Biodynamic Hypothesis for the Frequency Tuning of Motion Sickness

John F. Golding; Michael A. Gresty

INTRODUCTION: Motion sickness is often provoked by oscillatory translational (linear) acceleration. For humans, motion frequencies around 0.2–0.3 Hz are the most provocative. A current explanation for this frequency band is that it spans a region of maximum ambiguity concerning the interpretation of vestibular signals. Below 0.2–0.3 Hz, linear accelerations are interpreted as 'tilt', whereas at higher frequencies accelerations are interpreted as 'translation', i.e., linear motion through space. This is termed the 'tilt-translation' hypothesis. However, the origin of this particular frequency range is unclear. We investigated whether the differential perceptions of oscillations at different frequencies derives from the biodynamics of active self-initiated whole body motion.

METHODS: Video-films were taken of subjects running slaloms of various combinations of lengths/amplitudes to provoke a range of temporal frequencies of slalom (reciprocal of time to run a cycle).

- **RESULTS:** The usual tactic for cornering at frequencies <0.25 Hz was whole-body tilt, whereas >0.4 Hz lateropulsion of the legs with torso erect was observed. Between these frequencies subjects showed variable tactics, mixing components of both tilt and lateropulsion.
- **CONCLUSIONS:** This uncertainty in selecting the appropriate tactic for movement control around 0.2–0.3 Hz is the possible origin of 'tilt-translation' ambiguity. It also follows that externally imposed motion around these frequencies would challenge both perception and motor control, with the consequence of motion sickness.

KEYWORDS: motion sickness, nausea, tilt-translation, frequency, locomotion, transport, vestibular.

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Susceptibility to motion sickness is tuned to the mechanical frequency of vehicle motion;⁴ for example, a cycle of motion lasting 5 s would impose an oscillation of 0.2 Hz on a sailor. The key nauseogenic motion component is thought to be a variation in the direction and magnitude of the gravito-inertial force vector (GIF), which is usually the addition of the force of gravity and the imposed acceleration due to vehicle motion.² For human subjects, maximum susceptibility is observed in a frequency range around 0.2 to 0.3 Hz. Susceptibility declines progressively at both increasing and decreasing frequencies away from this region.⁴ Motion sickness can also be provoked by motions of the visual field, as would be seen looking out from a moving vehicle or in a simulator, and this is also most readily provoked in a similar (0.2–0.4 Hz) frequency band.³

A change in linear acceleration of the body can be due to either tilt with respect to gravity or to translational acceleration of the body through space. Normally, visual information of the situation will resolve this ambiguity. However, if a blindfolded subject experiences linear, earth-horizontal motion, his perception of self-motion varies with frequency.^{10,11} For example, at oscillations below around 0.2 Hz, the preferential perception is of tilting from earth upright, whereas at higher frequencies the preferential perception is that the person is moving (translating) through space. This dilemma of interpretation is often referred to as the 'tilt-translation hypothesis' as to how the brain resolves such perceptual ambiguity. Tilt versus translation is also reflected in eye movement reflexes. With low frequency acceleration 'compensatory' torsional eye movements

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are evoked, as if the subject were tilting, whereas with high frequency acceleration eye movements are predominately lateral, appropriate for maintaining fixation on earth stationary targets while the body is moving ('translating') through space.¹⁰

It is a commonplace observation that the tactic for running around low temporal frequency slaloms (corners) is alignment of the body with the GIF, which is tilted into the turns. In contrast, on high-frequency slaloms, the body is displaced laterally to round the turns by thrusting sideways with the legs, which we term 'lateropulsion,' while the torso remains approximately upright. We propose the hypothesis that the biodynamics determining these self-initiated tactics are ultimately responsible for interpretations of tilt versus translation in response to imposed motion.

At the 82nd Annual Meeting of the Aerospace Medical Association in 2011,⁶ we presented a poster concerning the use of tilt versus translation tactics during whole-body self-motion, i.e., during locomotion. This is given in more detail below. The aim was to investigate the frequency ranges through which GIF alignment (tilt) and lateropulsion are preferred tactics for changing direction during human running, i.e., self-imposed translatory acceleration, and whether this relates to the frequency characteristics of motion sickness and 'tilt-translation.'

METHODS

Video-films were taken of subjects while they were timed running slaloms of various lengths and amplitudes on a level playing field with the intention of provoking a wide range of temporal frequencies of running the slalom. Markers on the field defined sinusoidal pathways for the runners to follow. The camera viewed the long axis of the sinusoidal slalom, giving an adequate view of the subjects cornering to the right or left (see Fig. 1). Since there was no pre-existing guidance to the size of slaloms which would give a wide range of temporal frequencies, sinusoidal paths were marked at a wide range of sizes in terms of length along the axis of the sinusoid \times peak amplitude, (long imes wide): 20 m imes 2 m; 16 m imes 1.4 m; 12 m imes 1.4 m; 8 m imes2 m; 8 m \times 1 m; 6 m \times 1.5 m; 6 m \times 1 m; 4 m \times 1 m; 4 m \times 0.4 m; 3 m \times 0.75 m; 1.8 m \times 0.65 m. This distribution of approximately sinusoidal slalom sizes yielded temporal frequencies of running the slaloms ranging from 0.15 Hz to 0.75 Hz, where Slalom Frequency = 1/(time to pass first and)last sinusoidal marker).

Four adult male subjects, height 1.7-1.9 m, weight 60-75 kg, all of normal BMI, gave their informed consent to the study, which was performed under the approval of the Ethics Committee of the Department of Medicine, Imperial College London. They were allocated randomly to the various slalom sizes, with each subject running five or six different sizes of slaloms and with two to four trials at each size of slalom, depending on the quality of the video recording. The entry trajectory, running firstly toward the right or left peak turn, was randomized. Subjects were encouraged to run as fast as comfortably possible. Cornering tactics were identified from video frames at the

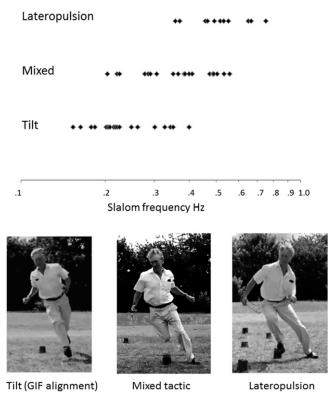


Fig. 1. The three types of body tactics (Tilt, Mixed, Lateropulsion) observed on cornering during slalom running are illustrated in the lower panel. The upper panel shows individual occurrences (diamonds) of these three types, which are plotted against the slalom frequency (X-axis, Hz) at which each was observed.

moments that runners rounded the peak lateral displacements of the sinusoidal course, i.e., when they were rounding the bends at the tightest points, which are the points of greatest lateral acceleration. The spatial orientations of the legs, torso, and head were observed.

RESULTS

Inspection of the videos yielded two distinct tactics used on cornering. These were 'Tilt,' alignment of both legs and torso tilting in to the corner, and 'Lateropulsion,' lateral thrusting of the legs with the torso maintained relatively upright or even tilted out of the bend, presumably as an inertial response to the strong lateral leg thrust. An intermediate 'Mixed' tactic was also evident in which legs and torso were misaligned, with legs aligned with the GIF and torso partially upright and head variably upright or tilted.

The results are summarized in Fig. 1. When running around corners of low spatio-temporal frequencies, the whole body tilted, en mass, with head-trunk-limbs in alignment with the tilt of the GIF vector induced by cornering, just like a motorcyclist will lean into a bend. This is the commonplace observation for low spatial frequency slaloms during skiing, cycling, and skating, as but a few examples. For high spatio-temporal frequencies of cornering, the head and trunk tended to remain earth upright while the legs push the body from side to side in a tactic of 'lateropulsion.' Lateropulsion is also displayed for very rapid slaloms, for example, in skiing, skating, and mountain biking. The tendency for the body to tilt during slaloms decreased with increasing frequency. By contrast, the proportion of lateroplusion increased with increasing frequency. A third 'mixed' pattern of coordination was seen at slalom in the middle frequency ranges. In this mixed tactic of cornering, head, legs, and torso were tilted separately by various amounts (Fig. 1, middle panel), giving the overall appearance of awkwardness.

For an initial quantitative analysis, the data were allocated into three equal numbers of observations, producing tertile frequency bins: < 0.25 Hz; 0.25-0.4 Hz; > 0.4 Hz, which were cross-tabulated with the three types of body tactics to satisfy the Chi-square rule for minimum 'expected' cell counts. The results were significant ($\chi^2 = 34.0$; df 4; P < 0.001), reflecting the different probabilities of occurrence of the three types of tactics across the three frequency bins. The data were then analyzed by ANOVA, where the independent factor was Tactic (3 levels: Tilt, Mixed, Lateropulsion) and the dependent variable was Frequency (observed frequency in Hz for each run). The effect for Tactic was highly significant (F = 31.4; df 2,47; P < 0.0001), with each of the three types of Tactic significantly different from the others by post hoc tests (Scheffe Tests, all P < 0.001). The source of this effect was the progressively higher (mean \pm SD) slalom frequencies, from Tilt (0.24 \pm 0.07 Hz) through Mixed (0.38 \pm 0.11 Hz) to Lateropulsion (0.53 \pm 0.12 Hz). This pattern of effects was robust and remained significant when subanalyzed for each individual (P < 0.01).

DISCUSSION

The key to understanding the relationship between cornering tactics and spatio-temporal frequency lies in fundamental mass-energy relationships for human body motion. Tilting with the whole body GIF-aligned is the most effective way of controlling and balancing the various body segments during rapid cornering at low frequencies. But the mass of the body is too great to be tilted at high turning frequencies; fortunately the legs are sufficiently powerful to effect rapid sideways translations, which we have termed 'lateropulsion.' Since the biomechanical characteristics of the human body are fundamental limitations, it follows that orienting reflexes and perception are adapted to complement the types of maneuvers the body executes and are tuned accordingly. This is why the frequency tuning of perception of imposed linear motion and vestibular ocular reflex dynamics^{10,11} are such that prolonged linear acceleration is interpreted as tilt, as the body would do in low frequency slalom, whereas rapidly changing acceleration is interpreted as translation, as in lateropulsive maneuvers. Thus the perception of an externally imposed acceleration, such as in a cornering vehicle, is driven by the brain's expectations of what would be normally happening in self-initiated motion.

Sensory signals provoked by cornering are ambiguous in that they could arise either from tilt with respect to gravitational upright or from reorientation of the GIF vector due to centripetal acceleration around a curved trajectory: the otoliths of the vestibular apparatus respond similarly to either. However, the demands on balance are different at high and low frequencies. Low-frequency cornering and actual tilt require a similar balance response of maintaining alignment with the GIF vector, whereas at high frequencies the trunk may be balanced just by lateropulsion using the legs. At the cross-over frequency, circa 0.2-0.3 Hz, there is a 'zone of uncertainty' where perception of motion in space may be uncertain and, as we have now shown, whole body maneuvers exhibit a mixed pattern of tilt and translation. This zone of uncertainty corresponds to the frequency band within which motion sickness susceptibility is at a maximum. The proposed hypothesis is that motion sickness susceptibility, in humans, is frequency tuned with a peak at circa 0.2-0.3 Hz because motion around this frequency presents a significant challenge to the coordination of whole-body movement: specifically, whether to tilt or translate. The resulting mixed pattern of coordination implies components of response to both tilt and lateral translation, which has an awkward appearance and must imply more complex motor processing than simple tilt or translation. From this viewpoint motion sickness is a consequence of an inability to make an optimized motor response, threatening incoordination. This view gives an explanatory and quantifiable framework for various postural instability hypotheses of the origin of motion sickness.7,15

Our biodynamic hypothesis predicts that animals with similar body mass to humans should have similarly tuned motion sickness susceptibility, whereas smaller animals should have their peak susceptibility tuned to higher frequencies. Although data are scant, this does seem to be true, since pigs¹⁴ with similar mass to humans are made sick during transportation by low-frequency oscillatory motion circa 0.2 Hz. By contrast, the small shrew *Suncus Murinus*⁸ and broiler chickens¹³ both have peak susceptibilities at much higher frequencies: 1-2 Hz. As with humans, animals round low-frequency bends with body tilted and change direction at high frequencies using leg movement without body tilt.

Reducing the issue of motion sickness provocation to limitations in fundamental mass energy relationships in moving the body subsumes the major theories of motion sickness, viz: the 'toxin theory,'16 that incoordination of movement could be interpreted as a sign of intoxication, thus provoking emesis; the 'aversion theory,⁷ in which movements threatening incoordination must be avoided, with nausea being the deterrent; and the 'conflict theory,'12 where nausea is provoked not only by conflicting sensory signals, but also in selecting appropriate tactics of motor behavior. Our hypothesis also explains why visual sensory input alone, for example rotation and tilt of the visual field, can induce motion sickness.⁵ The reason is that body movement is essentially predictive¹ and, as such, moving visual fields evoke an internal simulation, perhaps through an 'internal model;¹¹ of how body movement would be challenged by an equivalent, real, physically unstable environment.

Although couched in the framework of self-motion, this biodynamic hypothesis of the origin of motion sickness

transfers readily to the actual circumstances of imposed vehicular motions which typically provoke symptoms. Controlled laboratory observations have not been conducted given the limited capabilities of current motion simulators; however, from quotidian 'natural history' observations, it is evident that the tactics of tilting and lateropulsion are used differentially when moving about on moving platforms with different frequency characteristics. Balancing and walking on a conventional train at speed involves high mechanical frequencies (approx. > 1 Hz) to which the primary response is control of equilibrium by differential ankle-leg-hip movements and lateropulsion and usually does not produce sickness. In contrast, walking the deck of a ship in heavy seas can be problematic, since it is difficult to adopt an appropriate locomotor tactic, e.g., the UK-French cross-channel ferries are notoriously nauseogenic, having a frequency in the region 0.15-0.2 Hz.⁹ However, sea sickness can be ameliorated to some extent by lying supine and thus evading the locomotor challenges.

Our proposed biodynamic hypothesis about the provocation of motion sickness shifts emphasis from perceptual ambiguity and mismatch, currently dominating theory, to the problems of controlling appropriate self-motion within an unstable environment. The uncertainty in selecting the appropriate tactic for movement control around 0.2-0.3 Hz is the possible origin of 'tilt-translation' ambiguity. It also follows that externally imposed motion around these frequencies would challenge both perception and motor control, with the consequence of motion sickness.

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