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TECHNICAL NOTE

Differences in Otolith and Abdominal Viscera Graviceptor Dynamics: Implications for Motion Sickness and Perceived Body Position

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Human graviceptors, located in the trunk by Mittelstaedt, probably transduce acceleration by abdominal viscera motion. As demonstrated previously in biodynamic vibration and impact tolerance research, the thoraco-abdominal viscera exhibit a resonance at 4 to 6 Hz. Behavioral observations and mechanical models of otolith graviceptor response indicate a phase shift, increasing with frequency between 0.01 and 0.5 Hz. Consequently, the potential exists for intermodality sensory conflict between vestibular and visceral graviceptor signals, at least at the mechanical receptor level. The frequency range of this potential conflict corresponds with the primary frequency range for motion sickness incidence in transportation, in subjects rotated about Earth-horizontal axes (barbecue spit stimulation), and in periodic parabolic flight microgravity research, and also for erroneous perception of vertical oscillations in helicopters. We discuss the implications of this hypothesis for previous self-motion perception research and suggestions for various future studies.

IN A SERIES of recent publications, Mittelstaedt (21,22) showed through several convincing experiments and detailed reasoning that graviceptors for static longitudinal (G_z) loading of humans are located in the trunk rather than in limbs and/or the skin. These conclusions are based on experiments on a "sled-centrifuge" with the axis of rotation adjusted by the subjects, so that the otolithic and visceral inputs counteract. Through tests with labyrinthine defective (LD) subjects, he determined that the centroid mass of the trunk graviceptor is located approximately at the height of the last ribs and concluded that the effects of the trunk input "on the z-axis component of the postural control system is thus, on average, equal to or even larger than that of the otoliths." His further experiments with paraplegic subjects attempted to localize two centers for the extravestibular graviceptors: one associated with motion of the cardiovascular system and one with motion effects on the kidneys. Mittelstaedts's observations derive primarily from conditions where the acceleration stimulus was static. The purpose of this note is to examine implications of these observations for motion sickness and self-motion perception during transient and oscillating acceleration.

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Mechanics of Visceral and Otolith Graviceptors

Biodynamic research on the effects of vibration and shock on people over the last three decades has established that in response to periodic vibration in the z-direction, the abdominal viscera vibrate as a whole, coherent mass or liquid-filled sac. It moves in and out of the rib cage, alternately compressing either the relatively soft air volume in the lungs, or part of the mass against the pelvic bone; on this caudal swing, the other part of the abdominal volume extends in the x- and even y- directions by stretching the abdominal skin (4,5,24). This movement of the abdominal viscera has a clear resonance maximum between 4 and 6 Hz, depending on body position, size, weight, muscle tension, etc. Frequently called the main body resonance, it has been implicated as one of the main factors during environmental vibration and impact conditions leading to discomfort, and, under extreme conditions, even to injury.

This resonance can also be excited to a lesser, and more damped degree, by x-axis and even y-axis forces. (For interpretation of animal experiments it is important to keep in mind that this resonance frequency increases approximately inversely with the body dimension [24]). At high levels of stimulation, this thoraco-abdominal resonance is responsible for respiratory and cardiovascular effects as well as discomfort (16). Excessive stimulation at the resonance frequency results in chest and abdominal pain. Cineradiographic studies in humans and animals confirmed that all organs vibrate in unison up to and through this main abdominal resonance range (5,25).

It appears likely that this mobility of the abdominal mass with a resonance between 4 and 6 Hz is the mechanical "receptor" for Mittelstaedt's extravestibular gravity receptor(s). Without going into details of the merits of trying to separate afferent signals coming from this abdominal area into two distinct systems (cardiovascular and the kidneys), it appears that such stimulation could originate from several broadly distributed areas all undergoing, with the same phase, the same stretching and compressive motion. Areas of maximum stress probably change with frequency and, due to nonlinearity, with amplitude. (In experiments like the one reported by Mittelstaedt, flexing of hips and knees by 90° can change the abdominal dynamics to some extent by changing abdominal muscle tension. Stature, body dimensions, weight, and exact body positioning need to be considered and reported in future studies if more detail on the primary origin of visceral signals is sought.)

Considering the dynamics of the vestibular-otolithic versus the abdominal graviceptor system, (Fig. 1), it appears that the resonance frequency of the visceral system would be higher by almost a factor of 100. Although otolith models exhibit somewhat different phase relations between exciting accelerations and, on the one hand, neural response rates (6) and on the other, perceptual reports (26) or physiologic responses (11), all models indicate a phase shift at frequencies above 0.01 Hz. For the mechanical model (7), the phase shift is approximately 90° in the frequency range of the long time constant (10 s). (A second phase shift of 90° occurs above 500 Hz due to a less well-established short time constant.) The otolith model derived from the behavioral and dynamic counterrolling data exhibits an approximately 90° shift at 10 times higher frequencies (26).

Based on the measurements by Clark, Lange and Coermann (4) and others (5), the abdominal viscera are modeled as a 1° of freedom system with a resonance around 5 Hz. The mechanical-neural transfer function for visceral graviceptors is unknown. However, the important point for the present considerations is that the transfer functions for the otolith system, with or without including neural transmission modification, exhibit an increasing phase shift relative to the abdominal viscera. Even if the functions assumed here are not exactly accurate, it is obvious that at frequencies above 0.01 Hz, otolithic and visceral responses undergo a relative phase shift, as is clearly demonstrated by the behavioral data (see Fig. 1). The phase shift is most likely combined with a decrease in the response amplitude of the otolith system. There is clearly a frequency range between 0.03 and 0.5 Hz where there could be conflict between the otolith and visceral graviception signals.

Several hypotheses about the origins of motion sickness, particularly the sensory conflict/sensory rearrangement theory, have considered inter- as well as intra-modality conflicts. Among the latter, conflicts between otolithic and canal vestibular inputs have been discussed. Although a possible phase error between the otolith and somatic pressure graviceptor signals is implied in Benson's discussion, (1), potential conflict between vestibular and visceral graviceptor signals during dynamic stimulation, due to phase difference between them, has not been pointed out before. Since vertical motion is the principal provocative stimulus for motion sickness, the predominant mechanical response of the visceral system in the z-direction would also support this potential conflict factor. In their natural environment, humans are rarely exposed to vertical oscillations in the frequency range that provokes motion sickness. Habituation to the conflicting inputs from the two systems would, therefore, not be expected. Humans are exposed to frequencies above 0.5 Hz continuously during walking and running; therefore, habituation in this frequency range would be mandatory for survival.

Implications for Previous Motion Sickness Research

Vertical motion is the principal stimulus for vibration induced motion sickness. Lawther and Griffin (12) and McCauley et al. (18) found the highest incidence of vomiting during vertical oscillation at 0.03 to 0.5 Hz (Fig. 1). The same frequency range is used in the International Standards Organization (ISO) (10) and British Standards Institution (BSI) standards (3) as the frequency range primarily responsible for motion sickness (Fig. 1—0.1 to 0.3 Hz and 0.125 to 0.25 Hz, respectively). Below and above this frequency range the probability of motion sickness decreases rapidly, although the decline in motion sickness for frequencies below 0.1 Hz is based on very limited data (12).

The potential conflict between otolith and visceral input over a limited frequency range might also be a key to understanding and explaining motion sickness studied in subjects rotated about Earth-horizontal axes (2,15). When the axis of rotation coincides with the subject's z-axis (original "barbecue spit" stimulation) or x-axis, a high incidence of motion sickness is reported; y-axis stimulation is slightly less provocative. In all cases, stimulation varies sinusoidally between +1 and −1G, with the force vectors at both the head and viscera rotating in the x-y plane for rotation about the z-axis, in the y-z plane for rotation about the x-axis, and in the x-z plane for rotation about the y-axis. In previous vibration research noted above, similar abdominal viscera resonances have been noted for linear stimulation along all three axes, although somewhat larger visceral displacement amplitudes have been observed for x- and z-axis stimulation. Consequently, combined stimulation along two or even three axes should not change the resonance range sufficiently to affect the hypothesis suggested here.

Although it has been reported that for the Earth-horizontal axis rotation, the nauseogenic effect increases with the rotational speed, no studies have been reported which would allow determination of a range of maximum motion sickness sensitivity including decline at higher frequencies. Most of the studies that have been reported were done at 2.5 to 45 rpm (i.e., 0.04 to 0.75 Hz), frequencies at the boundary of the motion sickness range observed for vertical vibrations (Fig. 1). However, a study in which four subjects experienced 10° off-vertical rotation, which exposed them to a small component of the rotating G vector discussed for Earth-horizontal rotation, reported maximum motion sickness susceptibility between 10 and 25 rpm (0.17 and 0.42 Hz) and reduced susceptibility below and above this range (20).

Implications for Previous Self-Motion Perception Research

Subjects seated in an upright position are unable to track accurately sinusoidal vertical motion across frequencies of 0.1 to 0.5 Hz (17). Responses were obtained from six subjects during stimulation using a computer-controlled helicopter that produced accelerations exceeding 0.4 G (peak to peak). Two subjects exhibited response phase lags of 0°- 60°, two reported lags of 120° - 190°, and two were even more erratic. This inability contrasts with the quite accurate tracking of x-axis, Earth-horizontal oscillation reported by Young and Meiry (26). The difficulty in vertical motion tracking is surprising because directional information from the otolith receptors is available at the neural level (6) and self-motion detection thresholds (independent of direction) for horizontal and vertical motion are not greatly different (19). This suggests that the tracking difficulty reported by Malcolm and Melvill Jones may relate to the different dynamics of the visceral and otolith graviceptors and their interaction.

LD subjects report motion direction accurately during horizontal x-axis translation. The abilities of LD subjects might be accounted for by activities of extra-labyrinthine receptors, including the proposed visceral graviceptor.

Discordance between otolith and visceral graviceptor signals during "barbecue spit" rotation may also account for the illusory perceived self-motion reported during this stimulation. Guedry (9) reported that subjects exposed to constant velocity 0.167 Hz Earth-horizontal rotation around their z body axis experienced a "wobble" self-motion. The head and feet were perceived to move through orbital paths; however, when the head was moving upward the feet moved downward and vice versa. This was associated with a perceived wobble axis at the thoracic or lumbar levels. Given the phase difference in the response of the otolith and visceral graviceptors at the stimulus frequency (Fig. 1), perception of wobbling self-motion is a reasonable interpretation of the neural signals.

Differences in otolith and visceral graviceptor dynamics might help explain the phenomenon of inversion illusion in microgravity, where subjective perception might be influenced by the dynamics, i.e., frequency content, of the motion which brought the astronaut to the position evaluated. The sudden reversal of up and down, perceived as a consequence of transition from one state to another, was not reported by LD subjects during zero G parabolic flights (8). If the motion spectrum has components in the potential conflict range of Fig. 1, the reported experiences would be plausible.

Potential Limitations

The hypothesis presented in this note focuses on sensory conflict as the primary mechanism of motion sickness. Based on numerous observations, the sensory conflict approach currently appears plausible; however, other models that include interaction between and/or summation of otolith and visceral signals might be proposed.

Our hypothesis derives from Mittelstaedt's suggestion that the principal extra-vestibular graviceptor is located in the trunk. Mittelstaedt's view is not universally espoused; several investigators (see ref. 1) have proposed that mismatch between otolith and skin pressure receptor signals may be a major contributor to motion sickness. (Needless to say, the visceral response discussed here results in skin stretching and compression with the same resonance and phase response as the viscera).

The foregoing hypothesis derives from observations and models of the otolith mechanical - neural response transfer functions and the visceral mechanical response presented in Fig. 1. There have been some discrepancies between observations derived from different procedures and performed by different laboratories; the otolith transfer function remains a topic of some dispute. Also, the mechanical - neural response transfer function must be determined for the visceral graviceptor(s) if the hypothesis presented here is to be supported.

Conclusions and Suggestions for Future Studies

The questions raised by the above comments and their potential implications for the interpretation of previous research cannot be answered without further analysis. The above discussion is only a first step toward evaluating some of the phase responses of the two graviceptor systems. It might assist in the planning of future studies to clarify the interaction of these systems and, above all, to make the studies themselves more revealing. Possible studies to evaluate the hypothesis presented in this note include:

1) The phase shift between actual and perceived vertical motion without visual or auditory cues all through the frequency range of Fig. 1 should be measured.

2) The objective motion pattern of subjects in zero G parabolic flights, as well as in microgravity, should be analyzed with respect to its frequency spectrum. Some of the acceleration spectra in zero G parabolic flights (0.02 to 0.03 Hz—ref. 13,14) are close to the lower edge of the frequency range where otolith - visceral graviceptor conflict would be expected, which might affect motion sickness, as well as perceived self-orientation and self-motion (See Fig. 1). Increasing the pull-out and pull-up G loads in these maneuvers can change the higher harmonics in the G-load excitation (13), thereby

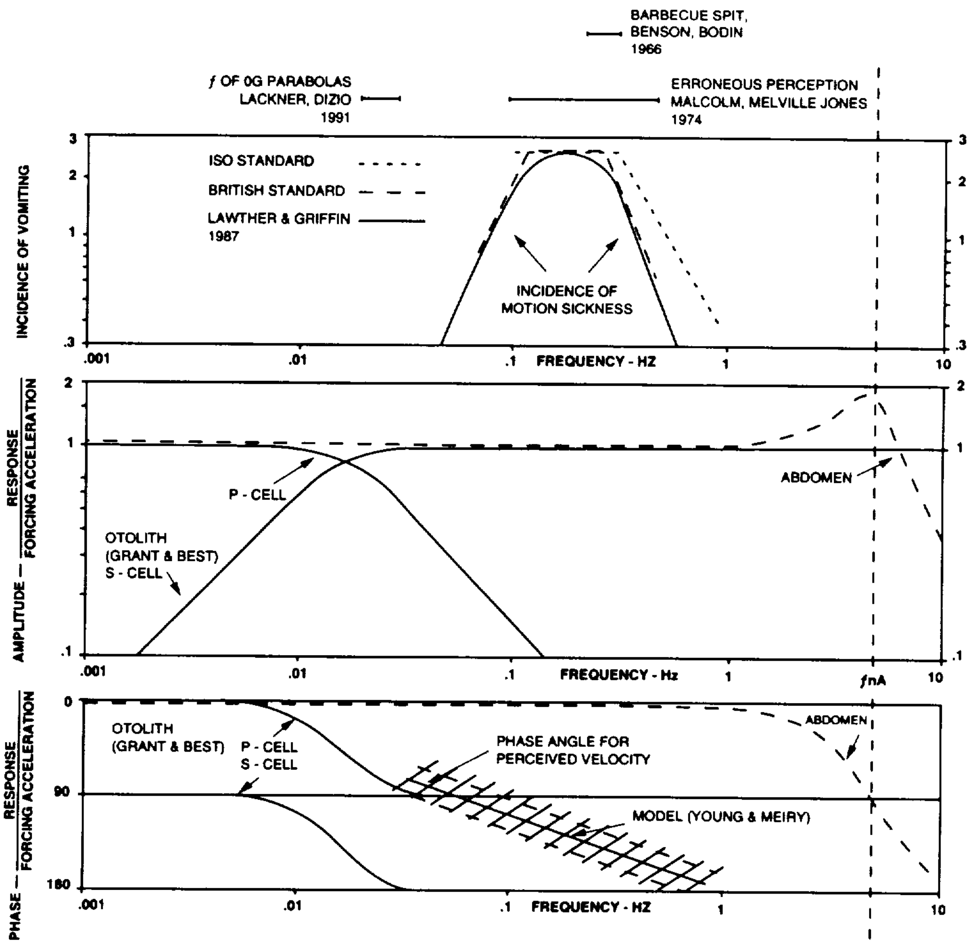

Fig. 1. The two lower panels present the amplitude and phase shift of the visceral and otolith response to constant acceleration input for the frequency range 0.001 to 10 Hz (4,7). For the otolith system, the responses of the peripheral (P) and striolar (S) cells are indicated. The phase shift between perceived velocity and actual velocity is also shown with the shaded area, indicating range of observations (26). The upper panel demonstrates the incidence and range of motion sickness [ISO (12, 10); BSI(3)]. Frequency ranges, in which motion sickness and/or erroneous perceptions were demonstrated (2,14,17), are also presented. See text for details.

shifting the effective frequency of excitation closer to the frequency range of highest incidence of motion sickness discussed above. Instead of distinguishing between motion sickness sensitivity in the "high force phase" versus the "free fall phase" (13), the complete dynamics of the receptor excitations (i.e., also the number of parabolas flown) might have to be considered in the future.

3) All of these experiments should be conducted with both normal, and LD subjects.

4) Subjective motion sensations (phase shift as a function of both ascending and descending frequency) should be observed in order to detect a potential hysteresis.

5) Motion sickness and subjective sensations should be determined during orbital flight across a range of frequencies, using the Microgravity Vestibular Investigations rotator (23) configured for "pitch" with the rotation axis through the subject's neck. In this configuration, the centripetal and tangential acceleration vectors which excite the otolith receptors are 180° out of phase with respect to those at the visceral receptors.

6) All mechanical accelerometers of the type assumed here for the viscera, as well as the otoliths, work as integrating accelerometers for short duration pulses; i.e., their output is proportional to the velocity change. For this to occur, the duration τ of a rectangular pulse, for example, has to be short compared to the systems' natural period ($\tau f < 0.3$). In threshold and latency experiments this would be approximately $\tau < 4.5$ s for the otoliths but $\tau < 0.057$ s for the viscera. Although threshold perception experiments with horizontal acceleration pulses point toward integration by the otolithic system in the range of 1 to 4 s, this would be expected to change for longer pulses. It might also change for vertical motion with the abdominal system being more sensitive. However, otolith integration would not be expected by LD subjects in which case the abdominal response would be predominant, unless the pulse duration were less than 50 ms. (In principle this type of constant velocity response has been observed in human impact tolerance experiments [24].)

The studies proposed, combined with a further extension of the modeling approaches, might answer the following questions: To what extent is there a conflict in the frequency range between 0.05 and 0.5 Hz between the signals from the vestibular and visceral graviceptor systems? Can such conflict help account for motion sickness, physiologic responses, and perceptual reports?

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