MASSACHUSETTS INSTITUTE OF TECHNOLOGY

PROGRESS REPORT

RESEARCH ON HABITUATION TO NOVEL VISUAL-VESTIBULAR ENVIRONMENTS WITH PARTICULAR REFERENCE TO SPACE FLIGHT

NASA GRANT NSG 2032

March 1975 - February 1976

MAN-VEHICLE LABORATORY
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Introduction

The research supported by this grant is aimed at the development of a cohesive theory of the underlying physiological mechanisms associated with spatial orientation in unusual environments. The knowledge gained through this study will be applied to providing means of preventing and/or minimizing the "space motion sickness" which has been observed during prolonged space missions.

During the past year, the work has been focussed along three major lines of endeavor:

(a) Studies of the interaction of visual and vestibular cues in conflict in the human

(b) Studies of the plasticity of the vestibulo-ocular reflex in monkeys

(c) Study of end organ function in the ray with particular emphasis on the effect of ionic concentration.

Significant progress has been made in these areas and is presented in the remainder of this report.

Motion Perception Dependence on Visual and Vestibular Cues*

The objective of this research is to develop a functional model of how vestibular cues and moving peripheral visual fields act in concert to produce a perception of body attitude and a sensation of self-motion in humans. Modelling of vestibularly induced motion sensation has been the subject of considerable research effort for many years, and the functional approach of describing input-output relations has met with a fair degree of success in predicting human subjective response to various rotational and tilt stimuli, in the absence of other sensory cues. A concommitant effort directed toward understanding how visual cues influence motion sensation has a more recent history, and models describing subjective response induced solely by moving visual fields are of a more qualitative nature, with the emphasis on identifying the visual field qualities most important in inducing motion sensation. This identification process is a prerequisite for the functional modelling of subjective response dynamics due to one or a few specific quantified attributes of the moving visual field; some work is thus currently directed toward developing an input-output model of subjective response due solely to visual cues, using techniques similar to those used in vestibular modelling. The natural extension of both the vestibular and visual studies is an effort directed toward understanding how

Performed by Greg Zacharias, Ph.D. Candidate, NIH Trainee, and L.R. Young simultaneous cues interact and contribute to motion sensation, and initial research in this area has already begun to uncover subjective response patterns not apparent in the separate vestibular and visual studies conducted in the past. It is the object of the proposed research to extend these efforts with more quantitative measurements of subjective response to combined visual and vestibular cues, and to integrate these results with those of past and current research in a functional model, one which relates the dynamics of the subjective response outputs of motion sensation and attitude perception to the sensory inputs of vestibular stimuli and moving peripheral visual fields.

It is anticipated that such a functional model would be a significant contribution in both the basic research area of understanding the properties of motion perception and the applications areas which rely on human motion perception models. In the research area, considerable effort has been devoted toward neurophysiological studies of cells along the "vestibular pathway", and work has begun on recording single unit responses to combined visual and vestibular stimuli. Because of the past success in correlating subjective response characteristics with single cell activity, it is anticipated that a dual-input functional model at the subjective level can complement neural response studies using the same visual and vestibular cues. In particular, it is felt that a subjective functional model can not only suggest appropriate stimulus sequences to be used in single unit experiments, but can also provide a mathematical framework for modelling the dynamics of the observed single unit responses. A second application of a functional model describing motion sensation is in the development of realistic moving base simulators, where it is desired to maintain a maximum of realism within the constraints imposed by the mechanical travel limitations and the sophistication of the projection system. In this instance, it is anticipated that a functional model could be used in an inverse sense, so that given a desired motion sensation to be simulated, the appropriate visual and vestibular cues to be supplied by the simulator could be backed-out of the model. Such an approach may not only minimize the current trial-and-error procedures used in simulator design, but may also indicate how simultaneous presentation of fairly simple visual and vestibular cues may be used to induce a relatively complex sensation of motion, one which is not particularly amenable to simulation by conventional moving base simulators. Finally, an extension of the dual-input functional model of subjective sensation would appear to be a tool particularly well-suited for the continuing effort directed at elucidating the causes of disorientation and motion sickness. Specifically, the functional model could be modified to generate, in response to a fixed visual and vestibular input stimulus pair, a spectrum of possible motion sensations, each assigned a particular probability consistent with experimental testing. The applicability of such an approach to motion sickness studies is supported by the "conflict theory" (see for example Guedry[22]), which suggests that an "inconsistent" set of sensory inputs (e.g. vestibular inputs with no corresponding changes in the visual field) can result in an internal conflict of how to process the sensory data in a physically meaningful way, which, in turn, can lead to disorientation and malaise. Thus a probabilistic dual-input functional model could be used to determine various combinations of visual and vestibular inputs which result in motion sensations characterized by consistently low probabilities, and hence, presumably, low probability of inferring correct orientation. Clearly, such a model could be used to test the "conflict theory" of disorientation and motion sickness.

1.0 Background

As noted above, research directed toward understanding the influence of combined visual and vestibular cues on motion sensation and attitude perception can be separated into three functional areas: experimental work involving only vestibular stimulation; similar studies utilizing only visual field stimuli; and research into the effects of simultaneous presentation of visual and vestibular cues. A summary of the relevant results of these efforts is given in the following sections, beginning with a brief review of vestibular modelling of subjective sensation and concluding with a discussion of the results of current dual-input studies.

1.1 Vestibularly-Induced Motion Sensation

Models of vestibularly induced motion sensation and attitude perception rest heavily on an understanding of the static and dynamic characteristics of the vestibular organ components: the semicircular canals and otolith organs. Perhaps the most influential model of end-organ dynamics was proposed by Steinhausen,[54] who developed a linear second order model of canal cupula dynamics to explain the observed characteristics of vestibularly induced eye movements in the pike. Neurophysiological support for this second order model was subsequently provided by the work of Lowenstein and Sand[36, 37] on the dogfish, who, by means of ampullar nerve and single unit recordings, showed that the primary afferent response to mechanical inputs also followed Steinhausen's model; the simplest interpretation of these observations assumed the hair cells to be approximately linear transducers of cupula motion, so that the basic characteristics of the afferent response is dictated by the dynamics of cupula deflection, and not the dynamics of neural transduction. It should be noted that Lowenstein and Sand[36,37] also made clear the bidirectional response capabilities of the canals, and suggested the possibility of a push-pull interaction between contralateral canals. The canal model became more formalized with the introduction of the "torsion pendulum" model of Van Egmond et al[57], who showed how the physical characteristics of the canal could be used to infer one of its time constants and, at the other end of the spectrum, how subjective cupulometry could also be utilized to infer the model's parameters. In particular, by monitoring motion sensation in response to a rotational stimulus, using a variety of experimental approaches, they were able to infer both a threshold and both time constants associated with subjective sensation; the implication was that subjective response characteristics are dictated almost entirely by the physical properties of the canal.

Further development of a functional model describing motion sensation was motivated on two fronts: the use of other measures of behavioral response to rotational stimuli, and an expansion of the scope of test stimuli used in vestibular testing. In the former case, a better understanding of the vestibulo-ocular reflex was made possible by quantitative cupulometry based on vestibular nystagmus experiments (see, for instance, Robinson[47] and Sugie and Melvill-Jones[55]). However, as shown in a study by Melvill-Jones et al[39], the long time constant of the torsion pendulum model takes on different values, depending on whether subjective response or nystagmus records are used for its calculation. This study also demonstrated that subjective and nystagmus time-constants varied with the subject's rotation axis (yaw, pitch, or roll, always about the vertical), further complicating the one-dimensional simplicity of the torsion pendulum model. Of course, this observation is consistent with different physical properties for each of the three synergistic canal pairs, but Melvill-Jones et al[39] point out that standard body-axis yaw, pitch and roll rotations excite all six canals to some extent, so that ascribing an axis time constant to one canal pair's physical properties may be entirely inappropriate. They also note that Ledoux[34] found no siginficant differences in time constants when cupulometry was performed about rotation axes (approximately) perpendicular to the three canal planes, and thus suggested a more central origin for the subjective dynamics observed during standard body-axis rotation tests.

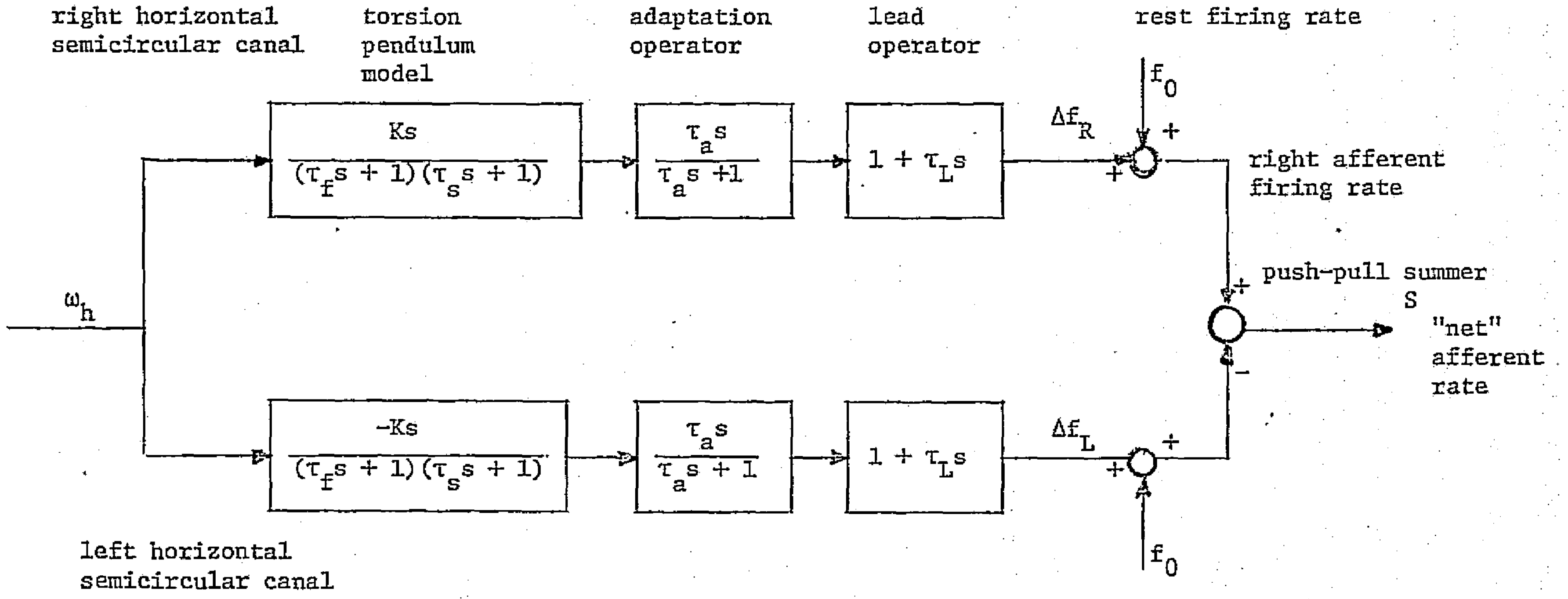
Similar differences are seen in threshold studies, both in terms of axis-by-axis dependence and in terms of dependence on the type of behavioral response measure used. Meiry[38] showed yaw-axis thresholds to be on the order of 1.0°/sec^2, with roll axis thresholds approximately 5 times larger. The idea of different "cupular" thresholds provides a possible explanation, as does the idea of a more centrally located processor working with body-axis coordinates and characterized by differing thresholds in each axis. However, neither of these explanations appears necessary in light of Clark and Stewart's[8] more extensive study of subjective thresholds about all three axes: they showed mean roll and yaw thresholds to be equal (0.4°/sec^2) and although the mean pitch threshold was slightly greater (0.6°/sec^2), the difference was barely significant. The suggestion is that all three subjective thresholds are approximately the same, across the test population, and might thus be ascribed to end-organ characteristics. However, single-axis studies using different response measures suggest a more central location for the factors influencing threshold behavior. For instance, in yaw rotation about the vertical, Brandt and Clark[9] show a mean subjective threshold of 0.4°/sec^2, and yet with the same test population, show a mean threshold for the oculogyral illusion[27] to be approximately four times smaller, or 0.1°/sec^2. Similar results were discussed by Oosterveld,[42] who noted that all three measures of vestibular function (subjective, oculogyral, and nystagmus) demonstrate differing threshold values, thus compounding the problem of attempting to fit the data with a simple torsion pendulum model.

The other development which has led to a less simplistic view of vestibular function has been the increasing interest in response to vestibular stimuli which consist of either linear accelerations or rotatory motion about non-vertical axes (the majority of the early studies having been concerned with rotary motion about earth-vertical). As discussed by Henn and Young,[30] Ernst Mach was perhaps the earliest investigator to study what is now generally considered to be otolith function, but approximately a century passed before quantitative studies of subjective responses to linear acceleration led to the functional models proposed by Meiry,[38] and Young and Meiry.[68] Here the subjective response is modelled as a second-order system with lead compensation, acting on specific force, so that static tilts away from the vertical and linear accelerations are equivalent stimuli. This model of subjective response was motivated by the known physical properties of the otolith organs, specifically the inertial reaction mass of the otoconia and the shear force input[49] due to head motions and/or gravity. The static characteristics of this model are also consistent with the single unit recordings of otolith afferents conducted by Fernandez, Goldberg and Abend,[17] who found a linear relationship between tilt angle (i.e., specific force) and steady state firing rate. It is appropriate to note that Fernandez and Goldberg are currently studying the response dynamics of otolith afferents due to sinusoidal stimulation, and it will be of interest to compare their unit frequency response curves with those associated with the functional model of subjective sensation.

Studies involving off-vertical rotatory stimulation have yet to result in definitive functional models, probably because of the complexity of higher-level processing involved in combining canal and otolith signals. As an example, Benson and Bodin[1] show that "barbecue mode" rotation, in which a subject's cephalo-caudal rotation axis is in the horizontal plane, results in an accurate subjective sensation of rotation, and is uncorrupted by the typical post-rotational turning sensation seen in vertical spin-axis studies. The simplest explanation assumes that subjective sensation in this situation is derived primarily from the otoliths signalling a rotating gravity vector, so that canal acceleration and deceleration transients are overridden; however, Benson and Bodin[1] argue for the notion of an additional mechanical influence of gravity on the canals (for example, the "roller-pump" theory of Steer[53]), motivated by their nystagmus records taken during the experiment. Specifically, they show barbecue-axis rotation to result in nystagmus patterns characterized by a sinusoidal oscillation in slow-phase eye velocity superimposed on a bias velocity. As argued by Young and Henn[67], who conducted similar testing with monkeys, the sinusoidal component is consistent with studies on "linear" nystagmus[53,62] (i.e., compensatory eye movement mediated by otolith transduction of linear acceleration), but the bias term is still not well understood.

Thus, model development of vestibular function has received impetus from both the use of more complicated stimulus patterns and the investigation of different response modalities (subjective sensation, eye movement, and visual perception illusions). The net result has been a better understanding of function both at the "component" level and at the "systems" level. In the former case, the torsion pendulum model of canal dynamics has been coupled to a non-localized "adaptation operator", proposed by Young and Oman,[69] to account for the above-noted discrepancies between parameter values calculated from subjective and nystagmus cupulograms. Such an operator also helps explain response reversals in experimental situations in which the torsion pendulum model predicts no such reversal[69]. Although the adaptation function could be implemented centrally, Goldberg and Fernandez [16,18] adduce neurophysiologic evidence to support the notion of peripheral adaptation, at least for some sub-population of the primary afferents. The other basic "components" of the vestibular organ, utricle and saccule, have received less attention, although functional modelling effeorts are continuing along the lines proposed by Meiry.[38] By using the results of past studies in perceived static orientation, Ormsby[43,44] has proposed a functional model of tilt perception which attributes non-linear processing of specific force information to the sacculus (which is supported by the unit recordings of Fernandez, Goldberg and Abend[17]), which, when combined with the presumed linear output of the utricle, result in a subjective perception of "down" consistent with the results of earlier psychophysical experiments.

On the "systems" level of model development, there has been a trend toward integrating the results of vestibular experimentation, with the goal of developing a unified model to explain motion sensation and attitude perception. Several workers have proposed various functional models[53,59,60,64,69] and it is appropriate at this point to discuss some of their salient features, so as to both summarize some of the points made earlier, and to provide a structure for later discussion. Shown in figure 1 is a block diagram which models the transduction dynamics of the horizontal canals, in which the input is the head's angular velocity component normal to the canal



ω_h horizontal canal component of head angular velocity (right ≡ positive)

Figure 1. Bilateral functional model of canal afferent dyanmics

plane, and the output represents an ensemble average firing rate of some cell population, presumably in the vestibular nuclei. Several points should be made regarding this model of afferent response. First, the two canals are modelled with opposite sign gains, in line with the observed excitatory response with ipsilateral rotations, and inhibitory response with contralateral rotations. The summer at the other end of the path complements this push-pull synergism of opposing canals, and provides for a single input whose sign indicates stimulus direction. Perhaps more significantly, it also provides for a linearization of canal-pair output in the face of individual canal saturation (observed in the inhibitory direction by Fernandez and Goldberg[18]), and thus allows the canal dynamics to be approximated with a linear gain K as shown. The adaptation and lead operators (the latter indirectly proposed by Nashner[41] to explain observed postural compensation and more recently by Fernandez and Goldberg[18] to better fit the frequency response curves calculated from primary afferent recordings) represent average behavior over the primary afferent population, as does the non-zero rest firing rate. As has been pointed out by several researchers, the torsion pendulum block provides for a relatively flat frequency response over the range of 0.01 to 1.0 Hz, thus acting as a velocity transducer for physiologic inputs; the adaptation operator is effective at only very low frequencies, while the lead term effects are seen at the other end of the frequency range. Finally, it should be noted that the model as drawn has identical parameter values for each path, an obviously unrealistic situation. It is presumed that any differences can be compensated for by more central processing and thus, the model is in some sense an equivalent of a more complicated peripheral model followed by a central compensatory logic. The simplest example would involve a difference in rest firing rates, f_0, so that the net signal S would be non-zero for a null input; clearly this firing rate asymmetry would be subracted off at some later stage to allow for a more accurate DC output.

This two channel model can of course be reduced to a single equivalent functional path simply by lumping the two canals together; shown in Figure 2 is the equivalent "cyclopian" functional model which not only is simpler, but avoids the problems introduced when one considers the question of left-right parameter mismatches. What is important to note here is that Figure 2 is a functional model of subjective sensation, and not afferent firing rate; the intimacy of the two measures of vestibular function should be obvious from the functional equivalence of their models.

Three other points should be made regarding this functional model of canal dynamics. First, it is generally accepted that such a model can be extended to the other canal pairs, where pairing is done on the basis of canal planes[43] (i.e., right superior with left posterior and right posterior with left superior) and thus a three-axis model consisting of three similar channels can be used to represent the transduction of an arbitrary angular velocity vector into a three dimensional

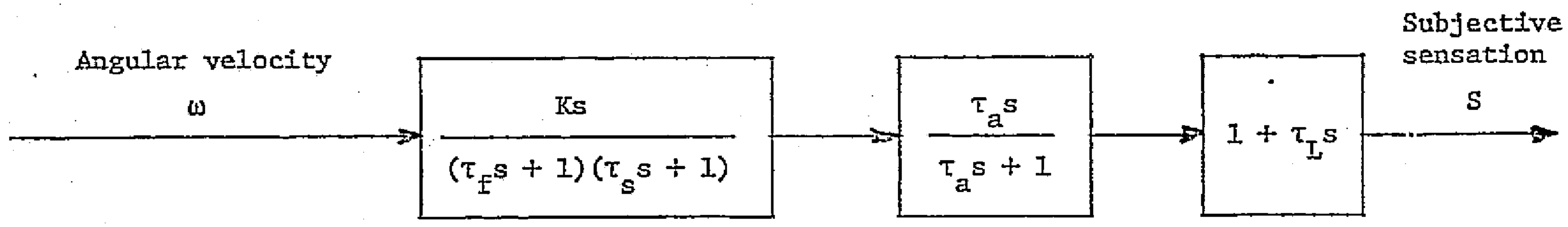


Figure 2. Functional model of subjective rotary sensation

sensor signal. Support for similar dynamic characteristics among the three channels may be found in the single-unit data of Fernandez and Goldberg[18] and in the psychophysical measurements of Guedry, Stockwell and Gilson.[23] A second point to be made concerns the location of the adaptation operator at the periphery. Young and Oman[59] argue for a more central location, so as to accommodate differences found between subjective response and vestibularly-induced eye movements; such an approach calls for two parallel paths beginning from the torsion pendulum block, with each path containing an adaptation operator whose parameters are consistent with the particular measurement being made. Since the concern here is with subjective response, the multipath model is unnecessary, and the simpler system of figure 2 will suffice, with no statement regarding location of the operator necessary. Finally, it should be recognized that this model makes no provision for threshold phenomena. The conventional approach is to simply apply a deadband non-linearity to the output, so as to match the threshold characteristics of the experimentally determined subjective response[69]. Ormsby[43] argues that this is too simplistic a view, and proposes a "signal-in-noise" model which attributes threshold behavior to signal detection confidence. Again this is supported by single unit studies,[16] which show no evidence of discrete threshold at the periphery, mechanical or otherwise. This issue will be set aside for now, since the proposed research will be concerned primarily with suprathreshold stimuli.

As noted earlier, less effort has been devoted toward modelling otolith function, primarily because of the difficulty in assuring canal non-involvement in experimental testing. Shown in Figure 3 is a subjective functional model whose superstructure was proposed by Ormsby[43] and discussed earlier, and whose individual "accelerometer" blocks are taken from the work of Young and Meiry.[68] The input is specific force ($\ddot{\underline{r}} - \underline{g}$) and the output is a vector signal, $\underline{s}$, which can be used to infer linear acceleration and/or tilt from the vertical. The saccular non-linearity is a particularly efficient means of modelling the results of past experiments involving illusions of determining the vertical, and is supported by recordings at the single unit level.[17] The actual utilization of the output of such a model in further sensory processing is an open question. Clearly, for the static situation, a simple vector normalization will provide an estimate of the "down" direction with respect to some body reference frame, and thus a measure of body attitude with respect to the vertical; what is not so obvious is how the sensory information is interpreted in the dynamic situation. One approach to this question is given by Ormsby[43], and is based on the different dynamic characteristics of the canals and otoliths, relying on frequency separation effects to differentiate between changes in body attitude and changes in the specific force vector. The model appears to fit the data well in certain instances, although it is far from the point of having been exhaustively tested.

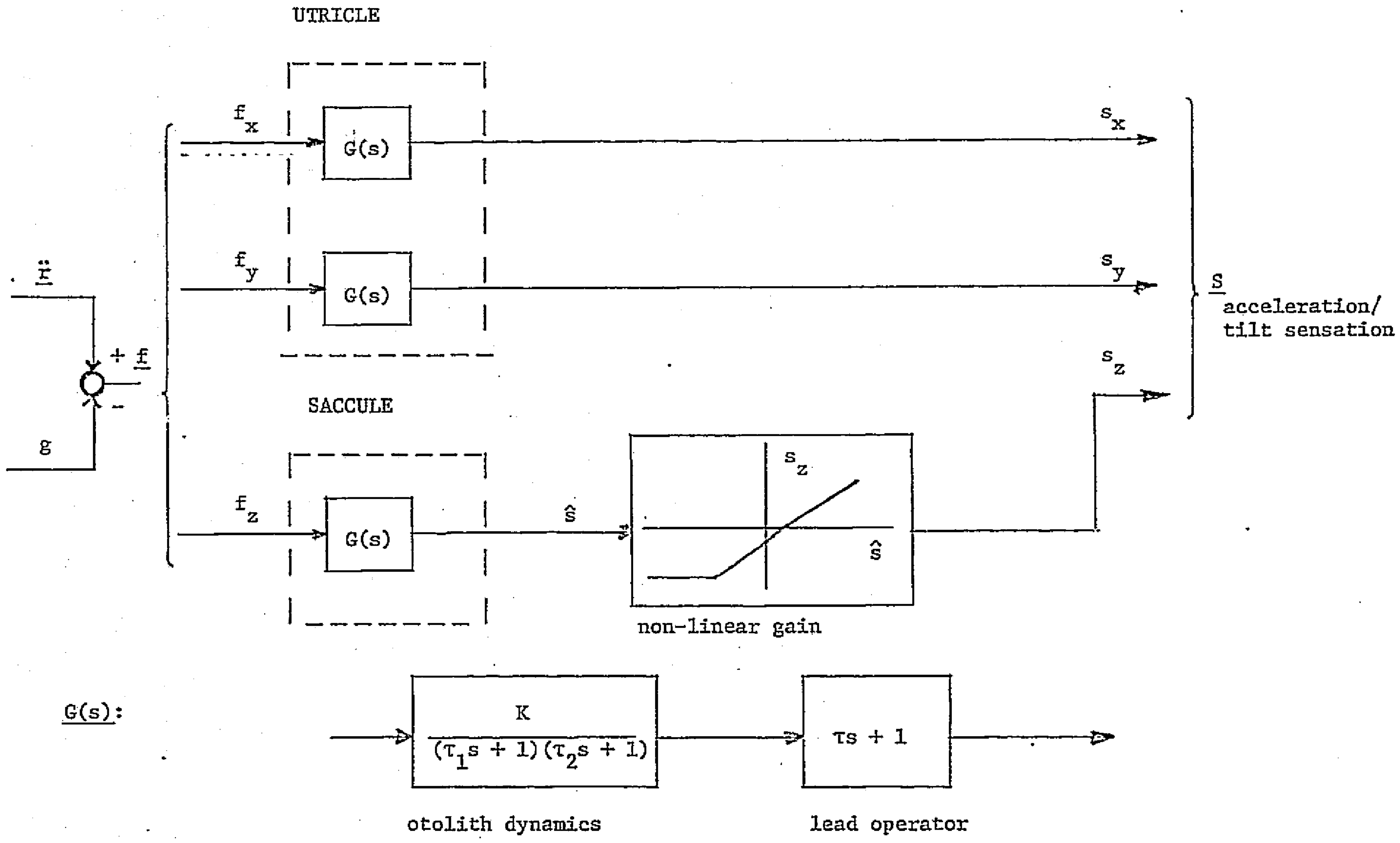


Figure 3. Functional model of subjective linear acceleration/tilt sensation

1.2 Visually-Induced Motion Sensation

Functional modelling of visually induced motion sensation and attitude perception is not nearly as well-developed as in the vestibular studies, nor does it have the relatively sound basis of extensive neurophysiological studies on which to base a relevant functional structure. For this reason, this section will briefly describe some of the findings of various experiments, on an axis-by-axis basis, and defer a discussion of a possible model until the next section.

Both rotatory and linear moving visual fields have been used to induce motion sensations (referred to as circularvection and linearvection, respectively), with the greatest concentration of effort being in yaw circularvection about an earth-vertical axis. The general aspects of the motion illusion have been knwon for some time:[30] initially, the subject feels himself fixed and the visual field to be moving; gradually, a transfer of differential velocity occurs so that the steady-state condition is reached in which the field appears stationary and the subject perceives himself to be rotating in the direction counter to the initially perceived field velocity. A more quantitative measure of this illusion, yaw CV, was undertaken by Brandt, Dichgans and Koenig,[3] who showed that the most important stimulus quality is its location within the visual field, peripheral stimulation being a necessary and sufficient condition for eliciting CV. In terms of subjective response characteristics, they found the following: CV latencies are slow compared to equivalent vestibular inputs, being on the order of one to five seconds, and are essentially independent of stimulus velocity or acceleration (over the range of stimuli used). CV rise times, in response to velocity steps of the visual field, were also relatively slow, being on the order of ten seconds, and displayed a tendency to increase with stimulus velocity. Finally, they found a linear relation of CV strength to stimulus velocity over a wide range, with saturation occurring only at the highest velocities (∿120°/sec). Subsequent tests reported by Young and Oman[70] showed a latency dependence on stimulus velocity which was most marked at very low stimulus velocities, below those used by Brandt et al.[3]

The illusion is quite convincing, and given adequate attention to the elimination of other motion cues, cannot, in the steady-state, be subjectively distinguished from true mechanical rotation. This suggests an intimate dependence of motion sensation on visual cues, with the mixing of sensory cues occurring at perhaps relatively low levels, possibly within the "vestibular" system. Evidence for this is given in the next section; it suffices at this point to note two other studies which support the equivalence of visually-induced yaw CV to the sensation associated with real rotation with a fixed visual surround. First, in a study by Dichgans and Brandt,[10] it was shown that motion sickness could be induced by a CV-inducing visual field and an appropriate head motion to the side, in a manner exactly analogous to inducing motion sickness with an actual body rotation and subsequent head tilt.

The results of this study are discussed in more detail later; what is important to note here is that the illusion is convincing enough to elicit symptoms indistinguishable from those of "real" motion sickness. A second study by Young and Henn,[66] demonstrated the presence of cross-modality habituation, in which vestibularly-induced nystagmus was reduced by pre-conditioning with a CV-inducing visual field. They argue that a necessary condition for a stimulus to be habituating is that it provide the same subjective sensation which will be encountered in the actual test for measuring habituation effects. Thus, the results support the conclusion that the habituating stimulus (the moving visual field) produces a sensation of motion equivalent to what would be experienced under true rotation, again lending credence to the "realism" of the illusion.

A moving peripheral visual field whose rotation axis is in the horizontal plane produces a qualitatively different response from the one just described. As discussed in a paper by Dichgans et al,[12] when the field rotation axis is along the observer's line of sight, the direction of the apparent vertical assumes a steady-state offset from the true vertical, in the direction of field rotation. Since the effect (referred to as roll CV) was measured by requiring the subject to adjust a reference line to the apparent vertical, it was necessary to determine if the effect was purely visual, or actually involved a change in the subject's internal representation of the "down" vector. A postural control experiment, reported on in the same paper,[12] confirmed the latter hypothesis, as it was shown that the "postural" upright also tended toward a steady-state offset from true vertical, again in the direction of field rotation. A quantitative study of the stimulus and response parameters was made by Held, Dichgans and Bauer,[28] who again asserted the importance of peripheral field stimulation on illusion strength. They noted latencies on the order of a few seconds, followed by a counterrolling sensation, which led to a steady-state perceived tilt approximately 30 seconds after stimulus onset. Latency dependence on stimulus velocity and acceleration was not reported on, but perceived tilt angle dependence on stimulus velocity was shown to be approximately linear with saturation occurring with stimulus velocities near 40°/sec.

Two additional points should be made regarding this study of visually-induced roll tilt, the first being the question of ocular torsion involvement in the subject's indications of the perceived vertical. Motivated by the appearance of unexplained response asymmetries observed during a combined tilt and visual stimulation experiment conducted by Tang,[56] Dolezal and Held [15] showed that ocular torsion does indeed occur in response to a roll CV display, and is on the order of a few degrees, in the direction of stimulus rotation. This is too small to account for the induced subjective tilt, but can account for observed response asymmetries. They propose that, in estimating the vertical with a movable reference line, the subject is unaware of his eye torsion, and thus the indicated response is merely the sum of eye torsion angle and perceived tilt angle. There still remains the question as to the source of the induced torsion, whether it is merely the response of the visual pursuit tracking system[47] or a manifestation of ocular counterroll,[27] perceived tilt being the adequate stimulus in this case, rather than the actual tilt.

The second point to be made regarding visually-induced roll tilt is its dependence on head position with respect to the vertical. One study by Young and Oman[71] showed that, with a fixed visual stimulus velocity, the induced subjective tilt was greater as the head was moved from its normal position to positions farther from the vertical. A parallel study was run by Dichgans, Diener, and Brandt,[11] using less tilt variation, but finding the same qualitative behavior. To ensure that this was not due simply to the well-known Aubert or Muller phenomena,[27] control studies were run so as to correct for vertical misperception due to head tilt alone. The results show that the roll CV induced tilt remains an increasing function of head tilt, and, further, that the variance in response measures also increases. Young, Oman and Dichgans[71] extended these results by parameterizing the responses over various stimulus speeds and a larger range of head tilts, to show that tilt response sensitivity to stimulus speed was a minimum with the head pitched 25° forward (so that the utricles are approximately normal to gravity) and increased significantly as the head approached the inverted position. As in the earlier studies, response saturation occurred with large stimulus speeds; the results show the induced tilt at saturation also to be an increasing function of head tilt.

Pitch axis CV, an illusion induced by a rotating visual field where the spin axis is perpendicular to the saggital plane, has received less attention then roll CV, perhaps because of the response ambiguities encountered during testing. As reported by Young, Oman and Dichgans,[71] there is an induced pitch tilt illusion which shows a similarity to roll CV in terms of its dependence on stimulus speed and head position. It differs however, in that there exists a marked directional asymmetry: for the same stimulus speed, the pitch down sensation is stronger than the pitch up sensation. No such asymmetry is seen in the population responses in the roll CV experiments, although individual asymmetries were noted (presumably due to the above-mentioned eye torsion asymmetry). In addition, the pitch CV experiments resulted in a substantial amount of vertical linearvection[70] (LV), a qualitatively different subjective response to be discussed shortly. Whether or not such a sensation contaminates the subjective indication of tilt is unclear at this time; Young and Oman[70] show how such a dual response can be minimized by appropriate masking of the visual field.

Linearvection, or the sensation of linear motion induced by a moving visual field, has received less qualitative study than the rotary analogs, and only a brief review of the results of two studies will be conducted here. By the use of a peripheral visual field moving in the fore-aft direction, Berthoz, Pavard and Young[2] were able to induce a sensation of linear motion oppositely directed to field velocity, a linear analog to yaw CV. They found that the stimulus properties of luminance and velocity necessary for LV induction were basically the same as those necessary for visual image motion detection in the periphery, and concluded that the visual image motion detection system was responsible for both threshold effects and LV loss at high stimulus velocity (due to fusion). With respect to response characteristics, they found latencies on the order of one second, and independent of stimulus velocity. By the use of a slow ramp in stimulus velocity, a non-linear saturating relationship between stimulus velocity and LV magnitude was demonstrated, although it is not clear how dependent such an input-output relation is on possible dynamic effects. In particular, it was shown that considerable adaptation occurs over the course of a few minutes, so that greater stimulus velocities are required for the same magnitude LV. Finally, the use of sinusoidal velocity profiles allowed for a describing function description of the response; the results show a gain roll-off at about 0.02 Hz, and a 90° phase lag at about 0.2 Hz. How these findings are corrupted by the predictive properties of the human observer and his manual control capabilities (of the indicator stick) is unclear at present. A second study, conducted by Chu,[4] investigated some of the properties of up-down LV induced by vertical peripheral visual field motion. Using a pseudo-random velocity profile to avoid subject prediction, and applying a small correction for manual control dynamics, he found the describing function gain-phase characteristics to be similar to those for the previously reported fore-aft situation, with slightly less gain at the low frequencies and more phase lag at the higher frequencies (possibly due to the non-predictive nature of the task).

A discussion of current theories which attempt to unify and account for many of the observations made in CV and LV studies will be deferred to a later section.

1.3 Visual-Vestibular Interactions in Motion Sensation

The studies just described have been primarily concerned with motion and tilt sensations induced by separate application of visual and vestibular stimuli; those to be discussed here have begun to answer the question of what happens with combined stimulation. Of course, it should be realized that any of the CV or LV experiments are fundamentally dual-input, because of the constant presence of gravity (assuming normal vestibular function in the subjects); thus many of the previously described observations should be directly applicable to a dual-input modelling effort. This section will briefly describe some additional studies using both inputs, and their implications for functional modelling of subjective response will be discussed in the next section.

Both psychophysical and neurophysiological studies support the theory that visual and vestibular cues are jointly processed to provide for a perceived sense of motion and/or body orientation. Support for such a convergence of sensory inputs comes from the identification of one possible interaction "site": the vestibular nucleus complex. Single unit recordings from the vestibular nuclei of goldfish, as reported by Dichgans, Schmidt, and Graf,[14] indicate that the majority of cells respond to both vestibular and moving visual field inputs. Their results may be briefly summarized in schematic form as shown in Figure 4. With the goldfish in the dark and using a yaw rotation stimulus consisting of a ramp to a constant velocity, a unit's response was seen to be consistent with the torsion pendulum model, returning to its rest firing rate after an excitatory period during the acceleration pulse. For the same unit, an oppositely directed rotation of the visual surround, with no vestibular input, resulted in a slight increase in the firing rate, which held constant during the constant velocity portion of the stimulus. Finally, when both stimuli were presented, in opposing directions consistent with rotation in the presence of a physically stationary visual surround, the firing rate was characterized by the faster response and greater sensitivity of vestibular stimulation, combined with the non-adaptive behavior of visual stimulation. The result is a signal which accurately indicates true body angular velocity. It was noted in the study that such a signal cannot simply be reconstructed by summation of visual and vestibular responses, but rather, represents a non-linear "modulation" of vestibular response by visual motion cues.

Similar results were found by Henn, Young and Finley,[29] recording from vestibular nuclei units of the monkey responding to visual and vestibular cues. They noted the "classic" vestibular step response to pure vestibular stimulation, and a very

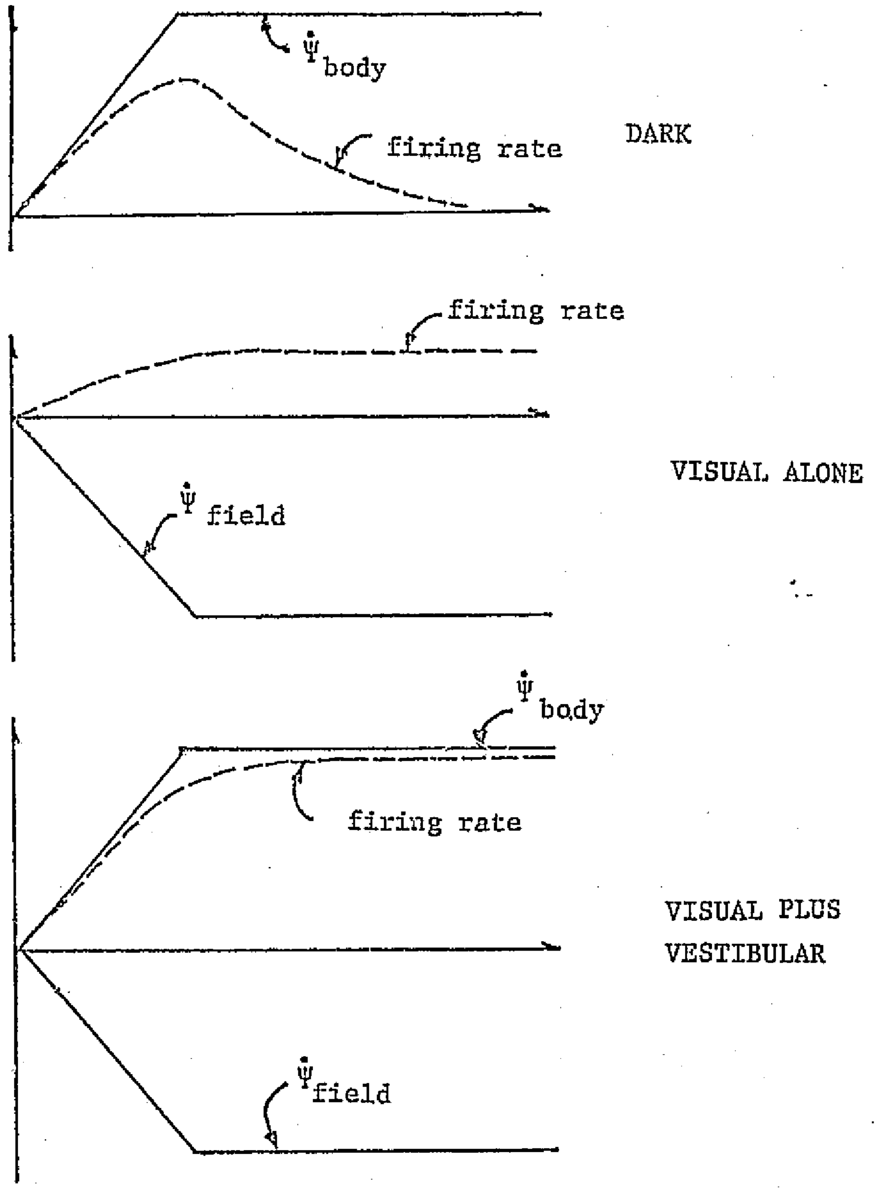


Figure 4: Vestibular Nucleus Recordings in the Goldfish.

slow change in unit activity in response to a pure visual field motion stimulus (again sign consistent as in the goldfish). Using sinusoidal stimulation, they noted the familiar low frequency phase lead in the response due to a vestibular input alone; the addition of a confirming visual field input abolished the lead, resulting in an accurate transduction of true velocity. Finally, the modulation effect of visual inputs was demonstrated by simultaneous application of sinusoidal rotation and constant visual field velocity. The unit response was seen to be basically sinusoidal, following the rotational stimulus, but its amplitude was modulated by the visual input. That is, if the field were moving in a direction which normally resulted in an excitatory response, the amplitude was increased over that observed during fixed-field rotation; the converse was also noted, decreased amplitude with inhibitory field motion. Such behavior cannot be modelled as simple amplitude modulation, because of the non-linear response asymmetry observed during a step change from one visual field direction to the other: in going from an excitatory to an inhibitory visual stimulus, response amplitude dropped quickly, while the converse transition resulted in a slow gain in amplitude.

Psychophysical studies of subjective response to simultaneous cues have also demonstrated the presence of subtle interaction dynamics. In one study by Young, Dichgans, Murphy and Brandt[65] subjective velocity and acceleration detection indications were made by subjects in response to combined yaw-axis rotational cues consisting of rotational acceleration pulses (of differing amplitudes and durations) in conjunction with a constant angular velocity visual field. They considered such a pulse to be "confirming" when it was in the direction of the induced CV, and "conflicting" when in the opposite direction. They found the following. First, the subjective velocity was found to be biased in the direction of the induced CV, but not to the extent of a simple summation of CV and expected vestibular response. Second, the detection of a confirming pulse was characterized by a lower threshold and shorter detection time compared to the detection of a conflicting pulse. Finally, the detection of a confirming pulse generally led to a moderate increase in subjective velocity, whereas a conflicting pulse, if detected, resulted in a marked decrease in subjective velocity, thus confirming the non-linear interaction observed in the vestibular nuclei recordings. It should be noted that a similar study was conducted by Berthoz, Pavard and Young,[2] in which linear fore-aft acceleration pulses were combined with linear field motion. They found qualitatively the same pulse detection dependence, showing detection to be considerably degraded when the pulse conflicted with the induced LV sensation.

1.4 Theories of Visual-Vestibular Interaction

As noted earlier, functional modelling of combined visual and vestibular stimulation is at a very early stage of development, with only qualitative theories to explain some of the experimental results; certainly there exist no detailed dynamic models comparable to those describing pure vestibular stimulation. What will be attempted here is a brief discussion of some of these ideas, how they relate to the research just described, and some of the questions which inevitably arise when attempting to fit fact with theory.

Basic to the study of visually induced motion sensation and tilt illusions is the concept of convergence of both visual and vestibular information at some point in the CNS, and that the output of this site is somehow intimately related to the sensation induced. As noted earlier, support for this idea comes from the "realism" of the visually induced illusion experienced during psychophysical experiments, and the identification of vestibular nuclei units which mimic the subjective CV response. This latter point was brought our by Henn, Young and Finley,[29] who, in describing vestibular nucleus unit activity in response to combined stimuli, noted that:

> "The slow gain of activity when visual and vestibular responses agree in direction, the sudden drop in activity when they disagree, the delay in onset of activity following optokinetic stimulation, and the outlasting of activity after the end of a moving visual stimulus are all qualitatively similar to the pattern of circularvection sensation in equivalent psychophysical experiments in humans."

One is clearly tempted to suggest that not only is the vestibular nucleus a prime candidate as a convergence site, but that it codes motion sensation, a function significantly different from relaying primary vestibular efferent activity. Although highly speculative, such an idea has support on two fronts. First, Henn, Young and Finley[29] showed that their recorded unit activity was only loosely correlated with nystagmoid eye movements, and was present even when animal drowsiness precluded nystagmus. This observation is consistent with the notion that the unit output is not merely a signal in the vestibulo-ocular reflex arc,[47] although more recent findings[32] have indicated a higher degree of correlation between unit activity and nystagmus than originally reported. Parallel supporting evidence was provided by Henn and Young [31] in an extension of this study by investigating the time course of reflexive head torques during stimulation: they were unable to find a consistent relationship between intended head movements (signalled by torque changes) and vestibular nuclei unit activity, thus suggesting that the unit output is not merely a signal in the vestibulo-colic reflex arc either. It should be noted that obvious counterarguments can be made against the conclusion that vestibular nucleus activity in this experimental situation is the neural equivalent of motion sensation, but they will not be pursued here, as the question is still open. This idea of neural equivalency of subjective sensation is not without precedent however, since it has been an implicit foundation of subjective response studies involving only vestibular stimulation; that is, the functional model of vestibularly-induced motion sensation (at least for yaw about the vertical) is almost identical to the model used to describe primary afferent response. Thus the relay-like behavior of the vestibular nucleus units (during pure vestibular stimulation) implies that unit output is the neural equivalent of motion sensation, whether or not this has been explicitly stated in the literature. The success of this approach would certainly argue for its application to the present study of combined stimulation.

One further comment should be made at this point concerning the site of visual-vestibular interactions. Recording from the canal afferents of a paralyzed goldfish, Klinke and Schmidt[33] found that a rotating visual surround caused a modulation of canal activity qualitatively similar to that seen in the previously described vestibular nuclei studies. Thus one suggestion is that the end organ itself acts as a convergence site, with the appropriate visual information transmitted via the vestibular efferents. An alternative interpretation, however, is that the modulation is due to the initiation of a postural reflex triggered by the moving visual field; although the reflex is not observed because of the induced paralysis, a collateral motor signal is sent to the end organ via the vestibular efferents, and results in the observed afferent activity. Functionally, such a view holds that vestibular efferents serve to lower the canal's gain, in anticipation of large mechanical inputs due to self-induced motor activity. Such a view is also supported by Russell's study[48] of the lateral line efferent system of Xenopus, in which he found a high correlation between the end organ's efferent activity and the activity of large motor nerves controlling rapid postural movements, i.e., those movements which would result in large vestibular inputs. Thus, Klinke and Schmidt's findings are not inconsistent with visual convergence at the vestibular nuclei: the postural reflex could be the result of a visually induced motion sensation, generated at the vestibular nuclei, with the modulation of primary vestibular afferents simply a response to the anticipated mechanical input from the reflex.

Turning to the functional modelling of this convergence process, one proposal by Young[61] suggests that the resolution of sensory cue conflicts is fundamental to the understanding of multiple cue interaction dynamics. Specifically, it is proposed that the visual and vestibular cues can be independently processed to infer two estimates of body "state" (i.e., attitude, angular, and/or linear velocity); should the two estimates be consistent with one another, then the perceived body state is calculated from a weighted sum of the two estimates, the weighting in turn dependent on the a priori knowledge of sensory cue reliability in the given situation.

Should the two estimates be inconsistent, that is, in conflict with one another, then a choice is made to accept one of the two on the basis of cue reliability and the subject's set; i.e. how well each inferred state falls within the range of expected states. Although this model has yet to be formalized in a mathematical framework, it has served, with various extensions and modifications, as the basis for qualitative explanations of some of the observed facts. One particularly important extension of this model postulates the use of frequency separation of sensory cues, both in generating the weighted estimate of perceived state and in the resolution of conflict situations. Specifically, it is assumed that the high-frequency components of a vestibular cue are weighted more heavily than those of a visual cue, with the reverse holding true for low-frequency components. To see how this conflict model qualitatively explains dual-input behavior, it is instructive to review some of the experimental results described earlier.

The studies of response to yaw rotational stimuli applied about the earth vertical are perhaps the simplest to model, because of the presumed non-involvement of otolith function. As is well known, the vestibular response to a velocity step exhibits an approximate exponential decay to zero (with slight overshoot due to adaptation) with a time constant on the order of 15 seconds; thus, in the face of constant velocity rotation we can expect no steady-state vestibular contribution to subjective velocity sensation. In the yaw CV illusion experiments, we observe a very slow build-up of subjective sensation (10 to 20 seconds), until the sensation is indistinguishable from true rotation in the presence of a fixed visual field. The conflict theory argues that the steady-state sensation of CV is the result of no visual-vestibular conflicts, since the null vestibular signal is entirely consistent with what would be expected three or four time constants after the start of a velocity step. Since the visual information also implies rotation at constant velocity, the two cues agree and it is merely a question of combining them to get a good estimate of subjective velocity in the steady state. This is a fairly trivial problem, since the null vestibular signals imply no acceleration and hence constant velocity, the particular magnitude and direction of which is supplied by the visual component.

The initial response during the CV illusion is not as straight-forward to explain. Here there is clearly a conflict between the two cues, since the visual information indicates a step change in velocity while the null vestibular cue denies the presence of any acceleration. If we presume heavy weighting of high-frequency vestibular information, then we should expect the visual information to be initially discounted, resulting in a null subjective response following stimulus onset. As time from stimulus onset increases, the conflict lessens since the expected vestibular step response decays to zero, approaching the actual vestibular signal. If we assume the existence of a threshold logic which begins to accept the visual information once the conflict is "below" some level, then we should expect to see CV latency times which are on the order of the vestibular long time constant (15 seconds). As noted earlier, this is what is observed, with CV latencies of one to five seconds, at least an order of magnitude larger than individual visual, vestibular, or manual control latencies.

The growth of CV to its steady-state value (following onset) can be modelled in several ways, and it is appropriate to consider at least two such possibilities. First, it could be assumed that the visual information is weighted by some parameter inversely proportional to a measure of the visual-vestibular conflict, and added to the actual vestibular signal, which is zero in the CV experiments. Thus, as the conflict disappears in the course of a run, the visual information predominates and the illusion grows stronger. Since the time course of this conflict is determined by the vestibular system's long time constant, this model is consistent with the observed slow rise in motion sensation; other implications are discussed below. A second model simply proposes that only the low frequency components of the visual cue are used in generating a sensation of motion, so that a functional model may be implemented which low-pass filters the visual signal and adds it to the vestibular signal (again zero). The filter time constant can then be chosen to mimic the time course of CV, with the steady-state response automatically accounted for by the filter.

One possible block diagram implementation of these ideas is shown in Figure 5, and deserves only brief comment. For simplicity, the vestibular dynamics are represented by only the torsion pendulum model, and (presumed) high-frequency visual dynamics are ignored. The diagram serves to illustrate the use of an internal vestibular model to generate an expected vestibular signal from the generally reliable visual information. The difference of this expected signal with the actual vestibular signal provides a measure of the conflict, which, in turn, is used to gate the visual information through a low-pass filter for summation with the vestibular signal to provide the motion sensation "signal"; note that the internal vestibular model could be used in place of the low-pass filter, but the distinction is made in the diagram for clarity. The waveforms shown illustrate the time histories of various signals in the pathways, for the situation in which CV is induced by purely visual means. A walk-through of the model will also show it to be consistent with responses to pure vestibular stimulation and to combined inputs when they are confirming.

It should be recognized that this model only serves to illustrate some of the concepts just described, and should not be taken too seriously. In fact, its value probably lies in pointing out the shortcomings of such a functional description and of the concepts behind it. For instance, it should be

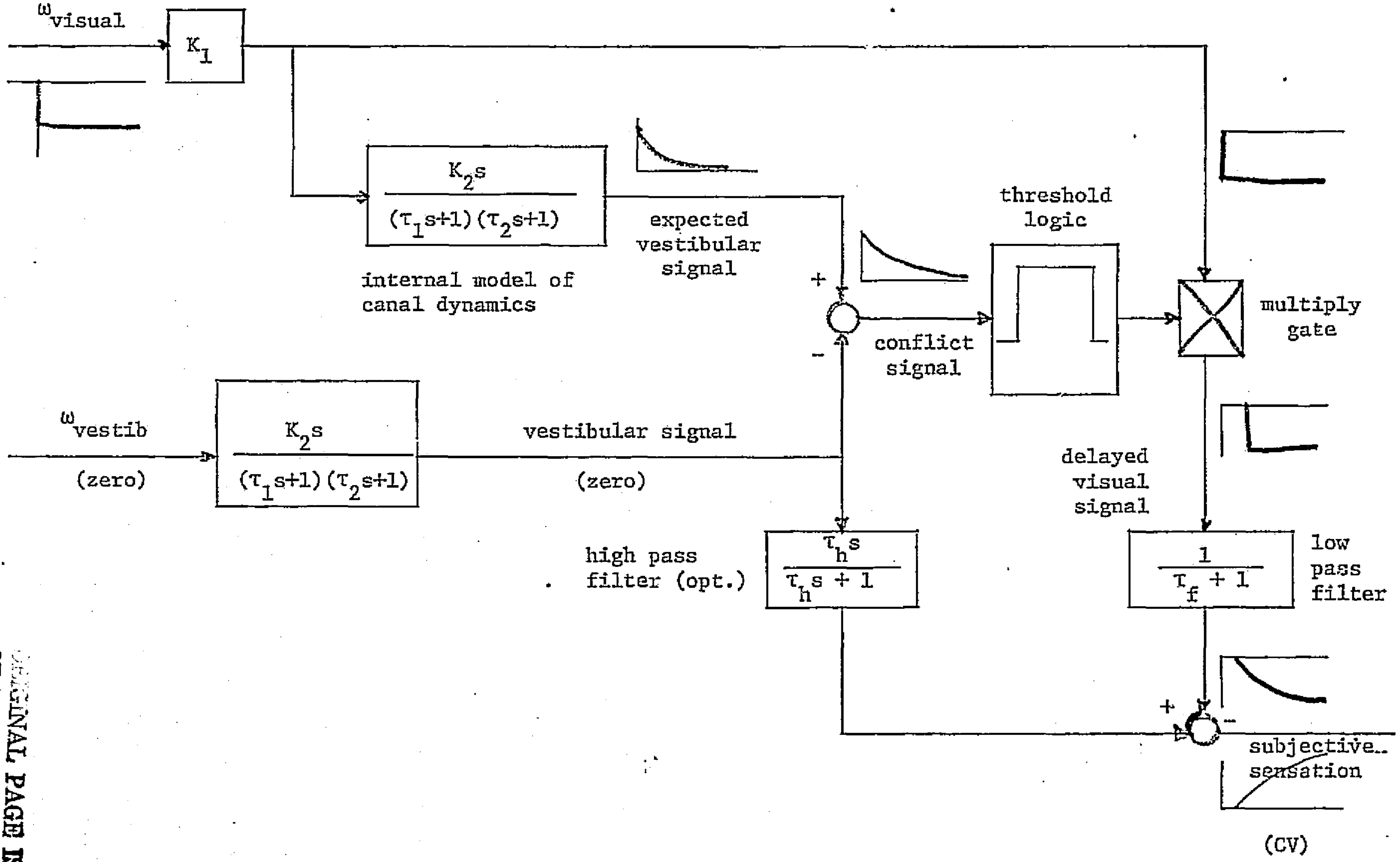


FIGURE 5: Illustrative Model of CV Induction

noted that the diagram illustrates a basically linear system, consisting of a single non-linear gate and a linear complementary filter, the latter acting to high-pass vestibular information and low-pass visual information. This is at odds with the vestibular nuclei unit recordings in goldfish[14] and monkey[29] which showed fundamentally non-linear behavior. In particular, the goldfish studies showed that visual stimulation alone resulted in a steady-state firing rate which was only a fraction of that observed when the visual stimulation was accompanied by confirming vestibular input; the model presented here would predict equal steady-state rates, if, of course we went so far as to assume equivalence between unit firing rate and subjective sensation. In the monkey studies, constant visual-field velocity superimposed on a sinusoidal vestibular stimulation resulted in unit activity resembling amplitude modulation, and not the linear summation of a sinusoid and a bias (which would be the steady-state response predicted by the model). In addition, the unit recordings show a response asymmetry in that they exhibit quick inhibition and slow build-up with alternating field velocities, a property which would not be present in the functional model. Of course, these arguments can be countered by recognizing that unit responses are being compared to the responses predicted by a subjective sensation model; however, the high correlation between the two for pure vestibular responses would suggest that such a comparison is not unreasonable.

The model also runs into difficulty when viewed in terms of the results of subjective sensation studies described earlier. Perhaps the most fundamental problem revolves around latency dependence on visual-vestibular conflict. Specifically, one would predict, either from the block diagram representation, or from the more general framework discussed earlier, that CV latencies would decrease with smaller visual stimulus velocities, since the conflict would be resolved in a shorter period of time. In fact, just the opposite occurs. Young and Oman[70] show that latencies are longest with the lowest field velocity, and decrease by a factor of 5 with a twenty-fold increase in stimulus speed. In addition to this, the model fails to predict the variable threshold behavior witnessed in the study by Young et al[65], in which the probability of vestibular pulse detection during CV was enhanced if the pulse was confirming and degraded if conflicting. Whether or not the more general statement of the conflict theory can adequately treat this case is unclear at present. It is also appropriate to note that the same study demonstrated the response asymmetries seen in the unit recording studies; that is, the quick loss of CV when a conflicting pulse was detected, and the moderate gain when a confirming pulse was detected. Again, the simple functional model presented fails to exhibit such behavior, and it is unclear at present how the conflict theory should be formulated to account for this type of response.

These last points of discrepancy suggest a fundamental structural change in the conflict theory as presented earlier. Specifically, it appears that the observed response patterns are highly correlated with the subject's perception of motion at the time of stimulus application. Stated another way, his expectation would appear to be a direct function of his current perceived state, so that if new sensory cues are integrated according to his expectation, then the cues are effectively weighted by the current perceived state. Thus, the open loop processing of sensory cues proposed by the conflict theory and illustrated by the block diagram would appear to be an incomplete description. Specifically, it is suggested that the output of the system, subjective sensation, must be fed back to the "front-end", so as to appropriately affect the processing of incoming sensory cues. How this should be accomplished in a functional model is not obvious at this point, but the following description of one remarkable motion illusion certainly suggests the necessity for such a pathway.

The Coriolis Effect (CE) is a motion sensation illusion which is reasonably well-explained by our current understanding of vestibular function. Briefly, a subject is rotated at constant velocity in the dark, until all motion sensation dies out; if he then performs a neck bend away from the vertical, he experiences the illusory sensation of rotation about an axis obtained from the cross product of the original angular velocity vector and the vector defining his neck bend. Thus, with yaw rotation to the right, a head roll to the right shoulder results in a pitch up sensation. A simple explanation of this illusion is presented by Peters,[45] who shows it to be due to the AC characteristics of the canals and a straightforward resolution of angular velocities in the head coordinate system. Of importance here is the fact that the illusion is unexpected, but completely determined by the sensory inputs. The pseudo-Coriolis Effect (pCE), on the other hand, is an illusion which has yet to succumb to a coherent functional explanation. Here, the subject is not rotated, but his visual surround is, so as to induce yaw CV. When the subject perceives himself moving at a constant velocity, a head tilt produces the same cross-axis illusion; that is, a left-moving field produces right yaw CV, which when combined with a right head roll, results in a pitch-up sensation. The problem is to reconcile this behavior in view of the fact that the canals are receiving no stimulation (except transiently in roll) since there is no actual rotation vector involved.

Dichgans and Brandt,[10] who conducted a series of pCE experiments, noted two important points. First, the basically null vestibular signal (with the roll transient) is a necessary component of the illusion, since tests with labyrinthine-defective subjects failed to elicit pCE; and second, rolling of the visual field during head tilt is not implicated as a cause, since pCE was elicited in the absence of a visual field once CV had been induced. What this leads to, then, is the following line of reasoning. Prior to head tilt, the subject perceives himself to be rotating about the vertical and thus infers the presence of an earth-vertical angular velocity vector. Assuming the presence of an internal model of the canal dynamics (as in the earlier discussion) and a knowledge of their orientation with respect to the vertical, then the subject should be capable of predicting the coriolis tilt illusion. That is, with right CV he would expect a right head tilt to result in a pitch up sensation generated by the vertical canals. Now, one explanation of pCE would suggest that, during the head tilt, the null vestibular signals are ignored, and the illusion is specified entirely by the expected sensation. This, of course, is entirely at odds with what is seen during CE, in which the illusion is specified entirely by the canal inputs, since the expected sensation is simply one of head tilt. An alternative explatation of pCE presumes the logical strategy of predictive compensation. That is, since the internal model predicts illusory canal responses, cancel the illusion by subtracting the expected canal output (generated by the internal model) from the actual output during the head tilt maneuver. This idea is supported by the observation that rotation in the presence of an earth-fixed visual field results in a substantial dimunition of the tilt illusion,[10] although it is far from being completely cancelled. In the face of no vestibular inputs during a purely visual pCE experiment, such a strategy model would predict a sensation which is the negative of the internal model expectation; that is right CV and right head tilt would result in a pitch down sensation, since the null vestibular signals would be overcompensated. This, of course, is exactly the opposite of what is seen during pCE, a discrepancy pointedly referred to by Dichgans and Brandt.[10]

Resolution of this problem is obviously not the objective of this discussion; rather, it is intended to motivate the incorporation of perceived state feedback into any functional model which attempts to explain the processing of multiple sensory cues. In this way, it is felt that the complex interactions associated with simultaneous visual and vestibular cues need not necessarily be modelled with a complex open-loop functional structure; rather, a more economical model which uses perceived state to process incoming sensory cues may prove to be considerably more appealing. It should be recognized that the idea is not new, as an extension of it was proposed by Young,[61] in which expected state is used to process sensory cues, using the formalized structure of an optimal linear estimator.

The results of studies of motion and tilt sensation about the roll axis are better understood in terms of the conflict model, but this is probably due to the lack of any dynamic visual-vestibular interaction studies, rather than to any inherent simplicity in roll-axis motion perception. Roll axis motion is, of course, compounded by otolith involvement, but the basic ideas applied to the explanation of yawing sensations can be used successfully here. Specifically, the steady-state tilt illusion experienced in roll CV is explained as a compromise between conflicting visual and otolith cues, the canals not being involved because their null signal is in agreement with what an internal model would predict in the face of constant velocity rolling. An internal model of the otoliths, however, would predict an approximately sinusoidal response (approximate because of saccular non-linearity), undamped, and with a period equal to the rotation period of the visual field. Since the actual otolith response indicates the presence of a non-rotating gravity vector, the conflict is never resolved, even in the steady state. What results is a compromise in which the perceived gravity vector is shifted in the direction of the visual field rotation, so that the DC quality of the otolith sensation is preserved, and the visually-induced sense of counter-rotation is in some sense satisfied. It should be noted that although perceived tilt has been shown to be an approximately linear function of field velocity,[28] it is unlikely that a simple linear relation exists at the more basic functional levels.

The dynamics of roll CV build-up are explained in a fashion similar to that used for yaw CV development. Specifically, it is proposed that the lack of confirming roll acceleration sensation from the vertical canals, during the start of visual field rotation, results in an initial conflict resolved in favor of the canals, in turn resulting in the relatively long latencies seen. As the expected canal output dies out, the conflict lessens and the tilt sensation slowly grows to its steady-state value. Of course, otolith conflict is also present during this time and it seems reasonable to assume additional response lags from this quarter. It is worth noting that no studies have described latency dependence on stimulus speed, so that it is unclear whether or not the paradoxical latency relation which characterizes yaw CV carries over to roll CV; it would seem likely that it does.

The conflict model, with its weighting schema, provides a reasonable qualitative explanation of the dependence of steady state perceived tilt magnitude on head inclination with respect to the vertical. As noted earlier, estimates of the apparent vertical exhibit larger errors and increasing variance as the head is tilted from the vertical; the interpretation is that the otoliths become less reliable indicators of the vertical. If it is assumed thatthe otolithic information is weighted according to its reliability, then, in a roll CV experiment, the visual-vestibular conflict should result in a compromise perceived tilt which is more heavily influenced by the visual cue (whose variance should be unaffected by head tilt because of symmetry about the line-of-sight). Of course, this is precisely what Dichgans, Diener, and Brandt[11] observed; the finding by Young, Oman and Dichgans [71] that CV induced tilt was at a minimum when the utricular plane was normal to the earth-vertical is also consistent with this explanation, if it is assumed that the head attitude for maximum transduction accuracy corresponds to that for maximum tilt sensitivity. Also noted in the roll CV experiments[11] is an increased variance of the subjective tilt indications with increased head tilt, a finding consistent with the increased variance of the otolith component of the tilt sensation. Formalized functional models have yet to be proposed which examine some of these ideas in greater detail, and dynamic studies, comparable to those conducted about the yaw axis, have yet to be reported in the literature.

As noted earlier, the qualitative findings for pitch CV resemble those of roll, with two notable exceptions: up-down asymmetry and LV involvement. Young and Oman[70] propose the possibility of a visual origin for the former, and advance a plausible explanation for the observed dependence of LV on visual field placement. Modelling the subjective response is also complicated by the lack of knowledge concerning saccular otolith funtion, a perpheral organ which may prove to be intimately involved in the visual-vestibular processing. It may eventually prove possible to apply the same basic functional model used to describe roll CV, but it should be clear that the additional features of pitch CV serve only to complicate an already difficult task.

One final note should be made regarding the application of the conflict model to the fore-aft LV study[2] discussed earlier. It should be apparent that this illusion is the linear analog of yaw CV, with the linear accelerometers of the otoliths replacing the canal angular accelerometers. Thus, a step input in film speed initially conflicts with an otolith signal which denies the presence of an acceleration impulse, resulting in a conflict resolved by accepting the (null) high-frequency vestibular information, and manifested by relatively long latencies to onset. The slow acceptance of the visual information is consistent with the long otolith time constants, as the internal model of the otolith signal gradually agrees with the null signal. Finally, the steady-state sensation of constant linear velocity is a no conflict situation in view of the otoliths signalling the absence of any accelerations. Actually, this is not exactly in accord with the observations, as Berthoz, Pavard and Young [2] demonstrated the presence of a fairly sizeable adaptation effect, in which progressively higher visual field speeds were required to maintain a constant velocity sensation. That this is not an artifact of the closed-loop procedure used in the study is indicated by qualitatively similar results found in open-loop testing.[50] Whether or not this adaptation is mediated entirely by the visual system is an unsettled question. Although it is not known if a similar adaptation effect is present in yaw CV responses (because of measurement techniques), the two motion illusions exhibit one other common property: vestibular threshold dependence on vestibular pulse direction. Thus, as noted earlier, detection of a linear acceleration is enhanced if it confirms the LV direction, and degraded if it conflicts. Again, such behavior points to a closed-loop functional dependence of cue incorporation on perceived state.

Additional support forthis last point comes from a finding observed during the LV experiment, and concerns visual perception: with LV induced by a constant visual field velocity, a vestibular acceleration doublet often resulted in an apparent stoppage of the visual field. No compensatory eye movements were detected, and although the results are preliminary, the suggestion is that there exists a vestibular-into-visual coupling effect. If LV is considered to be a visually-induced "vestibular" illusion, then this is certainly its converse, a vestibularly-induced visual illusion. Whether this is a case of direct cross-coupling or the effect of perceived state feedback is unclear; it does, however, suggest the reevaluation of the simple open-loop dual-input model.

2.0 Research Objectives

It was noted in the introduction that the overall objective of the proposed research is to develop a functional model which describes subjective response to combined visual and vestibular cues, and which extends our current understanding of motion sensation and attitude perception. Although the research just described and the theories which have been proposed to explain the experimental findings provide a solid base on which to begin a functional modelling effort, it should be clear that a large gap exists between our current understanding and an explanatory, comprehensive functional model. This is due to the need for additional studies covering other aspects of the subjective response in various situations, coupled with the lack of suitable quantitative functional models describing single-axis behavior, let alone coupled multi-axis behavior. In particular, the research summary given above clearly points out the following areas needing attention:

1. The development of a single-axis functional model to describe yaw sensation in all the experimental cases described, one which helps explain the following response patterns:
    i. CV rise-time dynamics and latency dependence on stimulus speed,
    ii. changes in vestibular threshold as a function of CV,
    iii. vestibularly-induced non-linear build-up and drop-off of CV, and
    iv. CE and pCE responses

2. Further study of yaw response patterns, with emphasis on:
   - i. quantitative measurements of non-linear CV modulation due to vestibular inputs,
   - ii. testing for the presence of CV adaptation, and
   - iii. testing for the presence of vestibularly-induced visual illusions.

3. The development of a similar single-axis functional model to describe roll sensation, which accounts for the responses described earlier and which incorporates new experimental findings.

4. Further study of roll response to support model development and aimed at quantitative measures of:
   - i. CV rise-time, latency and adaptation,
   - ii. vestibular threshold dependence on CV,
   - iii. modulation of CV-induced tilt due to vestibular inputs,
   - iv. possible vestibularly-induced visual illusions, and
   - v. ocular counterroll dependence on tilt sensation.

5. Additional qualitative and quantitative studies of pitch CV aimed at determining:
   - i. CV rise-time, latency and adaptation,
   - ii. characteristics of up-down response asymmetry,
   - iii. vestibular threshold dependence on CV,
   - iv. modulation of CV-induced tilt due to vestibular inputs, and
   - v. possible vestibularly-induced visual illusions.

6. Additional quantitative measures of fore-aft LV response, such as vestibular pulse modulation of subjective velocity, and incorporation into a single-axis functional model.

7. Additional qualitative studies of up-down LV and pitch CV interaction dynamics, directed toward the development of a coupled two-axis model.

8. Integration of the above models within a consistent multi-dimensional framework and the specification of test procedures to uncover cross-axis behavior not predicted by an axis-by-axis amalgam.

Motivation and justification for this list follows fairly directly from the background review given earlier; however some points deserve further comment. First, it should be clear that the order of presentation no way implies the suggested order of research, and that parallel efforts should be pursued to take maximum advantage of cross-fertilization of findings and models. Second, it is presumed that any modelling effort will build upon the ideas of the conflict model and the concept of perceived state feedback involvement in cue perception. This is the motivation for further yaw-axis testing of vestibular influence on CV development and visual field perception, the latter presuming a parallel with the results found during fore-aft LV experiments. Finally, it should be obvious that the above list represents many man-years of research effort by several investigators, and is beyond the scope of any single study. In fact, the last three items concerning LV and pitch CV are deliberately less specific, because it is felt that the proposed research should be of reduced scope, with the concentration on yaw motion perception and roll and pitch attitude perception.

Restriction of the proposed research to rotational sensations is motivated by other factors besides the practical consideration of the effort involved. First, the data concerning yaw responses is the most comprehensive, and thus offers the greatest probability of success in developing a useful functional model, one which aids our understanding of the motion perception process. Second, the development of a roll model would extend our understanding to the qualitatively different sensation of tilt orientation, and yet, because of its anticipated similarity to yaw, should involve reasonable bounds in terms of time and effort. It is felt that, in this case, roll model development can build on the features present in a yaw model, once the necessary attributes of roll sensation have been experimentally measured. It is felt that a strong modelling effort in both axes will yield a fundamental understanding of motion sensation and attitude perception which can be used to extend the model to the other axes currently under investigation, and, in particular, provide a sound basis for pitch-axis research. Although the pitch-axis model is anticipated to be quite similar to that developed for roll, the previously-noted response asymmetries suggest a qualitatively different phenomenon occurring in pitch, thus motivating the extension of the proposed research to pitch-axis subjective tilt. The resulting three axis rotational model should then provide a solid foundation to aid other researchers in understanding visual-vestibular interactions in the linear displacement axes, and in situations where more complex stimulus patterns are used for testing.

Thus, the proposed research will concentrate on yaw motion sensation and roll and pitch tilt sensations caused by combined visual and vestibular stimulation. The detailed objectives are given above in points one through four, and involve further experimental studies in all three rotation axes to support subsequent functional model development.

3.0 Research Plan and Experiment Designs

The proposed research will initially concentrate on yaw motion sensation about the vertical, for the reasons given above, and gradually shift its emphasis to roll and pitch sensation as the yaw-axis functional model becomes better defined. The experimental descriptions given below reflect this emphasis, in that the yaw-axis experiments are covered in considerably more detail than those of roll and pitch; a correspondingly detailed specification of the roll and pitch programs will be proposed later in the research. The descriptions are loosely organized along functional lines, not necessarily reflecting the anticipated experimental sequence, and contain the following information:

1. The qualitative or quantitative aspects of the subjective sensation being measured and how these observations support the functional modelling effort.

2. A description of the experimental design.
3. Anticipated problems in the design and possible solutions.
4. Preliminary results from already-conducted pilot studies, if applicable.

3.1 Subjective Velocity Measurement

The object of the following experimental series is to investigate more closely the effect of vestibular inputs on the non-linear build-up and drop-off of CV. Basically, this series is an extension of the work of Young, Dichgans, Murphy and Brandt[65] discussed earlier, which provided a quantitative measure of vestibular threshold variation due to CV, but only qualitatively investigated the non-linear modulation of CV by vestibular pulses. Their approach used a non-repeatable vestibular acceleration pulse profile in conjunction with a constant velocity visual field to elicit magnitude estimates of subjective velocity. However, no comparisons were made with experimentally derived responses elicited by pure vestibular stimulation with a fixed visual field. To better identify the contributions of the two cues, the following test sequences are proposed:

1. A simple acceleration pulse profile for suprathreshold vestibular stimulation combined with a peripheral visual field which is fixed with respect to the subject.

2. The same vestibular input combined with a counter-rotating or confirming visual field.
3. Again, the same vestibular input, but combined with a constant velocity (with respect to the subject) visual field.

By the use of a center-loaded stick and meter for bidirectional magnitude estimation of perceived yaw velocity, the response histories should allow for the determination of:

(a) a subjective gain curve relating vestibular stimulus amplitude to subjective response amplitudes; and

(b) the approximate time constant(s) of response, inferred by relating the data to a first- (or second-) order dynamic model.

The dependence of these calculated parameters on the visual field velocity and/or on CV indication can then be inferred by comparing the results from the three visual environments presented. The objective here, of course, is to derive a functional model which concisely explains the observed CV modulation by vestibular inputs, and which provides an analytic base for other experimental designs.

One of the primary concerns of the design of this experiment is the fidelity of the subjective velocity responses, and how they are interpreted as indicating true subjective velocity sensation. Specifically, subjective response calibration to a pre-test velocity modulus must be a dynamic process, because of both the equipment's acceleration limits (necessitating a velocity ramp-step rather than a step) and the well-known AC canal transduction properties. However, by use of a short acceleration time (approximately 1 second) and instructions to the effect that the indicator modulus is to be associated with the maximum perceived velocity occurring during the first few seconds, it is felt that response variation due to calibration can be minimized. Variations due to change in memory of the modulus, however, are not as easily controlled, and, in fact, may be inseparable from habituation effects. To combat this, several short runs may be made, each initiated by the modulus (and made known to the subject); or one long run may be made with repeated applications of the modulus (unknown to the subject), so that long term drift in the subjective modulus can be measured. The latter course has been taken in designing current stimulus patterns, primarily to maintain short test sessions. Ordering effects, in which the preceding stimulus affects the current response, may also prove troublesome, especially since it is not obvious how they may be separated from perseveration effects, in which the preceding response affects the current response. However, adequate randomization of the stimulus patterns combined with sequential correlation analysis on a single run should allow for minimization and/or correction of these effects.

Preliminary experimental runs measuring subjective velocity due only to vestibular stimulation are underway, and testing with added visual stimuli will begin shortly. The results obtained so far indicate that considerable response differences occur between subjects, the naive subject tending to indicate in an all-or-nothing fashion, and the practiced subject tending toward a more graded response pattern. It is felt that this is indicative of a perceptual learning process, as the subject becomes more attuned to slight changes in subjective velocity.

3.2 Closed-Loop Velocity Nulling (yaw-axis)

To complement the information derived from the above series, a similar set of runs could be proposed in which the vestibular stimulus, rather than being a simple acceleration pulse profile, consisted of a "pseudo-random" velocity profile generated by summing a number of non-harmonically related sinusoids. By examining the frequency content of the subjective velocity history, the motion sensation process could then be approximated by a linear transfer function, one whose parameters were dependent on the class of visual input (i.e. fixed, counter-rotating, or constant velocity). The approximation accuracy would depend on system non-linearity and would be evident by the magnitudes of the remnant frequencies present in the response signal. An alternative means of interpreting the data would involve the inference of a non-linear gain characteristic from the results of the previous experimental series, coupled with a linear system model, so that the cascaded elements had a frequency response consistent with the results of pseudo-random testing.

Perhaps the most fundamental finding of such an experimental series would be the demonstration of frequency separation effects during the processing of combined visual and vestibular stimulation. That is, a closer look can be given to the conflict model premise that the high-frequency components of the subjective sensation are primarily determined by the vestibular inputs, whereas the low frequency content is determined primarily by the visual field velocity. Although this may be true in certain situations (e.g. when vestibular pulses are superimposed on a constant visual field velocity) a closer examination of its validity may show how the complementary filter approach discussed earlier could be modified to account for some of the response features seen during combined stimulation.

A short pilot study using a pseudo-random vestibular profile in conjunction with a fixed visual field showed that subjective velocity indication was too difficult a task. Results were inconsistent within subjects, and confusion with regard to velocity sensation often led to a more conservative strategy of simply indicating when a pulse was detected. This detection mode behavior thus caused the subjective response history to be a poor indicator of velocity sensation, and this series of open-loop pseudo-random testing was terminated. It should be recognized that had this series yielded more consistent results, it still would have been subject to the magnitude estimation problems mentioned in the previous section, particularly those of calibration and memory.

A less direct method avoids these problems by giving the subject the task of closed loop control over his own (sensed) velocity. Specifically, the subject is requried to maintain at zero the yaw velocity of a platform on which he is seated, by use of a velocity control stick coupled to the platform drive. Loop closure is provided by the subject's own sensation of velocity, which in turn is derived from visual and vestibular cues. To avoid a null response, the pseudo-random signal mentioned above is added to the platform drive signal, so that the subject must perform disturbance compensation throughout the run. This scheme is illustrated in block diagram form in figure 6; the subject is represented similarly, and is indicated by the dashed outline. Visual field environment, generated by the projector, is controlled by the switch shown, which allows for counterrotating, fixed or constant velocity visual field motion.

Changes in the subject's input-output characteristics, as a function of the visual stimulus used, can be obtained by relating platform drive noise to compensatory stick deflection. Assuming that the subject's control strategy is unaffected (see below) then presumably, these changes can be ascribed to changes in perceived self-velocity. For example, by using a constant velocity visual field input, a dynamic estimate of the magnitude of the visually induced motion sensation (CV) can be obtained by low-pass filtering the platform velocity. Such an approach clearly avoids the problems associated with open-loop magnitude estimation procedures. This closed-loop approach can also be used to develop linear models of subject response under various visual environments, so that the question of frequency separation of cues can be examined. Shown in figure 7 is a linear equivalent of the loop, with remnants ignored for simplicity. It assumes that the control strategy C(s) is linear and works on the perceived rate error, generated by another linear block E(s), which represents the motion perception subsystem; the stick is represented by a pure gain and the

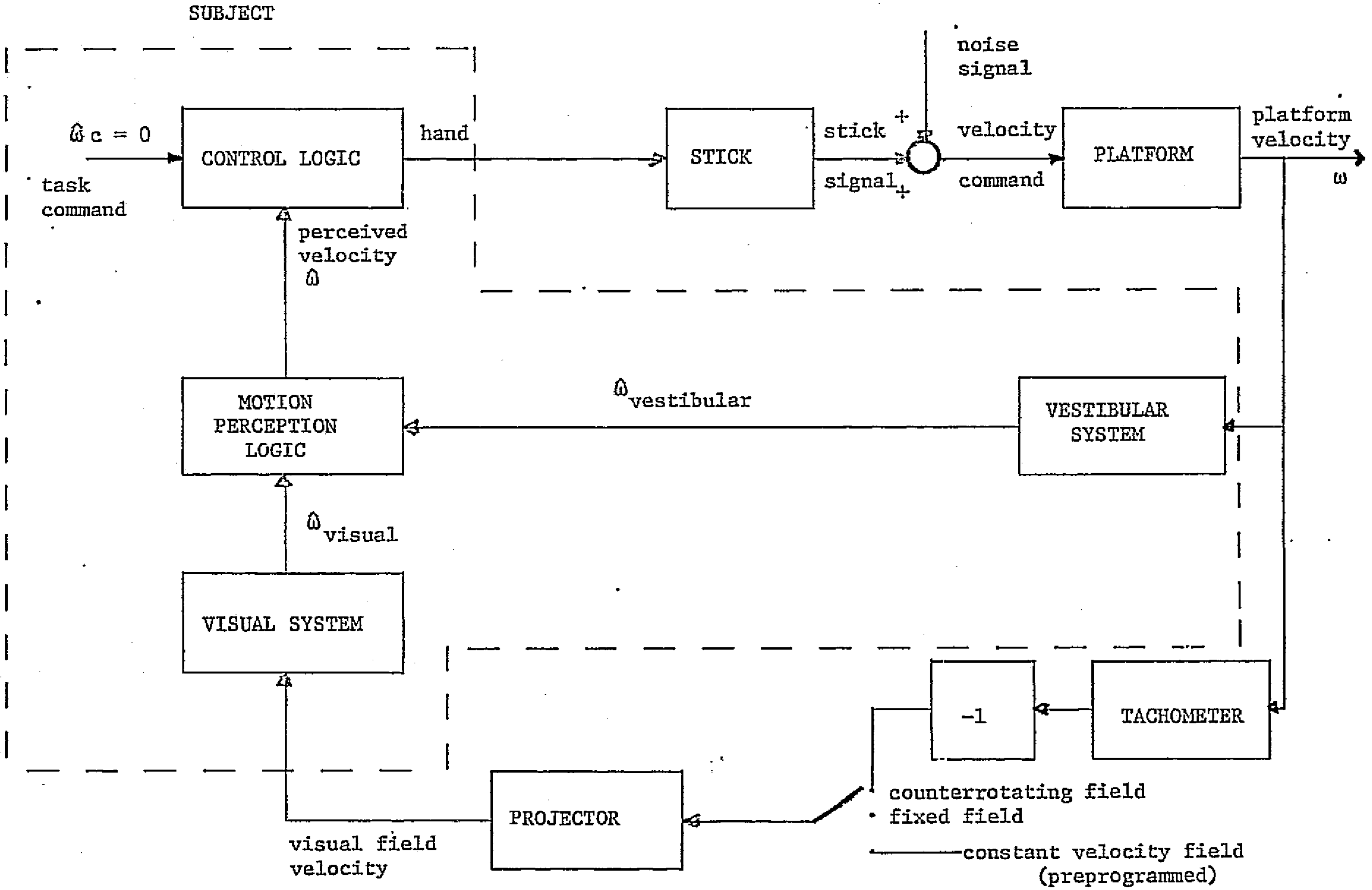


FIGURE 6: Closed Loop Velocity Control (Yaw Axis)

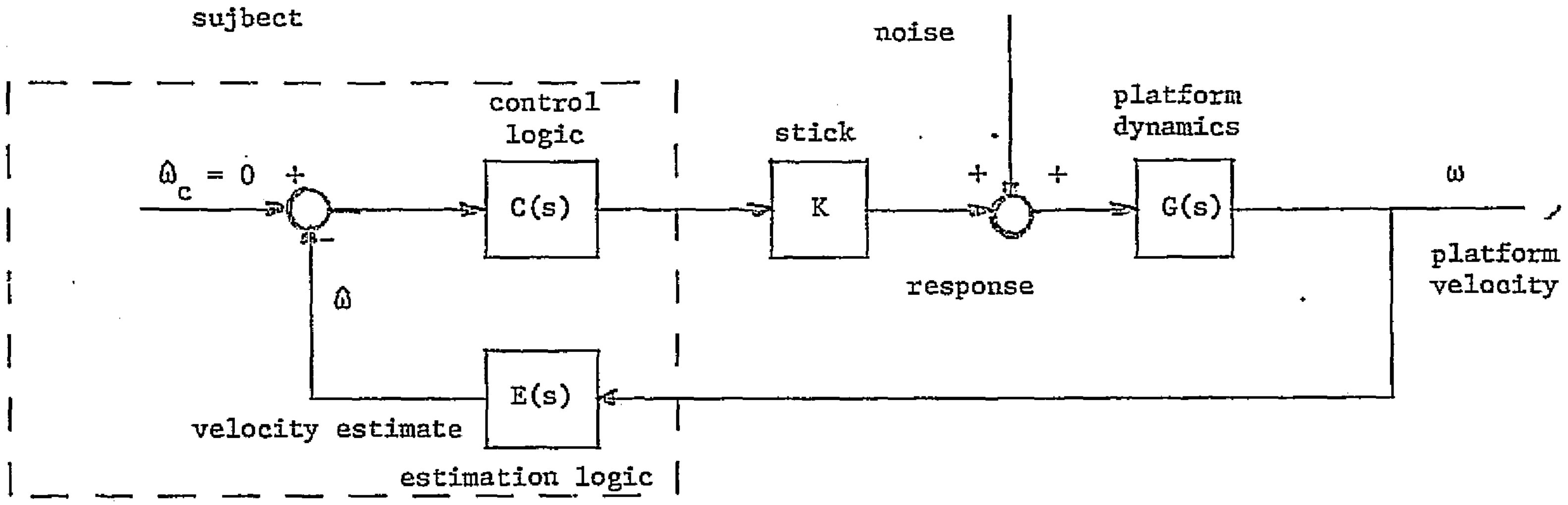


FIGURE 7: Linearized Closed-Loop Model (Yaw Axis)

platform dynamics by G(s). Simple block diagram arithmetic shows that

$$\frac{\omega(s)}{n(s)} = \frac{G(s)}{1 + KG(s)C(s)E(s)} \;\; ; \;\; \frac{r(s)}{n(s)} = \frac{KG(s)C(s)E(s)}{1 + KG(s)C(s)E(s)}$$

so that division of the two relations results in an expression for the subject's linear elements

$$C(s)E(s) = \frac{1[r(s)/n(s)]}{K[\omega(s)/n(s)]}$$

Since the individual transfer functions [r/n] and [ω/n] may be determined experimentally from the Fourier transforms of the recorded histories of r, ω, and n, this relation affords a convenient means by which the cascaded control and estimation functions can be linearly modelled. If the input disturbance n is a pseudo-random signal consisting of summed sinusoids at the discrete frequencies $_{i}$, then the above relation can be reduced to:

$$C(s)E(s) = \frac{1}{K}\left[\frac{r(s)}{\omega(s)}\right]_{\omega_i}$$

where the notation indicates that CE is only computed at the input frequencies, to yield the human estimator/operator describing function.[52] As discussed by Shirley,[52] the operator remnant, responsible for injecting into the loop power at frequencies not present in the input n, can be similarly calculated, so as to arrive at a describing function plus remnant noise model of the subject in the loop.

Although magnitude estimation problems can be avoided in this closed-loop task, it should be clear that this approach is not without its own problems. From the above discussion, it is obvious that, for a single run, control and estimation functions cannot be separated without additional information on subject response. This can be obtained by comparisons of describing functions obtained with differing visual environments; with the presumption of control strategy constancy across the stimulus ensemble, inferred changes in the estimation function can be related to changes in the visual inputs. An alternate approach would be to use one of several human operator models (see for example, Shirley[51]) appropriate to the task, input spectrum bandwidth, and controlled plant dynamics, so that the control portion of the overall describing function can be divided out from the experimental results, thus allowing the estimator function to be inferred. Of course, this assumes that the controller describing function found from human operator response studies is an appropriate model of the subject's control strategy in this experimental series, and that it is not significantly affected by changes in the estimator logic (which might be expected in the face of changes in the visual field cues). Should this problem of separating the effects of control and estimation be successfully overcome in this experimental series, there remain two other potential problems. First, response variations due to learning the task can certainly be expected. Since this probably involves both changes in the control strategy and in estimating self-velocity (due to the subject's becoming more "attuned" to the sensory inputs), the simplest approach may be to allow sufficient pre-run training to ensure that the subject is at a plateau. The second problem concerns the question of possible differences in motion sensation due to active versus passive head (and body) motion, and whether the results of this experimental series can be expected to correlate directly with the open-loop results obtained by subjective velocity measurements. Support for possible differences comes from the findings of Klinke and Schmidt,[33] discussed earlier, which suggest modification of end organ gain in anticipation of self-generated vestibular inputs. Of course, this need not imply a change in perceived velocity at the higher levels, but psychophysical studies do suggest differences due to active versus passive movements. Some of these points are discussed by Young[61] in relating the efferent copy notion to the idea of expected state, and are clearly central to the issue of realistic flight simulator design, and in understanding motion sickness etiology. It suffices to note here that the results of this closed-loop test series may prove to be significantly different from those obtained from open-loop testing.

Preliminary experimental runs measuring nulling performance in the presence of fixed and counterrotating visual fields are currently underway. With a fixed visual field, most subjects allow a subthreshold velocity drift rate to build up, which is on the order of $0.1°/\text{sec}^2$, and is bidirectional across the test population. The presence of this drift obviously supports the notion of frequency separation of inputs, in which velocity perception at low frequencies (in this case, zero frequency) depends heavily on visual input. Those few subjects who performed in a drift-free manner with a fixed visual field may have been using the self-centering properties of the control stick as a cue to zero mean self-velocity (since the noise signal used is zero mean); it may prove appropriate in the future to replace the stick with a smooth knob so as to avoid such cueing. Frequency response curves have been computed for some subjects operating with a counterrotating visual field, and, at the high end of the frequency range of interest (0.5 to 1.0 Hz), there appears to be little difference between these curves and similar curves computed from runs in which the visual field was fixed. Comparison of the curves at low frequencies is yet to be done because additional processing is required to eliminate the drift velocity in the fixed visual field runs, a necessity because of overflow problems with the signal processing software package used. An additional series of runs has recently been completed to verify these preliminary findings and to ensure that stimulus presentation ordering effects are minimized, and to provide internal control for learning effects throughout a run. This series also includes stimuli sequences in which a constant visual field velocity is present, so as to determine the contribution of CV bias to the frequency constant of the subjective response signal. The response histories from this series are currently being analyzed.

3.3 Closed-Loop Position Tracking (Yaw Axis)

To complement the velocity response data obtained from the experiments described above, it would appear appropriate to attempt some quantitative measure of subjective rotatory displacement, as a function of visual and vestibular inputs. At present, the relation between subjective velocity and subjective displacement is not well-defined, although it would appear that an approximate integral relationship between the two exists for a certain class of vestibular inputs. This was shown to be the case for short duration acceleration pulse doublets (i.e., velocity triangles) used in a study by Guedry, et al,[24] in which it was demonstrated that subjective estimates of total displacement were quite accurate. In fact, it was proposed as a method of inferring the vestibular time constants, an alternative to the conventional cuplogram testing which involves subjective estimation of velocity following an acceleration impulse. If this displacement method can be extended to measure subjective response to a more general class of visual and vestibular inputs, it may prove to be an accurate means of inferring subjective velocity, thus allowing for a consistency check on the estimation procedure proposed for open-loop testing.

The advantage of subjective displacement estimation over that of velocity, lies in the fact that neither modulus nor training are necessary for the subject to provide reasonably consistent results. This is made possible by the use of an indicator wheel riding with the subject and whose spin axis is approximately vertical. The subject is asked to perform a null tracking task by maintaining the wheel fixed in the lab frame, by appropriate counterrotation in response to his sensed rotary displacement; the wheel displacement with respect to the platform is then interpreted as the negative of the subject's sensed displacement. This method also has an advantage over the closed-loop velocity nulling task just described, in that the subject is responding to sensations induced by passive head motions; thus, his wheel control strategy should not effect his sensation and the measured response should be a good indicator of perceived displacement (corrections may need to be made for the manual control task of moving the wheel).

It is anticipated that the stimulus patterns for this experimental series will be the same as those used for the subjective velocity measurements: a simple acceleration pulse profile providing vestibular cues in conjunction with a fixed, counterrotating, or constant velocity visual field. The wheel displacement history can be differentiated to yield an estimate of subjective velocity, which, in turn, can be used for estimating the subjective gain curve and the response time constants, in the manner suggested for processing the subjective velocity data of the first experimental series. Should differentiation prove too noisy, an alternative approach would be to analytically model subjective displacement as a simple integration of subjective velocity, and use the response history directly to infer dynamic parameters and gain characteristics. This information can then be used to infer parameter dependence on visual field environment, as in the previous two series.

Preliminary runs have been made to check out the suitability of the wheel design for convenient response indication, although no detailed response studies have been conducted to date.

3.4 CV Adaptation Measurement (Yaw Axis)

It was noted earlier that long term adaptation of fore-aft LV response has been observed, although a corresponding adaptation of yaw CV has not. The purpose of this short series is to determine if such behavior is indeed present, and if so, measure and model it. The proposed approach is the same as that used by Berthoz, Pavard and Young[2] in their LV study, in which the subject assumes control of the visual field velocity once CV is induced with a constant field velocity. With the task of maintaining constant CV, any observed increase in field velocity can be interpreted as a long-term decreasing effectiveness of the visual field in inducing motion sensation, and thus may be modelled as response adaptation.

As in the closed-loop velocity nulling experiment, the measurement proposed here avoids many to the problems associated with open-loop magnitude estimation, but does require the assumption of memory constancy; that is, adaptation effects cannot be separated from a growth of the remembered initial sensation which is the set-point for the subject's closed-loop control of CV. Whether this is functionally significant is not clear at present, although it may motivate the use of pre- and post-run open-loop subjective estimates as controls.

3.5 Visual Field Velocity Estimation (Yaw Axis)

A simple view of visual field influence on motion sensation is based on the assumption that perceived visual field velocity is the "visual" input to the functional block devoted to generating motion sensation. It thus seems appropriate to measure the subject's estimate of the visual field velocity, as a function of the actual field velocity. This can be done by having the subject provide magnitude estimations of visual field velocity, in response to relatively short velocity pulses of the visual field. The large acceleration involved in a pulse will preclude any fast onset of motion sensation (due to conflict with null vestibular signals), while the shortness of the pulse (a few seconds) will not allow for CV onset.

As the experiment is currently conducted, the visual field is entirely peripheral and rotates in yaw about the vertical. The subject makes verbal magnitude estimates of perceived visual field velocity using a numerical scale tied to a velocity modulus presented repeatedly at the beginning of a run,[46] and is instructed to fixate on a point directly forward. Fixation is used as a control to minimize response variance across the population, since Dichgans, Korner, and Voigt[13] showed a dependence of subjective velocity estimates of the visual field on eye velocity. The primary output of this experiment is a power curve relating input magnitude to subjective output magnitude, although additional data processing may prove capable of revealing directional preponderances and/or sequential effects (i.e. memory variation, perseverance effects, and neighboring stimulus influence). The power curve can then be incorporated into the overall functional model, and may help explain some of the observed response non-linearities during simultaneous cue presentation.

It may prove worthwhile to extend this experiment to determine the dependence, if any, of subjective field velocity on either vestibular inputs or motion sensation. The possibility of vestibular dependence is motivated by the fore-aft LV findings discussed earlier, in which vestibular pulses often led to an apparent stoppage of a constant velocity visual field; looking for a perceived field velocity dependence on motion sensation is motivated by the previously-mentioned feedback model, in which sensory cues are processed according to perceived state. One method of measuring this dependence would consist of rotating the platform with the same simple acceleration pulse profile used in the subjective velocity estimation runs mentioned earlier, and requesting the subject to estimate visual field velocity. Should the resulting power curve prove to be significantly different from the one obtained during fixed platform testing, it may then prove possible to model a cross-coupling block which functionally relates changes in perceived field velocity to vestibular inputs, or to motion sensation. This latter dependence could be inferred from the subject's subjective velocity estimates in response to the same acceleration pulse profile presented during previous subjective velocity testing. Of course, such modelling may prove to be complicated by the subject's inability to completely suppress vestibularly-induced eye movements (by attempting to fixate), and thus may necessitate the use of eye movement monitoring equipment during testing. In this way, responses associated with nystagmoid motion can either be eliminated during data processing, or an attempt can be made to adjust the responses according to one of several models of perceived visual field velocity (see, for instance Yasui and Young[58]).

This experimental series is currently underway, a visual field velocity pulse sequence having been designed and several fixed platform runs having been conducted. Current effort is directed toward a regression analysis of the log-transformed estimates to arrive at a power curve for the test population. Moving base runs will be delayed until more data become available from the subjective velocity measurements using simple acceleration pulse profiles.

3.6 Roll-Axis Studies

This section only briefly discusses proposed roll-axis experiments as it is felt that a better definition should await the results obtained in yaw, to take advantage of the experience gained in experimental procedure. This brevity is also justified by the fact that most of the proposed roll experiments are direct analogs of those already discussed for yaw, so that many of the procedures and possible problems are similar, and need not be repeated.

3.6.1 Subjective Tilt Measurement (Roll Axis)

The object of this series is to investigate the effects of vestibular inputs on visually-induced roll tilt, by use of a roll velocity pulse profile in conjunction with various visual field environments, in a manner completely analogous to that used for subjective velocity testing in yaw (see section 3.1); here, however the stick is to be used to indicate perceived tilt from the vertical. Basically, this is an extension of the static tilt tests reported on earlier[11,70,71] with the object of determining how dynamic changes in actual tilt angle are reflected in the sensation, as a function of the visual field. This will be accomplished by inferring static gain curves and first- or second-order time constants from the observed data, to arrive at a functional model. The same problems of subjective estimation are anticipated as in the corresponding yaw experiment.

3.6.2 Closed-Loop Attitude Nulling (Roll Axis)

The roll analog of maintaining zero yaw velocity is the task of maintaining the upright, and it is proposed that such a series be conducted to investigate the frequency dependence of roll tilt sensation on visual and vestibular cues. The experimental procedure and analysis techniques described earlier (section 3.2) are applicable here, as are the comments regarding possible pitfalls in interpreting the data. It is anticipated that an additional problem may be encountered in this experiment due to possible changes in the subject's "operating point" due to incurring large tilt angles during a run; since the linear analysis requires fixed-point operation, the experimental design must preclude large deviations from the vertical and ensure zero-mean tilt error.

3.6.3 Closed-Loop Vertical Tracking (Roll Axis)

This series requires the subject to indicate the perceived vertical by giving him the task of space-stabilizing a vertical bar in the presence of roll acceleration pulses and differing visual environments. This may prove to be the simplest and most reliable measure of tilt sensation, and should provide a good check on the results obtained in the first proposed roll series utilizing magnitude estimates. The primary caution here is that indicator bar placement will be dependent on ocular torsion as in conventional roll CV measurements, and it may prove necessary to correct the data for this, necessitating an additional series of measurements devoted to measuring torsional displacements. This subjective tilt measurement technique is currently being used at the MVL in another experiment, and it is anticipated that some of the hardware, procedures and results will be directly applicable to this study.

3.6.4 CV Dynamics Measurement (Roll Axis)

It was noted earlier that the response parameters of roll CV are relatively poorly-defined in comparison to those for yaw. The object of this series is to look more closely at roll CV dynamics with the goal of specifying latency and rise-time dependence on field velocity and static head tilt, so as to provide a data base for the eventual modelling of visually induced tilt sensation. A secondary objective will be to look for adaptation effects, analogous to those seen in fore-aft LV.

3.6.5 Visual Field Velocity Estimation (Roll Axis)

It is proposed that visual field velocity estimation studies be conducted in roll as in yaw, with the object of uncovering any dependence on either vestibular input (roll velocity or tilt) or perceived tilt. The same experimental procedure is suggested as in yaw, with the results directed similarly toward a functional model of vestibular-into-visual coupling.

3.7 Pitch Axis Studies

At this time, it is suggested that the research into pitch axis subjective tilt sensation follow along the same lines as that proposed for the roll axis study. Specifically, it is proposed that the pitch axis experiments include: a) magnitude estimates of subjective tilt in response to combined visual and vestibular stimulation; b) closed-loop maintenance of the vertical in the face of vestibular "noise" and differing visual field environments; c) indication of the vertical in the face of combined stimulation; d) dynamic magnitude estimates of visually-induced pitch tilt; and e) estimates of visual field angular velocity about the pitch axis. It is anticipated that the roll axis findings will influence this list, and suggest the elimination of some tests and/or the addition of others, and thus a detailed description of the proposed pitch axis experiments is not appropriate here.

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Rearrangement of Vestibulo-Ocular Reflex *

This portion of our research is concerned with the investigation of the extent to which neural mechanisms associated with the vestibulo-ocular reflex are sufficiently plastic so that normal reflex patterns may be rearranged to be appropriate for altered visual-vestibular environments. In particular, we will alter the visual field of a Rhesus monkey by employing Dove prisms mounted at a 45° angle in front of the monkey's eyes to shift the visual scene by 90°. We will then assess the development of changes in the reflex pattern. In the new visual environment, the normal reflex response of the vestibulo-ocular loop will be totally inappropriate for image stabilization.

Any neural rearrangement present will be investigated under two conditions: vestibular input and visual input. More explicitly, this means:

(1) testing for the development of "orthogonal nystagmus" (vertical eye movements as a result of horizontal head movements in the dark, and vice versa) following continuous visual wide field stimulation with prisms attached, and

(2) testing eye movements resulting from optokinetic stimulation with prisms attached.

The ability of the monkey to maintain an image in space under normal circumstances is measured by the vestibulo-ocular

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Performed by Judy Shaffer, S.M. Candidate, with L.R. Young reflex gain which is the ratio between the slow phase velocity of nystagmus and the angular velocity of rotation in space. Calculation of the gain for both horizontal and vertical eye movements prior to attachment of the prisms and while the prisms are mounted to the monkey will indicate if a rearrangement has occurred and provide some indication of magnitude.

Preparation of Rhesus Monkey

The monkey has been trained to fixate a visual target to enable eye movement calibration. The apparatus used to train the monkey consisted of two single plane multiple projection readout displays. Each display sequences through four images. The four images consist of a *delay* during which there is no image, a *blank* during which the photocell is on, and a *horizontal* during which the photocell is on and a dark horizontal line is superimposed, and lastly, a *vertical* during which the light is on and a vertical bar is superimposed on the photocell. The monkey is trained to fixate on the displays and to press a bar when the vertical image is being displayed. The two displays are activated pseudorandomly, and the monkey is rewarded with a drop of water when he correctly presses the bar when the vertical image is being displayed. In this manner, the monkey is trained to fixate a target and to make distinct eye movements.

Four skull screws were implanted to allow attachment of the prism holder and head holder. A prototype for the mask to surround the prisms and limit the visual field of the monkey to the 90° displacement has been constructed from a thermoplastic material. A reshaping of the mask to fit the specific contours of the head of the monkey is required but the thermoplastic appears to be a suitable material.

In addition, throughout the rotation experiments, the eyes of the monkey will be covered with black felt to ensure total darkness. In order to allow for control of the effects of changes in corneoretinal potential with time in the dark, 20 minutes of dark adaptation will be allowed as nystagmus amplitude is a variable of interest.

Both vertical and horizontal eye electrodes were implanted, tested and found to be functional. Modifications of existing equipment used to hold the head stationary were completed and tested, and it was found that a slight pitching motion of the head was still possible. An additional support will be needed for absolute constraint of the head.

Apparatus

The chairholder has been designed, constructed and mounted on the top of the rotation table. The plastic chair which restrains the monkey is then slid into the chairholder and secured for recordings from stimulation of the horizontal canals. Although the table is capable of rotating 90° to stimulate the vertical canals, this would also cause stimulation of the otoliths. To circumvent this, the monkey will be placed on its side and the table again rotated in the horizontal plane. To maintain the monkey on its side, a metal sheet is bolted to the side of the plastic chair and this is secured to the chairholder. High density foam has been purchased to alleviate pressure points on the monkey.

A dual channel amplifier with its own DC power supply has been built and mounted on the table. In this way, only AC need be provided through the slip rings.

The last major piece of equipment still to be completed is the calibration board. Initially, we were prepared to utilize nine of the multiple projection readout displays. However, the high cost of such displays led us to look for an alternative piece of hardware. It was decided to attempt to simulate the delay, blank, horizontal, and vertical sequence using dot matrix LEDs. During the delay, the LED will be off. The blank will correspond to a 5 x 5 lighted matrix. The horizontal and vertical bars will be simulated by turning off the center horizontal row and center vertical row, respectively.

If the monkey learns to respond to the LEDs in the same manner as he responds to the readout displays, not only will the cost be cut by 80%, but the calibration board will be several factors more compact, lightweight and portable.

The LEDs will be mounted such that the distance between each of the lights corresponds to 10° of eye movement. The power needed to operate each light will be supplied via a 10 position rotary switch. In this manner, the lights will be manually sequenced through a specific protocol. One of the plates of the rotary switch will be used to produce a voltage indicative of the particular calibration light being currently addressed. This will be accomplished via a series of voltage divisions. Thus, a permanent record of the calibration points with respect to time will be available.

Calibration Theory

The design of an adequate calibration procedure is extremely important as data analysis can at most be as accurate as the calibrations. For this reason, a 9-point calibration procedure is used. The calibration procedure begins with the center light cycling through delay, blank, horizontal and vertical. When the monkey presses the bar and receives the reqard, the experimenter is fairly sure the monkey has fixated the proper target and advances the rotary switch to activate the next position in the 9 point matrix. This continues until all nine points have been sequenced. In addition, a final return to the center position determines if the point of gaze of the monkey returns exactly to the initial coordinates. Immediate duplication of the calibration scheme determines the reproducibility of the matrix.

Using a 10 position rotary switch to successively actuate each of the nine calibration lights provides the flexibility that allows the experimenter to remain at any light until the monkey has successfully fixated.

A nine point array has been tested on humans (Buchsbaum et al, 1973) and a typical calibration run appears as shown in the figure. The open circles indicate the coordinates of the lights. The small dots indicate the coordinates of the actual measured eye movement recordings.

The reason for using a 9 point matrix as opposed to the 5 points which could calibrate horizontal and vertical data is the theory that horizontal and vertical eye movements are coupled. The above data appears to support this. Thus, in order to analyze the EOG data from an experimental run, the two recordings must first be decoupled. This is essential as we are interested in seeing if after the prisms are worn, horizontal nystagmus becomes vertical nystagmus, and the converse. To accomplish this, it is important to isolate horizontal data independent of the influences of the vertical component (similarly, vertical data must also be isolated).

The initial assumption is

$$x_m = f(x_T, y_T)$$

$$y_m = g(x_T, y_T)$$

where m indicates the measured voltages and T the true voltages. Assuming a first order functional relationship,

$$x_m = K_1 x_T + x_0 + K_2 y_T + y_0$$

$$y_m = K_3 x_T + x_0' + K_4 y_T + y_0'$$

By adjusting the balance on the amplifiers and subtracting any dc components in the software, we can force

$$x_0 = y_0 = x_0' = y_0' = 0$$

leaving only

$$x_m = K_1 x_T + K_2 y_T$$
$$y_m = K_3 x_T + K_4 y_T$$

Using a least squares technique, we can determine estimates for the [K].

In order to reduce the error in our estimate of [K], we use the 9 points to form 4 quadrants. We can thus estimate four K matrices. Prior to the raw data being analyzed, it will initially pass through a software routine to assign the digitized raw data point to its appropriate quadrant. The raw data then gets multiplied by $[K]^{-1}$ for that particular quadrant and is therefore decoupled.

Software

The software for the calibrations consists of two processes. Initially, a program written in assembly language for our PDP-8 accepts the horizontal and vertical eye movement calibration voltages from FM tape after being digitized at a rate of 80 samples per second. An ideal set of calibration recordings would look like that shown in the figure.

However, even using a trained monkey, we expect that the actual recording will deviate a great deal. As such, the software was developed such that a variable size window is established for the -10°, 0°, 10° marks. In this way, those positions at 0° ± x° will correspond to an eye position of 0° and will be considered acceptable samples. The first 64 acceptable samples are stored and averaged. The 18 resulting averaged values are then used as input to the decoupling routine. Presently, the decoupling routine is written in Fortran and the four 2 x 2 gain matrices printed off line. These values would then be manually placed in the core of the PDP-8 and utilized during the actual data analysis.

Data from the experimental runs is initially A/D converted and each sample is assigned to its proper quadrant formed by the 9 calibration points. After being assigned to a quadrant, the measured x and y values are multiplied by the appropriate gain matrix and the resulting decoupled x and y values are used as input to MITNYS II.

It is anticipated that this work will be completed through the calibration of monkey eye movements by the end of June.

TRANSDUCTION MECHANISMS IN SEMICIRCULAR CANAL ORGANS* **

During the past two summers, Professors Oman and Frishkopf have worked at the Marine Biological Laboratory, in collaboration with Professor M.H. Goldstein of Johns Hopkins University. The goal of this work initially was to study the relationship between cupula motion and neural output in the semicircular canals of the skate, *Raja erinacea*. The research dealt with four issues:

a. cupula motion under physiological stimulus conditions
b. origins of adaptation
c. pharmacology of the afferent and efferent synapses
d. effect of Ca^{++} and Mg^{++} concentrations in Ringer's solution.

Methods

Studies were carried out on the semicircular canal in the excised ear of the skate. The horizontal and anterior ampullary nerves and portions of the canals were exposed and dissected nerve twigs raised on a platinum-iridium electrode. The ear was kept immersed in a Ringer's solution throughout

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*Performed by Professors L.S. Frishkopf and C.M. Oman.

the entire dissection and experiment to minimize trauma to the membranous labyrinth. Nerve spikes were readily recorded in this way and the preparation responded to a variety of mechanical stimuli. Single or multiple unit spikes were selected by means of a window discriminator. Pulse rates of spikes within the window were monitored and displayed continuously on a Brush 2 channel chart recorder. Raw spike data, discriminator output pulses and pulse rate were recorded on a multichannel FM tape recorder for further analysis. In recent experiments, analysis and display of pulse data has been carried out on-line by our computer.

A number of techniques have been developed to observe and control the motion of the cupula. During our first summer (1974) at Woods Hole, we succeeded in directly driving the cupula hydraulically through a cannula inserted into the severed end of a horizontal canal duct. We attempted to improve upon the techniques described by Dohlman (1938) and Flock and Goldstein (1973) by avoiding procedures which would impose a pressure difference across the ampulla. The cannula was filled with Alcian blue dy in simulated endolymph. Gently injecting the dye through the cannula allowed us to observe the cupula through a dissecting microscope. The cannula was connected to a microliter syringe, which was in turn driven by a modified loudspeaker coil. Electronic position feedback of syringe pluger position was used so that precise volumetric changes from 0.001 to 0.1 μl could be made. Although very precise cupula movements of sinusoidal, step, or truncated ramp waveform could be generated in this way, we became concerned about the possible traumatic effects on the cupula and crista of cutting and cannulating the canal. Monitoring the nerve response during the cutting and cannulating procedures showed large changes in afferent response. After the canal was cut, both spontaneous and evoked activity usually deteriorated rapidly. We experimented with a number of alternative techniques for severing or making a window in the canal duct, including electrocautery, without achieving substantial improvement in the results.

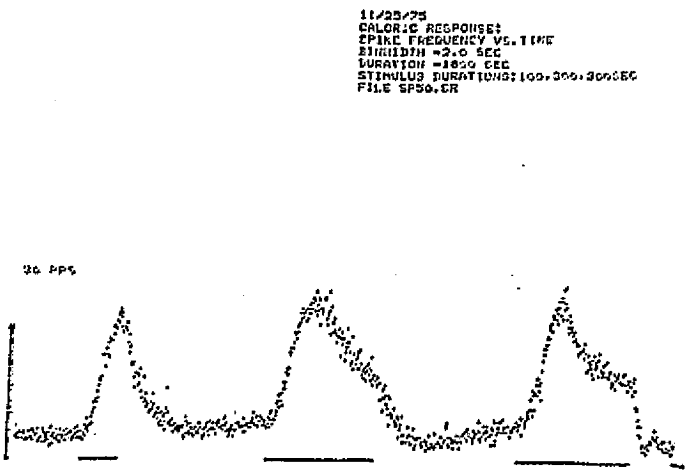
Eventually, however, we were able to bypass this problem by a second method of stimulation which required neither cutting the canal nor rotating the labyrinth. This consisted of focussing a small spot of light on the canal or ampulla, thereby producing a caloric response. The response was determined to be caloric (i.e. due to forces on the cupula generated by temperature induced changes in endolymph density) in that no response resulted when the canal torus was in a horizontal plane, and that excitation or inhibition of afferent nerve activity could be consistently produced depending on whether the light was focussed on the canal or utricular side of the ampulla. In experiments where visualization of the cupula was desired, a small puncture was made through the wall of the ampulla with a sharpened (10-20 μm tip diameter) double pipette filled on one side with Alcion blue dye in skate endolymph. The cupula was visualized by

C.2

slowly infusing a small amount of this fluid while monitoring activity in the nerve. In attempting to puncture the wall of the ampulla, we found that the wall displaced as the pipette was pushed against it. We have also attempted to use Collagenase to help penetrate the wall with only erratic success. Recently a method has been developed of pulling the ampulla onto the pipette which works with great consistency. This procedure causes a moderate transient change in activity, after which activity usually returns to prepenetration levels. In successful preparations, the caloric response before and after penetration and dye infusion is found to be within what we have observed to be the normal range of variation in the intact preparation. We conclude that under favorable circumstances--which can be evaluated in each preparation--these procedures leave the sensitivity of the canal to caloric stimuli essentially unaltered. The problems associated with cutting the canal, apparently the result of cupula damage, do not appear to occur in this method.

Caloric Response and Observation of Cupula Motion

After the stimulus light is turned on, a typical excitatory caloric response may start ten to fifteen seconds later, reach a peak frequency at sixty to one hundred seconds, and then gradually decline to some constant adapted level--in many cases above the spontaneous level. After the light is



Caloric responses obtained from the horizontal semicircular canal of the skate Raja erinacea to successive illumination stimuli. Multi-unit activity is recorded, and is counted in 2.0 sec. bins. The display shows spike frequency as a function of time over a period of 30 minutes. The height of the calibrating bar at left represents 30 pulses/sec. The horizontal bars at the bottom indicate the intervals of illumination (100,300,300 sec.) Note the marked adaptation and undershoot that occur in response to the longer stimuli.

turned off, the response declines rapidly and often undershoots the prestimulus spontaneous level, as shown in the figure. Return to resting activity may require several hundred seconds. As shown in the figure, successive identical caloric stimuli, presented at sufficiently long intervals to permit recovery, produce very similar responses. Increasing the intensity or size of the light spot increases the magnitude of the response. Most experiments thus far have been run using excitatory stimuli because of the relatively low level of spontaneous activity (10-20 spikes/second) present in the skate and the existence of silent units.

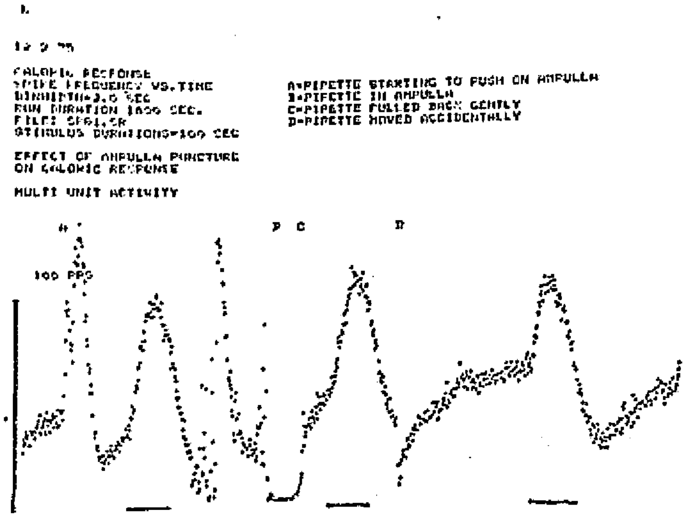
By applying caloric stimuli while recording afferent activity, we are able to examine the dynamics associated with the system comprising the closed canal, cupula, crista, and afferent nerve fibers. We found that although the small density differences produced by heating the canal endolymph stimulated afferent units in a repeatable way, differences in the dynamics of the responses of individual units were observed. Some units were found to be tonic in their response characteristics while other units in the same preparation appeared phasic. Phasic units often had higher thresholds. These variations in dynamics appear consistent with similar findings obtained by other investigators for response to angular acceleration in the semicircular canals of other animals. The absence of adaptation in some units strongly suggests that cupula displacement as a result of caloric stimulation is statically maintained.

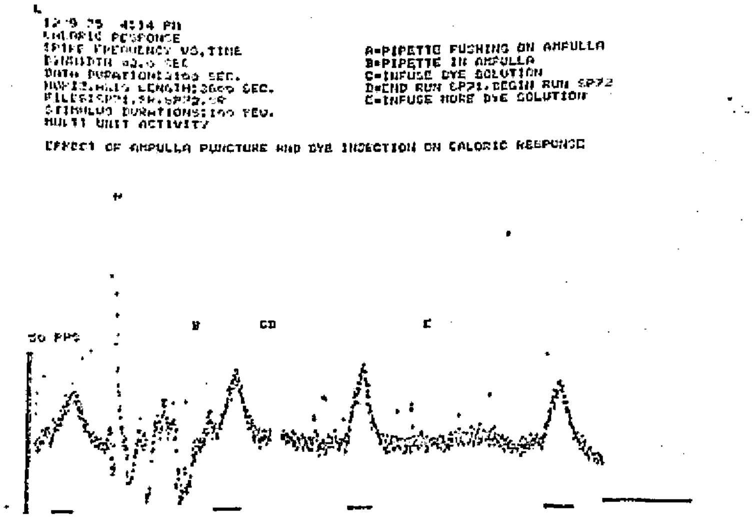
Very different observations of cupula motion and response sensitivity have been obtained using the two different approaches to cupula visualization described above.

In the case when the canal was cut and the cannula inserted, the cupula was seen to deflect visibly in the fashion of a swinging door, apparently free of attachment at the vault of the ampulla. This is much the same as the classical picture described by Steinhausen (1927) and Dohlman (1938). In favorable cases, threshold response as judged by visual and auditory criteria of change in nerve activity occurred for fluid injections of 0.01 - 0.1 μl, corresponding to a deflection at the center of the cupula of 4 - 40 μm. In favorable cases, hydraulic stimuli could then cause deflections so large that dye was seen to leak across the barrier. In unfavorable preparations (or under extreme stimuli) the cupula was seen to be torn or entirely missing. Even in favorable cases, the sensitivity and spontaneous activity usually deteriorated soon after cannulation.

A very different picture emerged from experiments in which the ampulla was punctured and the canal calorically stimulated. The preparation was extremely stable; repeatable caloric responses to identical stimuli were obtained over many successive stimulus presentations. Comparison of the nerve response to a constant caloric stimulus before and after puncture of the ampulla and before and after dye injection allowed us to assess the effect of these procedures on the sensitivity of the system. Large changes in response presumably indicate a significant change in the preparation. This approach provides a sensitive control on the effects of our procedures. Comparison of the caloric responses to identical stimuli before, during and after dye injection are shown in the figure. Data of this type lead us to believe that in such cases, the cupula deflects in a very similar way before and after puncture and dye infusion. Also in such cases no cupula motion has been seen at the highest resolution we have been able to obtain, with caloric stimuli which result in doubling or tripling the rate of firing in the nerve. We estimate this resolution limit with present optical techniques at 3-5 μm. The region of cupula best seen in the horizontal canal is where it meets the roof of the ampulla. We are in this case looking at the cupula in profile through the wall of the ampulla. In several instances it has been possible to see a point near the center of the cupula and again we have observed no cupula motion. However, if we infuse dye rapidly, we have, on occasion seen a sudden displacement of the cupula in the attachment region.

Thereafter, caloric stimuli identical to those that earlier produced no visible cupula displacement now cause the cupula to deflect up to 20 μm in the region of the roof of the ampulla. Our conclusion from these observations is that normally the cupula moves very little even when strongly stimulated calorically. It appears, however, that rapid





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OF POOR QUALITY

Caloric responses obtained in the horizontal semicircular canal of the skate to successive 100 second illumination stimuli The two displays represent the results of different experiments in which the ampulla was punctured with a pipette filled with Alcian blue dye (1.0%) in simulated skate endolymph. Responses to caloric stimuli before and after puncture (marked "B" in both photographs) and before and after dye infusion ("C" and "E" in lower photograph) are substantially the same. Touching the ampulla ("A") results in a large response. Note that response is erratic before "B" due to attempts to puncture ampulla (see insets for details).

infusion of fluid into the canal can cause wiper motion of the cupula along the ampulla vault. Thereafter, identical caloric stimuli produce visible wiper motion in our experiment, indicating that an associated reduction in the cupula stiffness has occurred. We suggest therefore that normally the skate's cupula is functionally adherent to the roof of the ampulla and only by traumatic breaking of this attachment does the classical swinging door action become possible. Further, if the cupula moves at its center or bottom in response to caloric stimuli, movements are less than 5 μm in amplitude. This is consistent with the model of Oman and Young (1972) who on theoretical grounds suggested that for the human, the range of normal cupula motions, whatever their mode, angular or linear or both, lies between 10^{-2} and 3 μm. A paper describing these results is in preparation.

Pharmacology

Recently it has been proposed that GABA is the transmitter in hair cell afferent synapses (Flock and Lam, 1974). These investigators base this hypothesis on their finding of GABA synthesis in a variety of hair cell organs and on the physiological findings of Flock and Goldstein (see Flock and Lam, 1974) that in the cut and cannulated semicircular canal of the skate, picrotoxin, a known specific antagonist of GABA at inhibitory synapses, blocked spontaneous and evoked afferent activity when perfused onto the base of the ampulla in concentrations of from 5 x 10^{-5} to 10^{-6}M, reversibly in some cases. In an attempt to repeat these experiments in our closed canal preparation, we applied picrotoxin to the ampullary nerve during a series of repeated caloric stimuli. Picrotoxin dripped onto the ampulla and nerve, or applied in the bath, was ineffective in reducing either spontaneous or evoked activity in concentrations from 10^{-6} to 10^{-3} M. Thus our data do not support the hypothesis that GABA is the afferent transmitter. This finding is consistent with recent results of Sand et al (1975) in lateral line organs. We also attempted to establish acetylcholine as the efferent (inhibitory) transmitter in this preparation. A variety of paradigms based on the known pharmacology of cholinergic synapses were employed in an attempt to establish an inhibitory action of ACH (and ACH analogs) by direct application of these drugs in the presence of an anticholinesterase, and to block these effects with curare and atropine (Russell, 1971). These experiments were equivocal; although some effects were observed, we were unable to reproduce them consistently. Presumably ACH is the efferent transmitter here as in other hair cell systems. Our inability to obtain repeatable effects suggests that insufficient quantities of these drugs are reaching the hair cell-efferent synapse. This may imply that a barrier to diffusion of large ions occurs in this system. The same barrier could prevent picrotoxin from reaching the hair cell-afferent synapse. Thus we may have shown that this system is not suitable for experiments which depend for their effect on large molecules reaching the synapse. Small ions such as Ca^{++} and Mg^{++} may be expected to pass through and effects on spontaneous activity of changes of concentration of these ions have been observed. However, an experiment in which we attempted to facilitate the release of ACH from the presynaptic terminals by shifting from low to high Ca^{++} concentration was also inconclusive. One could argue that the effect of spontaneous release of ACH in this procedure might be too small to achieve an observable effect. Electrical stimulation of efferent fibers would permit more definitive experiments of this type, however.

Developing An Improved Ringer's Solution: Effects of Ca^{++} and Mg^{++} Concentrations

We have developed a skate Ringer solution based on findings in the literature and the results of our own electron probe microanalysis of skate endolymph and perilymph (Peterson et al, in preparation) which permits us to work on the isolated ear of the skate for up to 24 hours. This represents a great improvement over the results we obtained initially using MBL skate Ringer (Marine Biological Laboratory, 1974) in which the spontaneous activity disappeared after 2-4 hours. The key discovery was that the longevity of the preparation was extremely sensitive to the concentrations of Ca^{++} and Mg^{++}.

Reducing these from 5.0 and 2.3 mM to 3.3 and 1.2 mM, respectively, produced the stability change in the preparation noted above.

Presumably these concentration changes in the external medium would reach the hair cell-neuron synapses but, due to tight junctions at the lumenal surface, would not reach the apical ends of the hair cells. We expect therefore that this finding has implications for our understanding of hair cell synaptic mechanisms.

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VISUAL INFLUENCES ON VESTIBULAR NEURONS IN THE BRAINSTEM

Volker Henn and Laurence Young

Presented at the Ninth Annual Center for Visual Science Conference on Eye Movements and Motion Perception, May 29, 1975, Univesity of Rochester.

This review is concerned with visual influences on vestibular neurons in the brainstem, i.e. mostly second order vestibular neurons. This requires knowledge about characteristics of these neurons during pure vestibular stimulation, i.e. turning the animal in the dark. The question then arises: how is this activity modified if visual stimuli are given together or without the vestibular stimuli. Then it is necessary to interpret the results. Suggestions given so far relate this phenomenon to the detection of self-motion or link it to eye and head movements.

In 1957, Duensing and Schaefer reported neurons in the vestibular nuclei which changed their activity with each quick eye movement or whose freqeuncy was related to eye position. Such units were also found in all other species investigated. This type of unit will not be considered in the present context, because these units seem to be related more closely to oculomotor output. Visual stimuli have an indirect influence on these units only as far as they induce eye movements. Fuchs and Keller and Miles reported about such units in monkeys; our data largely confirms their findings.

The first clear evidence that vestibular neurons can specifically be influenced by moving visual stimuli came from Klinke and Schmidt. In 1970, they reported about recordings from afferent vestibular fibers from horizontal canals in the relaxed goldfish. The spontaneous activity was depressed during the whole field optokinetic stimulation when the stripes moved temporally; it was increased when the stripes moved nasally.

During the last few years, several groups have independently investigated central vestibular neurons using similar approaches. Recently Allum and coworkers provided quantitative data from the relaxed goldfish. The animal is turned in the dark; the activity of a particular vestibular neuron (which was very probably a second order vestibular nueron) first increased during acceleration, then fell to a steady level during constant velocity rotation, and was inhibited during deceleration. When the stationary animal is exposed to optokinetic stimulation in the opposite direction, this unit increases its activity. If the animal is turned in the light before a stationary background, with the same velocity profile, a similar increase in unit activity as during acceleration in the dark is obtained, but unit activity remains almost constant and is more or less proportional to actual velocity. Results which are qualitatively similar have beel recently reported by Azzena, Azzena and Marini using the guinea pig.

We have been doing similar experiments in our lab using alert monkeys. Rhesus monkeys were chronically prepared with DC electrodes implanted around their eyes and a plug for the micromanipulator. During experiments, the head was positioned 25 degrees down, so that the horizontal semicircular canals were actually horizontal. In more recent experiments, strain gauges were attached to the head holder which allowed measurement of head torque. Monkeys could be turned in complete darkness or a drum totally enclosing the monkey could be turned. In earlier experiments, moving stripes were projected onto a screen in front of the monkeys. In both cases, the aim was to have almost all of the visual field moving including the periphery. In humans, this very quickly induces the sensation of circularvection, even if parts of the visual field are stationary relative to the observer.

Single units were recorded from the vestibular nucleus comples, mostly from the rostral pole of the medial nucleus and adjacent regions. All recording sites were checked histologically.

35 units from 4 animals showed a clear increase to rotation in the ipsilateral or contralateral direction, type I and type II units in the literature. Activity of these units was not correlated with eye movements. By their location and physiological characteristics, they were believed to be neurons cerebral to first order vestibular neurons.

To summarize our findings: In more than 90% of the 35 units investigated, clear and consistent visual effects upon vestibular unit activity could be shown. The change in vestibular unit activity was not causally related to nystagmus, nor could a consistent relationship to head torque be established. The modulation of unit activity during motion of the environment was usually much less than during turning of the animal in the dark with similar velocities. Also the visually induced activation or inhibition usually took 10 to 20 seconds to reach maximum.

During sinusoidal turning, lights on tended to reduce phase angle and tended to increase values for amplitdue relationships. During stepwise turning in the light, unit activity more closely reflected velocity than acceleration. Acceleration and deceleration from opposite directions induced the same unit activity in the dark, but completely different behavior in the light. Preliminary more quantitative analyses suggest a non-linear interaction between the input from the semicircular canals and from the visual system onto these central vestibular neurons.

In the experiments described, only short term exposure to visual stimuli were used; also direction of movement was changed often. Recently several experiments were done where the response of the vestibulo-ocular reflex arc was modified by habituation processes. Different experimental approaches used by Miles, Melvill Jones, Young and myself have all resulted in consistent although temporary changes of ocular response to vestibular stimulation. So far, there are no published reports on vestibular unit recordings under such conditions. It can be expected that under such experimental conditions vestibular activity would also be modified.

The question now arises: how can the phenomena described be interpreted? One of the basic functions of the vestibular system is to convey information about self motion. Receptors for such information are mainly the labyrinths and the eyes. At some level, information from these two systems has to converge. Experimental evidence suggests that such convergence takes place at the level of the second order vestibular neurons. The time course of unit behavior suggest that the phenomena described could be interpreted as information about real or apparent body motion. It should especially be stressed that the observed unit activity does not parallel nystagmus. For that reason there have to be two systems projecting from the visual to the vestibular system: one which determines frequency and amplitude of optokinetic nystagmus which is reflected in many units within the vestibular nuclei; and another system which can modify activity of the second order units as described.

It was Ernst Mach 100 years ago who after an extensive series of psychophysical experiments came to the conclusion: "Apparently, optical sensations can be modified by motion sensation. Conversely, motion sensation can be modified also by optical means". It seems that we can now give some fragments of physiological proof to that statement.