning. After conditioning, the threshold for motion detection was increased to 248% ± 31% (mean ± SD) of that before (P = 0.001). Perception of real rotations (30° - 180° over 5 s), in which non-vestibular sensory cues were also available, were significantly reduced by motion conditioning (with 16.1% in average). When using GVS, subjects reported larger illusionary movements before conditioning compared with immediately after. After conditioning, reported rotation to a given stimulus intensity nearly halved (from 113 to 61 degrees when exposed to 1 mA over 10 s). Interestingly, we also found that rapid vestibulospinal balance reflexes (latency ~300 ms), evoked by GVS and recorded as lateral shear force exerted on a force-plate, were halved in amplitude.

We conclude that, in healthy individuals, vestibular sensitivity is modulated by passive motion. The modulating process operates over short time frames and affects both perception of vestibular motion signals and automatic vestibular balance reflexes, suggesting sub-cortical or afferent regulation. Dysfunction in this process is likely to alter movement sensation and balance control.

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Introduction

"Every movement in bed now caused vertigo and nausea, even when I kept my eyes open. If I shut my eyes the symptoms were intensified. At first, I found that by lying on my back and steadying myself by gripping the bars at the head of the bed I could be reasonably comfortable. Later, even in this position the pulse beat in my head became a perceptible motion, disturbing my equilibrium."

This citation is from the essay "Living without a Balancing Mechanism", written by a physician who lost vestibular function through streptomycin treatment (1). Heavy demands are placed upon the human balance system as we stand and walk with upright posture, balancing our body on two legs. Interpretation of multiple sensory information allows perception of how our body is oriented in space. The vestibular system is of great importance for this task and acute loss of vestibular function often leads to dizziness, nausea, instability, difficulty focusing the gaze and sensations that the environment is moving (2). On the other hand, chronic loss can often be partially compensated for by other sensory systems (3-4).

Knowing and understanding the physiology of this complex system is essential for the recognition and interpretation of pathophysiology and furthermore, in the rehabilitation of patients with vestibular impairment.

The Vestibular System – a short presentation

A functional unit located in the bony structure of each inner ear forms the peripheral vestibular system that constantly provides the brain with information about movement and head position. Three semicircular canals, the anterior, posterior and horizontal, and two otolith sensors, the utricle and saccule, form this functional unit. The three semicircular canals sense rotational movement and due to the arrangement of the canals at right angles to one another, rotation of the head in any direction can be detected. Linear acceleration, like gravity, is sensed by the otolith organs, which are also oriented at right angles to each other to be able to resolve acceleration in three dimensions. Also when we are stationary, the brain receives information from the vestibular afferents about the force of gravity acting on the otolith organs. Combined, the semicircular canals and the otolith organs provide the brain with information about head movement and contribute to the perception of self and non-self motion, spatial orientation, navigation, oculomotor control and autonomic control. Thus, a

range of brain functions, from high levels of consciousness to automatic reflexes, depends on the vestibular system. Signals from the vestibular system are interpreted in conjunction with information from other sensory sources, such as vision and proprioception, to create an image of how our body is oriented in space.

In both the utricle and saccule, hair cells are activated when their embedded cilia are bent due to movement of the overlying membrane that consists of dense calcium crystals. When gravitational or inertial forces cause movement of the membrane, the cilia bend and the primary neurons discharge, thereby producing a signal of movement. The magnitude of the movement is encoded by the firing rate of the neurons. This also applies to neurons activated by hair cells in the semicircular canals. When the head rotates the endolymphatic fluid within the semicircular canals lags behind due to inertia. This causes displacement of the cupula, in which the cilia of the hair cells are embedded, resulting in altered discharge of the primary neurons. The semicircular canals are arranged as mirror images across the head, which means that corresponding parallel canals on each side of the head will generate inverse signals when exposed to natural stimuli. This arrangement, which increase, and decrease, firing compared with the tonic discharge rate, improves the directional sensitivity.

Despite rotation of the head, we are still able to focus our gaze on one point, for example, when looking into someone's eyes while nodding the head. This is largely because the vestibulo-ocular reflex counter-rotates the eyes to stabilize the visual image on the retina. When the head is moving, signals from the vestibular system influences eye movements so that if we, for example, look at a point straight ahead and then turn the head left, our eyes will turn right to fix gaze at the same point. To create appropriate eye movements the brain has to distinguish linear acceleration and tilt that stimulate the otolith organs identically. By combining signals from otolithic organs and the semicircular canals the brain can distinguish, for example, acceleration to the left and tilt to the right.

Galvanic Vestibular Stimulation

Galvanic vestibular stimulation (GVS) is a non-invasive method that enables isolated investigation of the vestibular system. A small current is applied between the mastoid processes leading to activation of the vestibular system on one side while the other is inhibited. Which side is activated and which is inhibited depends on current direction. This

method allows other sensory inputs to be excluded and not contribute to balance control. By modulating the firing rate of hair cells in the neuroepithelium of the semicircular canals and the otolith organs, GVS creates a false input signal to the balance system. This creates an illusion of motion if the body is immobilised and a galvanic sway response if unsupported during standing. That is, to the illusion of sway, a reverse actual movement is generated which involves the entire body with its segments (5-7).

By placing skin electrodes on the mastoid process behind each ear (an anodal and a cathodal electrode) a current is passed between the electrodes (bilateral bipolar GVS) (5). The current activates the vestibular afferents of both semicircular canals and otolith organs. Since a current with direction anodal towards cathodal is produced, the cathodal vestibular afferents increase their firing rate whereas the anodal vestibular afferents decrease their firing (5, 8). The galvanic sway response is therefore directed towards the anodal side if standing unsupported and if supported, an illusionary movement towards the cathodal side is produced (9). The sway response to GVS has been shown to be related to the head position. When standing unsupported, the net-effect of GVS, i.e. the direction of the sway response, is rotation around a sagittal axis that is directed backwards and slightly upwards from Reid's plane (an imaginary plane through the inferior of the orbit and the auditory canals). Different studies have shown that the rotational axis is sagittal with an angle between 16° to 19° from Reid's plane. The same axis of rotation is obtained by summing the vectors from the six semicircular canals. (5, 8). The response from the otolith organs needs more complex summations since the hair cells are arranged in opposite direction and the consequence seems to be that the vectors cancel each other out. However, the net result is thought to be a small acceleration, probably towards the cathodal side, while using bilateral bipolar GVS (5).

After GVS stimulation, EMG recordings of lower-limb muscles involved in postural control have shown post-stimulus activations of these muscles through vestibular reflexes, one short-latency of 56 ms followed by a middle-latency response of 105 ms. The activation of the lower limb muscles is a reciprocal response of the agonist and antagonist. The two vestibular reflexes cause a narrow postural sway, which is followed by a prolonged sway, described above as the galvanic sway response (6). The two vestibular reflexes appear to origin from activation of the semicircular canals and the otolith organs. In theories, it has been assumed that there are separate pathways preserving postural balance. The middle-latency response to GVS is emerged from activation of the semicircular canals and the short-latency response from activation of otolith organs (10). Although, a more recent survey claims that the otolithic

signal does not contribute to either the short-latency or the middle-latency response (11). Thus, probing the vestibular system by using GVS to create a perturbation of perception when standing, shows complex patterns of pathway activation to maintain postural balance.

Previous Research

Afference from several sources are of significance for awareness of body image and how we relate to the surroundings. This is of great importance to maintain an upright posture and balance. The vestibular system, vision and proprioception from muscle spindles and joints form these sensory systems and have been studied separately to learn more about their specific contribution during different tasks (4, 6, 12-14). Results indicate that vestibular input is of less importance during standing on a stable floor and that the vestibular system seems to influence lower-limb muscles only when vestibular cues are required to maintain balance (6, 12, 14). While proprioception from leg muscles is sufficient for postural stability, the vestibular threshold is too high to register sway as a threat to balance when standing on a stable floor (6, 12, 14).

Loss of vestibular function may lead to a wide range of symptoms including instability, dizziness and oscillopsia (15). If chronic loss, patients normally replace vestibular functions by visual referencing and an abnormally large sway is observed when standing on an unstable support with eyes closed (3). According to previous research, the main difference between healthy subjects and vestibular-loss subjects seems to be the ability to reference the perception of own body orientation in relation to the surroundings (16-18).

The vestibular system, like the auditory system, is built on hair cells that receive efferent innervation from related brainstem nucleus. In the presence of continuous sound, feedback through the auditory efferent system modulates and tunes incoming signals and produces a long-lasting inhibition of cochlear afferents so that a larger sound stimulus is required to evoke a response (19). The function of the vestibular efferent system is less understood but electrophysiological studies have shown that efferent activity, driven in large part by afferent feedback, can increase or decrease the responsiveness of vestibular afferents to motion stimulation (20-22). This suggests that the vestibular system, through efferent control on its sensors and afferents, can autoregulate its own afferent inflow, perhaps to keep it within a functional operating range for the prevailing conditions.

Objectives

We asked us if human vestibular sensitivity is regulated according to previous or ongoing motion and, if so, whether it involves both perceptual processes and automatic balance reflexes?

We hypothesized that vestibular perception is down regulated after a time of motion conditioning in terms of passive, stochastic, rotating movement while blindfolded. Further, we hypothesized that postural vestibular reflexes would not be affected by the same conditioning.

Method

10 subjects with an age range between 23-59 years (4 females) were recruited from staff and students at the University of New South Wales to participate in this non-invasive study. None of the subjects had a history of repeated periods of nausea or dizziness, neurological disease or trauma. The tests were approved by the Human Research Ethics Committee of the University of New South Wales and subjects provided informed consent before participating.

Two setups were used (Fig. 1), consisting of one or three tests, respectively. As mentioned above, we were interested in comparing perception before and after passive activation of vestibular input. Therefore, each test was performed at least twice, i.e. once before motion conditioning and once immediately after. Test one and two in Setup 2, which are threshold for motion detection and perception of virtual rotation using GVS, were performed once before conditioning and immediately, 30 minutes and 60 minutes after.

To create a period of passive activation of vestibular input, the subject was sitting, blindfolded and wearing ear defenders, in a chair on a platform (described below in Setup 2) and passively and stochastically moved (0.5-2.5 Hz, -40 dB/decade roll-off), with a peak velocity of ~100 deg.s^{-1} and a peak acceleration ~300 deg.s^{-}2, for 10 minutes. As during all tests in Setup 2, the position of the head was in a forward tilt so that Reid's plane and the horizontal canals become close to vertical. Thus, semicircular canals were activated in a corresponding way during both tests and motion conditioning (5). This position was used as it is the position that evokes a sensation of whole-body yaw rotation with GVS. Subjects leaned with the forehead resting on the hands to lessen head-on-neck motion. The time frame of 10 minutes as well as the rotation of the platform in different direction, velocity and amount of degrees were preprogrammed using custom LabView software.

Setup and Protocol

Setup 1: GVS reflexes

The subject stood bare-foot on a stable forceplate (KISTLER) with an area of 40 x 60 cm. Centre of pressure and sheer force data were recorded using custom LabView software. The subject was instructed to stand upright with the head facing forward and feet together, similar

to the setup during Romberg's test.

Bilateral bipolar galvanic vestibular stimulation, GVS, was applied during this setup, to measure postural sway due to stimulation of vestibular afferents. Ag-AgCl electrodes with an area of 3 cm^2 were attached bilateral to the mastoid processes. The current generates a medio-lateral sway response (i.e. rotation about a sagittal axis, backwards and 16° to 19° upwards relative to Reid's plane), if standing with head facing forward (5, 8). Subject responds with a sway to one side, depending on the direction of the current, since the sway response is towards the anodal side (6, 9). A controlled current source with ±70 V compliance delivered a current of 1.0 mA between the electrodes. The current was plateu-shaped with duration of 2 s and the recording of movement was applied during the first second.

The subject stood on the stable platform with eyes closed. GVS with a current of 1.0 mA was applied every five seconds. The subject was exposed to 20 currents with the polarity in a randomised order. The purpose of this test was to investigate if the sway response due to activation of vestibular afferents was affected by a period of motion conditioning.

Setup 2: Perception of rotation and threshold

A chair with armrest was placed upon a circular platform that was 1 meter in diameter and every tenth degree was a written number, from 0° to 350°, with 0° right in front of the chair and 180° just behind. The chair was placed so that the head of the person sitting on it was in the center of rotation. The subject held the head tilted forward during the whole setup, so that the position of the head was similar during both the galvanic stimulation and the real movement. The subject was blindfolded and wore ear defenders and the lights in the room were turned off except for a weak dimmed light. The motion of the platform was under computer control through custom LabView software.

Three tests were made.

1. Threshold for motion detection

The platform was rotating only a few degrees, between 1° and 15°, and the subject was instructed to tell the direction of any movement he or she detected. No response within 3 s or wrong direction was scored as non-detected. This test estimated the subject's threshold to perceive passive yaw motion. The threshold was determined by fitting a cumulative Gaussian psychometric pseudo function, which in practice means that the threshold was defined as 7 correct answers out of 10. When movements were detected correctly the next test rotation was

reduced and *vice versa*. In these stimuli, angular displacement (θ) velocity (ω) and acceleration (α) all co-vary such that: $\omega_{peak} = \theta/2.5$ deg.s^{-1}, and $\alpha_{peak} = \theta/4$ deg.s^{-2}.

2. Perception of virtual rotation

GVS was used to create an illusionary movement. The electrodes were applied to the mastoid processes as in Setup 1. A controlled current source with ± 70 V compliance delivered a current of either 0.5 or 1.0 mA between the electrodes. The current was applied during 10 seconds, together with a small stochastic motion (2-6 Hz, zero mean, $\omega < 1$ deg.s^{-1}) of the platform, in six trials. Subject, still sitting on the chair with eyes and ears covered, bent forward to make the head parallel with the floor. In this position the net effect of GVS is an illusionary movement of yaw rotation to the right or left, depending on the current direction, with an axis in the vertical plane (5).This means that the subject will feel as if the platform is moving. We asked the subject to tell direction and point at where he or she started from. Since the platform was not rotating during this test, the number of degrees from zero represents the illusionary movement. We hypothesized that perceived movement would be down regulated after a time of passive motion compared with before, i.e. subjects would report smaller illusionary movements after motion conditioning.

3. Perception of real rotation

Subject sat on the motorized platform, blindfolded and with ear defenders. Rotations of θ = 30°, 60°, 90°, 120° and 180° with a sin-square velocity profile were delivered, with ω_{peak} and α_{peak} co-varying as above. Rotations were both clockwise and anticlockwise, in randomized order, and superimposed on a small background stochastic motion (2-6 Hz, zero mean, $\omega < 0.1$ deg.s^{-1}). After each rotation, subjects reported its direction and displacement by pointing to the estimated start position, which the experimenter measured (5° resolution) with a protractor scale on the platform perimeter. There were eleven trials and before each one the subject was asked “ready?” from behind so that the subject would be prepared for each trial. The room was silenced and instructions were always given from directly behind the subject.

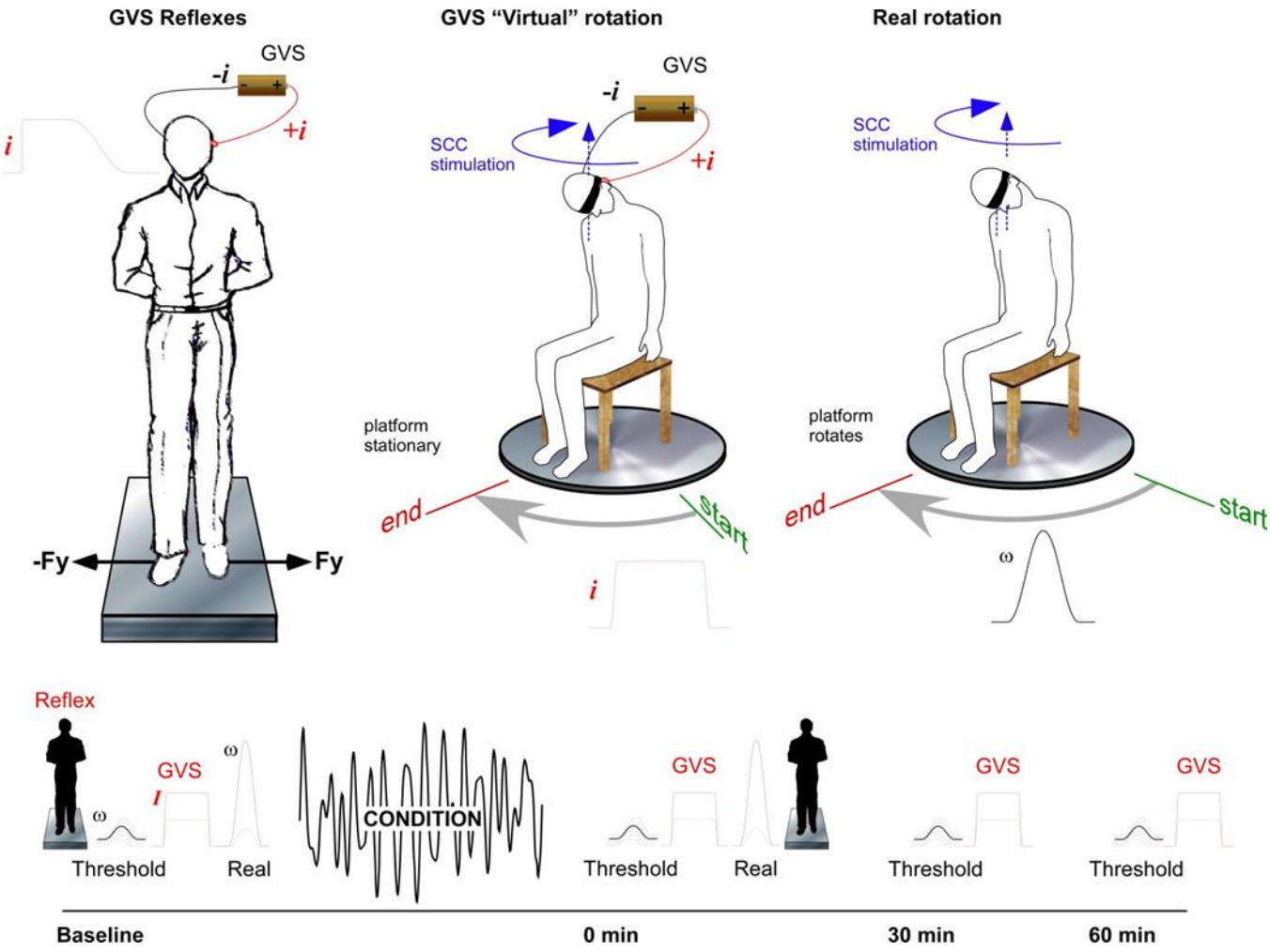

Figure 1. Method. *Setup 1: GVS reflexes*. Blindfolded subject stood on a forceplate and received electrical stimulation of the vestibular system (i.e. Galvanic Vestibular Stimulation) with a current of 1.0 mA. The current was delivered 20 times and the sway response was recorded. *Setup 2: Threshold for motion detection, Perception of virtual rotation* and *Perception of real rotation.* Subject was blindfolded and comfortably seated in a chair with the head tilted forward. The platform rotated only a few degrees and subject reported any motion detected by telling the direction. Perception of rotation was measured with both GVS to create an illusionary movement and when the platform rotated for real. The timeline displays the order in which the tests were performed. After each test was done, the subject was exposed to 10 minutes of passive movement, i.e. conditioning. Subsequently, the threshold for motion detection and perception of virtual rotation were tested three times more while GVS reflexes and perception of real rotation was performed only once after conditioning.

Measurements and Analysis

To measure the vestibular reflex responses, lateral shear forces were recorded from the forceplate at 1 kHz. Anode-left and cathode-right trials were normalised to the anodal direction and pooled for within-subject averaging. From these, the peak shear force of the short-latency response (at ~120 ms) and the medium-latency response (300-350 ms) were identified for each subject. Pre- and post-conditiong responses were compared by paired t-test.

Detection thresholds were determined by fitting a cumulative Gaussian psychometric function to individual responses (0 = wrong, 1 = correct) and identifying the rotation amplitude estimated to produce 50% correct responses (P_{50}, with its SE). Repeated-measures ANOVA with Dunnett's post-hoc test was used to identify significant effects of motion conditioning on *threshold for motion detection* (4 times), on *perceptions of virtual (GVS) rotation* (4 times, with stimulus intensity as a factor) and on *perceptions of real rotation* (4 times, with rotation angle as a factor). Significance was set at $P\alpha = 0.05$.

Results

Setup 1: GVS reflexes

Reflexive force responses evoked by electrical stimulation of vestibular afferents were recorded before and after motion conditioning. Both showed typical biphasic shear reaction force responses (Fig. 2). The short-latency response (~120 ms) was unaffected by motion conditioning (t_{18} = 0.44, P = 0.66) whereas the medium latency response (300-350 ms) was halved in amplitude (-6.64 to -3.18; t_{18} = 2.86, P = 0.011).

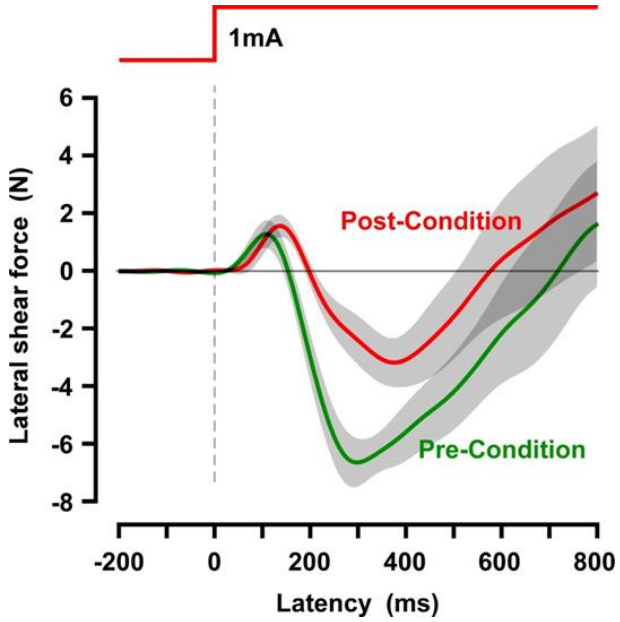

Figure 2. GVS reflexes. The curves represent the mean value (N = 10) of sway response, when exposed to a current of 1 mA, before versus after conditioning.

Setup 2: Perception of rotation and threshold

1. Threshold for motion detection

Subjects could detect the direction of whole-body rotation of a few degrees (threshold P_{50} = 3.9º, SD 1.5º) when delivered as a sine-square function over 5 s (Fig. 3). For this threshold movement, peak angular velocity was 1.6 deg.s^{-1}, and peak angular acceleration was 1.0 deg.s^{-2}. As thresholds had to be established rapidly with a limited number presentations,

the confidence intervals for individual estimates were relatively wide compared with customary psychophysical estimates (mean 95% CI = ± 0.22%). There was a significant main effect of conditioning (pre, post) on threshold (P = < 0.001). Immediately after motion conditioning, the detection thresholds more than doubled (subject mean 248% ± SD 31%). At 30 minutes post conditioning, thresholds were still elevated significantly (mean 151% ± SD 19%) but at 60 minutes the increase was no longer significant (mean 141% ± SD 23%).

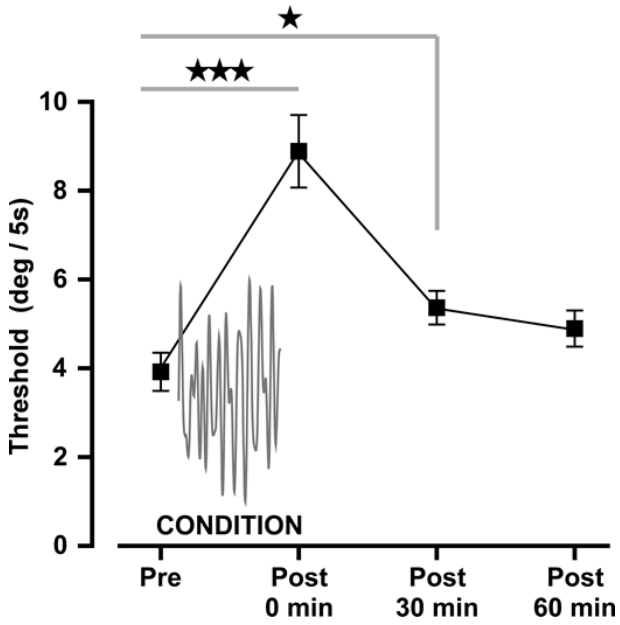

Figure 3. Threshold. Mean value (N = 10) of the threshold before conditioning (3.9°) as well as 0 minutes (8.9°), 30 minutes (5.3°) and 60 minutes (4.9°) after conditioning. ★P = 0.05 ★★★ P = 0.001 by Dunnett's test.

2. Perception of virtual rotation

All subjects reported strong sensations of illusory motion when the galvanic stimulus was applied in the absence of real rotation (Fig. 4). For a 1 mA stimulus delivered for 10 s, the mean reported rotation was 113º (range 53º -205º). Reported displacements were on average 54% greater with the 1.0 mA stimulus current ($F_{1,79}$ = 22.5, P = 0.001) compared to the current of 0.5 mA. Immediately after motion conditioning, reported rotations to the same stimuli were reduced by 44% overall and at 1 hour after conditioning, the reported rotations were reduced by 24% compared to pre-conditioning levels (P < 0.01 and P < 0.05 respectively by repeated-measures ANOVA and Dunnett's test).

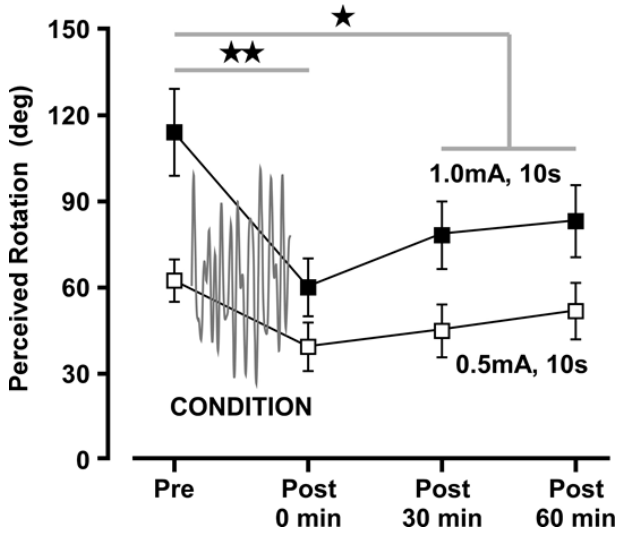

Figure 4. Perception of virtual rotation. Group mean (N = 10) perceptions of rotation after 10 s exposure to GVS (0.5 and 1.0 mA). Motion conditioning resulted in an immediate reduction in perceived rotation. ★ $P = 0.05$ ★★ $P = 0.01$ by Dunnett's post-hoc test.

3. Perception of real rotation

In this test we did not use GVS and perception of rotation was reported when the platform was moving for real. Subjects reported their perceived rotation by pointing to their start position for each rotation. In Figure 5, clockwise and anticlockwise results are pooled as there was no difference in report errors ($F_{1,189} = 0.15$, $P = 0.70$). For each movement, perceived rotation error was calculated as a proportion of the actual rotation. Before conditioning subjects overestimated the real rotation by a mean of 41.1% (33.3-48.8) but after motion conditioning this was reduced to a 21.5% (13.0-30.0) overestimation ($F_{1,189} = 6.4$, $P = 0.033$), which represents a 16.1% mean reduction in the perception of the imposed movement.

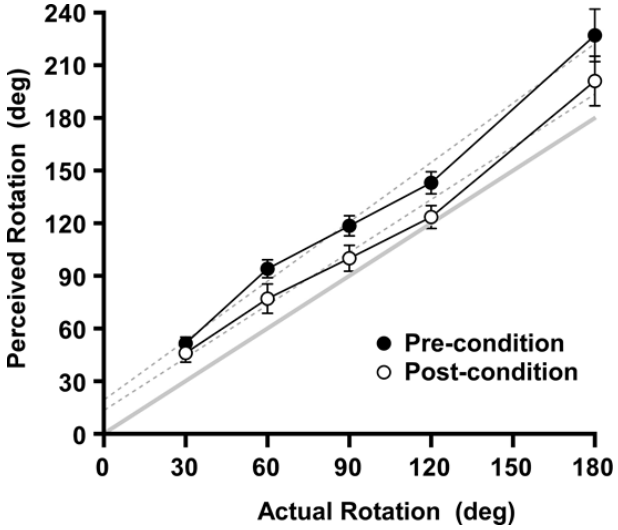

Figure 5. Perception of real rotation. Group mean (N = 10) ± SEM perceptions of rotation after different whole-body rotations, before and after motion conditioning. Broken lines are regressions through the raw data. The solid is the equality line. Motion conditioning reduced perceived rotation although it remained greater than actual motion.

Discussion

Generally, it is likely that it is physiologically useful to adjust perception from sensory systems depending on the situation. For example, recent findings suggest that long-term training involving vestibular adaptation allow dancers to perform pirouettes with only slight dizziness and can explain dancers' vertigo resistance (23). To be able to operate in a specific environment you may want to ignore some information while other information requires more attention. Usually, neural processes such as habituation or adaptation enable perception of repeated or continuous stimulus to decline. Habituation and adaptation occur at different levels down the neural pathway – from peripheral habituation with receptor desensitisation to central mechanisms that lead to disregard of an irrelevant stimulus.

With galvanic vestibular stimulation it is possible to investigate response to activation of the vestibular system without influences from other sensory sources (5). Perceptual adaptation has previously been explored using both GVS and kinetic stimuli (24). With kinetic stimuli, signal transformation occurs both at the canal-cupula and centrally, whereas GVS input seems to act at the hair cell and bypass the canal-cupula operator (25). It was shown that constant GVS was interpreted as angular acceleration about a specific head-referenced axis (24). Previous findings also indicate that changes in the brainstem and afferent system are responsible for a long-term adaptation (24). It has previously been shown that neuronal resting discharge and motion sensitivity can be influenced, either excitatory or inhibitory, by vestibular efferent neurons that synapse with hair cells and afferent neurons (26).

The purpose of this study was to investigate whether vestibular sensitivity can be modified by passive movement of the whole body. We hypothesized that perception of self-motion is down regulated after a period of motion conditioning. The ability to adjust sensory information would facilitate operation in an environment with a lot of redundant signals.

The results of this study are unequivocal and suggest that vestibular sensitivity is modulated by passive whole-body motion. Most evident was how perception of virtual rotation decreased after conditioning. The threshold for motion detection and the perception of real rotation were also affected indicating down regulation of vestibular sensitivity.

It was also hypothesized that postural vestibular reflexes would not be affected by motion conditioning. However, this hypothesis was falsified. A standing subject was exposed to GVS and the sway response was recorded. Results reveal a decrease in sway response after the 10 minutes of passive movement compared with before. However, the first 100 ms of the sway response was unaffected by motion conditioning (Fig. 2). The sway response recorded can be divided into two, a short response after only 50 ms, not affected by conditioning, and a larger response towards the anode after 100-150 ms. Given the time frame, both responses are automatic reflexes and could not be voluntary (6). It is possible that the two sway responses represent the short-latency and the middle-latency reflex response, previously studied with EMG recordings (6). The sway responses recorded in this study correspond with the latency of these reflexes.

Overall, the results indicate that vestibular sensitivity can be modulated. The following question is where in the nervous system this modulation takes place and how? The fact that rapid reflexes are affected suggests that habituation occurs at receptor level or in the vestibular nucleus rather than on a higher level. Since the first sway response was not affected by conditioning while the second response was, the vestibular nucleus is more likely to be the level of modulation. Galvanic stimuli bypass the first level of possible signal modulation since the inputs act further down the neural pathway and do not influence the canal-cupula mechanism (25). Perception of virtual rotation was largely decreased after conditioning which means that modulation must occur proximal from the canal-cupula in addition to possible peripheral habituation. This supports the theory that signal transformation takes place in the vestibular nucleus. It can also be considered that additional adaptation occurs on a higher level and affects the vestibular contribution to interpretation of self-motion. The perception of self-motion would, in that case, rely more on other sensory information in comparison with signals from the vestibular system. Since GVS evokes a pure vestibular signal without influences from other sensory sources, the habituation shown in the results is, most likely, a consequence of vestibular afference (5). The modulation does not necessarily occur down the vestibular neuronal pathway, though the latency of the second sway response, affected by conditioning, is consistent with modulation at brainstem level (24). The results of this study could be compatible with previous observations made by R. Fitzpatrick et al (24) who suggest that changes in the brainstem and afferent system are responsible for a long-term adaptation. In this study, however, it is more a question of habituation rather than adaptation since the conditioning was a series of unpredictable movement and not a constant rotation.

Methodological Considerations

Both perception of real and virtual rotation were examined. A large difference between these two tests is that other sensory information, in addition to the vestibular, were available when exposed to real rotation. Centrifugal forces could, for example, contribute to somatosensory cues. Moreover, it is conceivable that sound from the engine gave additional clues to perception of the rotational movement even if the subject was wearing ear defenders. During the test of perception of virtual rotation using GVS, the platform was stationary and either centrifugal forces or sound from the engine were present. Awareness of this difference is important when analyzing the results.

Another reflection that emerged during data collection regards how subjects reported perceived rotation in Setup 2. One subject said he rotated 180°, but as we noted the number of degrees that the subject pointed to, he was asked to point. When he did so, he pointed at 130° instead of 180° which would indicate an underestimation of the movement. The difference between the told number and the number to which he pointed could be explained by either negligence or difficulty to proprioceptively direct the arm to the estimated start position. In this situation, however, it is more likely that the difference is because of negligence, i.e. if the subject thought he already had made the report of the movement, he might not be as exact when asked to point. Proprioception difficulty is less likely since error of active reproduction of the joint position has been shown to be only a few degrees for the shoulder (27). It is difficult to estimate whether this is a general methodological issue since a similar situation never occurred for another subject. We assume that this was a onetime event that does not affect the results.

A possible approach for Future Research

Vestibular dysfunction is common in the general population and more prevalent in older adults among whom it predisposes to falls (28). A condition were the pathophysiology is unknown is termed Mal de Debarquement (MdD). Patients describe perception of rocking, bobbing and/or swaying and usually the symptoms occur when going back to stable conditions after being passively moved – for example when disembarking from a ship (29-31). It is quite common that healthy individuals experience this phenomenon, but patients describe persistent sensations of imbalance months to years after being exposed to a motion

environment (29-31). Still, little is known about what leads to this persistence, but a part of the explanation may be inability to adjust vestibular sensitivity. In this study, of neurologically healthy individuals, it has been shown that vestibular sensitivity can be modified depending on the situation. It would, therefore, be interesting to investigate if the vestibular sensitivity in patients with MdD is modified in a corresponding way when exposed to motion conditioning.

Previous observations of patients with Mal de Debarquement indicate that these patients are more sensitive to exposure of rocking compared to yaw rotation (personal communication, Linda Forsberg). When seated in a swing with a rotational axis in the horizontal plane, at the level of the head, and being pulled sideways, patients report larger perception of movement compared to controls (personal communication, Linda Forsberg). This applies to both real movement and illusionary movement created by GVS. An interesting approach for future research would, therefore, be a case-control study to investigate how patients with MdD and controls perceive rocking movement before and after motion conditioning. Unlike this study, where seated subjects were exposed to rotational movement with a vertical axis through their body, a setup with rocking movement and an axis in the horizontal plane would involve gravitational forces. Further investigation of the gravitational component and the ability to adjust vestibular sensitivity in a rocking environment might contribute to increased knowledge of the syndrome and pathophysiology of Mal de Debarquement.

Another condition which would be interesting to study further on the basis of these findings is phobic vertigo. The cause of the symptoms is not established, and patients tend to report greater experience of dizziness and unsteadiness than what can objectively be seen in tests (32). A possible approach for future research of phobic vertigo might be investigation of how patients perceive vestibular signals, evoked by either real movement or electrical stimulation, in relation to previous or ongoing passive motion.

Conclusions

The results of this study lead to the conclusion that vestibular sensitivity is modulated by passive whole-body motion. Altered vestibular sensitivity was seen up to one hour after passive motion. Vestibular perception was shown to be down regulated after a time of conditioning consisting of passive, stochastic, rotating movement while blindfolded. Postural vestibular reflexes were also affected by the same conditioning. This means that our first hypothesis was confirmed while the second hypothesis was falsified. A possible explanation to this could be that the modulation and transformation of vestibular signals occur further downstream than first thought. The results of this study rather suggest that a system of vestibular sensory autoregulation exists and that this most likely involves afferent and brainstem mechanisms. We propose that failure of these regulatory mechanisms could lead to disorders of movement perception and reflexive balance control.

Populärvetenskaplig sammanfattning

Ständigt hanterar vi en mängd information utan att vi är direkt medvetna om det. I innerörat finns balansorganet som sänder signaler till hjärnan om hur vi påverkas av olika rörelser. Tillsammans med information från muskler och leder och sinnen som syn och känsel, skapar vi en bild av hur vår kropp förhåller sig till omvärlden.

I den här studien frågade vi oss hur känsligt balansorganet är för att uppfatta rörelse. Vi undersökte också huruvida vår förmåga att uppfatta rörelse, med information från endast balansorganet, är annorlunda efter en period av passiv rörelse jämfört med innan. Vår hypotes var att vi blir sämre på att uppfatta rörelser, efter en tid av passiv rörelse, till följd av att vi omedvetet sorterar bort information från balansorganet. Vi antog att den här sorteringen skulle ske i hjärnan och att de snabba reflexer som balansorganet ger upphov till inte skulle påverkas av passiv rörelse.

För att aktivera balansorganet användes antingen en verklig rörelse eller elektrisk ström. En elektrod placerades bakom vardera örat och en liten ström, 1.0 mA, skickades emellan. Strömmen aktiverar balansnerven på ena sidan, medan den andra sidan inaktiveras, och det ger upphov till en känsla av att man rör sig mot den sida som aktiveras. I stående leder känslan av rörelse till ett balanssvar i form av en rörelse åt motsatt håll. Det här balanssvaret kan man både se och mäta. Om försökspersonen istället sitter på en stol när strömmen aktiverar balansnerven kan man inte se eller mäta något balanssvar. Istället efterfrågades då personens upplevelse av rörelse. På så sätt har vi, i den här studien, kunnat studera personens uppfattning av verklig rörelse samt upplevelse av rörelse då balansnerven aktiverats med en ström. Samma försök gjordes före och efter 10 minuter av passiv rörelse för att kunna jämföra resultaten och se om, och i så fall hur, uppfattningen av rörelse var påverkad efter perioden av passiv rörelse.

Resultaten av den här studien visar tydligt att balansorganets känslighet är nedreglerad och att det därmed är svårare att uppfatta rörelser efter passiv rörelse. Tröskelvärdet för att detektera rotationsrörelse fördubblades efter passiv rörelse jämfört med innan. Dessutom visar försöken att vår uppfattning av rörelse blir betydligt mindre. Resultatet är också entydigt för reflexer som balansorganet ger upphov till. Vi antog att reflexerna skulle vara bevarade, men det visade sig att reflexsvaret blir mindre, liksom vår förmåga att uppfatta rörelse.

Det är vanligt att hjärnan hanterar informationsflöde genom att ignorera vissa signaler så att andra, som är mer användbara i den givna situationen, kan få mer utrymme och uppmärksamhet. Den här studien visar att balansorganets känslighet är minskad efter en period av passiv rörelse. Det är inte bara vår förmåga att uppfatta rörelse som försämras utan även balansreflexer, som vi kan se och mäta som balanssvar, blir mindre. Innan studien trodde vi inte att reflexerna skulle påverkas och en förklaring till att så faktiskt är fallet skulle kunna vara att nervimpulser från balansorganet påverkas redan innan signalerna når hjärnan och inte i hjärnan som vi tidigare förutspått.

Att det nu är visat att information från balansorganet regleras beroende av situation innebär vidare möjligheter att förstå var och hur balanssjukdom uppstår. En del patienter beskriver en kontinuerlig upplevelse av att underlaget gungar och att det känns som att de ska falla. Det har tidigare föreslagits att symtomen beror på en oförmåga att reglera signaler från balansorganet beroende av situation. Eftersom resultaten från den här studien tyder på att friska individer har denna förmåga är det en fullt rimlig förklaring till uppkomst av sjukdomen. En intressant aspekt för framtida forskning är hur dessa patienter hanterar och reagerar på samma typ av passiv rörelse som studerats i den här studien. På så sätt kan teorin om sjukdomens uppkomst förkastas alternativt få ytterligare stöd, vilket är ett exempel på hur resultaten från den här studien kan komma att användas.

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