

Simulation of Vestibular Semicircular Canal Responses During Righting Movements of a Freely Falling Cat

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Abstract. The righting maneuver of a freely falling cat was filmed at 1000 pictures per second, and the head position about the roll axis was digitized from each film frame using a graphics input tablet. The head angular velocity and acceleration were computed from the roll axis position trajectory. Head acceleration trajectories approximated two periods of a damped sinusoid at a frequency of 26 Hz. Head acceleration peak amplitudes exceeded $120,000 \text{ deg/s}^2$. These trajectories were used as stimuli for the horizontal semicircular canals in a computer simulation of first-order afferent responses during the fall. Linear system afferent response dynamics, characterized in a previous study of the cat horizontal canal using pseudorandom rotations, provided the basis for linear predictions of falling cat afferent responses. Results showed predicted single afferent firing rates that exceeded physiological values; and variations in afferent sensitivities and phase were predicted among different neurons. Fast head movement information could be carried by ensemble populations of vestibular neurons, and a phase-locking encoding hypothesis is proposed which accomplishes this. Implications for central program versus peripheral vestibular feedback strategies for motor control during falling are presented and discussed.

Introduction

The cat's ability to right itself while falling from an inverted position has been studied previously in various ways. High speed films recording the sequence of motions during falling were described in reports spanning nearly a century (Brindley, 1965; Magnus, 1922; Marey, 1894; Muller and Weed, 1916; Rademaker and Ter Braak, 1935). Biomechanical models of this phenomenon were developed using motion sequences from films and anatomical measurements (Kane and Scher,

1969; Rademaker and Ter Braak, 1935). Qualitative descriptions and speculations complemented the other studies (Brindley, 1965; McDonald, 1960). Results of previous studies of this phenomenon show that striking communication and control are required among the cat's sensory and neuromuscular control systems, in order to accomplish this maneuver. The visual, proprioceptive and vestibular systems appear to act together to provide appropriate synergistic information to brainstem and spinal motor command centers. Surprisingly, cats could still execute righting in the absence of bilateral vestibular input by using vision, although with certain sacrifices in speed and accuracy. Learning, through repeated trials, appeared to increase the reliability of righting in the absence of vestibular information (Muller and Weed, 1916; M. Igarashi, personal communication).

Quantitative studies of the peripheral vestibular system have resulted in useful descriptors of afferent information processing, on the basis of data from input-output experiments which employ physiological stimuli. Controlled rotational acceleration inputs to the semicircular canals have resulted in linear system transfer function descriptors of the afferent responses. The system is sufficiently linear, as demonstrated by coherence values close to 1, that linear descriptors provide useful approximations of the afferent response dynamics (O'Leary and Dunn, 1983). Tomko et al. (1981) characterized horizontal semicircular canal afferents from anesthetized cats in response to pseudorandom, or bandlimited "white noise", rotational acceleration. Afferent gain and phase data were fitted with transfer function zeroes, poles and gain factors, to provide parametric descriptions of the response dynamics. The results showed diverse response characteristics, particularly above 1 Hz.

The cat horizontal semicircular canal is stimulated during righting by rapid turning about the animal's roll axis. Other vestibular receptors are undoubtedly

important for stabilization and detection of yaw and pitch rotations that occur during bending of the spine (Kane and Scher, 1969). These considerations raise the following question. Are there sufficiently fast response components in the afferent dynamics from the horizontal canals to enable them to carry such fast head movement information? If that is the case, dynamic control during falling could depend on semicircular canal information as peripheral feedback. An alternative control strategy could be based on central programming, analogous to the ballistic control of saccadic eye movements, which would be independent of peripheral vestibular information from the canals.

The purposes of this report are: 1) to characterize cat head movements about the roll axis during falling; 2) to simulate horizontal canal afferent responses to those head movements using linear prediction theory; and 3) to examine hypotheses of fast neural information processing in order to suggest possible mechanisms of vestibular control of fast head movements.

Methods

Filming of Cat Righting Movements

Movements during free fall were filmed at a rate of 1000 pictures per second with a rotating prism movie camera (Redlake Corp., Seattle, WA). The cat was held by the feet in an inverted, head down position, with its back 50 cm above a table surface, and its head nearest the camera with roll axis parallel to the optical axis. Filming began just prior to releasing the cat and continued until all four feet contacted the table top with the cat upright. Six falling trajectories were filmed from one cat on each of two experimental days separated by 14 days. The cat rested quietly for at least 5 min between falls, showing no sign of agitation. The twelve filmed trajectories of the falling cat were inspected visually by projecting them at slow speed. No apparent differences in the trajectories were observed. The trajectory showing the best view of the cat's head was selected for frame-by-frame digitizing, and subsequent motion analysis.

Computer Processing of Head Movements

Each film frame was projected onto a vertical translucent screen using a stopframe projector (Redlake Corp., Seattle, WA). The projected frame image, of approximately 60 by 80 cm, was bordered on two sides by linear microphones of a sonic digitizer (Science Accessories Corp., Southport, CN), which produced x- and y-coordinates of the position of a stylus. The vectorial direction of a dark stripe along the sagittal midline of the cat's head was digitized from each film frame, by entering the position coordinates of two

points along the middle of the stripe with the digitizer stylus. During the later frames, the projected stripe image was not centrally located, so the positions of two new marks were digitized: the nose and a dark spot between the eyes. Both vectorial markers were digitized on overlapping frames from the two segments, permitting alignment of the two different sequences, and their subsequent concatenation in the completed computer file. The result of this procedure was a sampled time series of head position at 1 ms intervals, projected on a 2-dimensional plane normal to the cat's long axis. The translation component in the vertical direction was removed, resulting in a trajectory of head rotation about the roll axis.

The head angular position trajectory was smoothed by low-pass digital filtering to reduce high-frequency digitizing noise prior to differentiation. The smoothing filter was a non-recursive double-sided design which did not cause phase shifts in the data. It was constructed by (Hamming, 1977, Fig. 6.1-4): 1) specifying the frequency domain transfer function, 2) truncating higher-order Fourier coefficients, 3) transforming to a time domain finite impulse response, and 4) convolving the latter with the trajectory data. Cosine-tapered window functions were applied to reduce filter ringing due to the Gibbs phenomenon. The filter cut-off frequency was 56 Hz.

The smoothed trajectory was differentiated by backward differencing adjacent points to obtain head angular velocity. The backward difference algorithm has a bandwidth twice as large as the two-point central difference algorithm, and its phase differs from that of a true derivative by $-\omega T/2$, where ω is the frequency and T is the sampling interval (Bahill et al., 1982). With $T=1$ ms, the phase shift introduced by this operation at frequencies below 56 Hz was less than 0.4° , which was negligible. The velocity trajectory was again smoothed with the same digital filter, prior to backward differencing once more to obtain the projected head angular acceleration about the roll axis.

Semicircular Canal Afferent System Identification

Cat eighth nerve afferents were characterized in a previous experimental study (Tomko et al., 1981) by pseudorandom binary sequences (bandlimited "white noise") of rotational acceleration to result in linear system transfer functions. The transfer functions were of the general form

$$H(s) = \frac{K \prod_{i=1}^{N-1} (\alpha_i s + 1)}{\prod_{j=1}^N (\tau_j s + 1)}, \quad (1)$$

where K is a gain constant, α_i are zeroes, τ_j are pole time constants, and s is the Laplace operator.

Linear System Impulse Response Functions

The transfer functions determined previously were transformed to time domain system impulse response functions via Laplace transformations. The result was a truncated exponential series of the general form

$$h(t) = \sum_{i=1}^n A_i \exp(-t/\tau_i), \quad (2)$$

where A is a component amplitude at time $t=0$, τ_i is the component time constant, and n is the system order. A FORTRAN program computed the impulse response parameters of (2) from the transfer functions of (1).

Linear Prediction of Afferent Response to Cat Head Movements

Response predictions to cat head movements were computed by linear convolution of the head acceleration trajectory with afferent linear system impulse responses. The convolution equation was

$$r(i) = \sum_{j=0}^i h(j)b(i-j), \quad (3)$$

where $r(i)$ is the predicted spike rate at the i^{th} sample time, $b(i-j)$ is the acceleration at time $i-j$, and $h(j)$ is an afferent impulse response. Predictions were computed at each ms over the range 1–149 ms.

Results

Cat Head Motion Trajectories

Figure 1 shows a typical sequence of one animal's position at different times during the fall, as drawn from individual film frames. Time after start of the fall (in ms) is shown above each frame. The background lattice grids were traced from those superimposed onto each film frame by the camera. Most of the head rotation occurred during the first 80 ms. One rear foot contacted the table at 115 ms, and all four feet were on the table at 160 ms. In addition to roll axis body rotation, the other body motions were also complex, including bending and arching of the spine, counter-rotation of the tail, and relative phase differences between rotations of rostral and caudal body segments, as described previously (Kane and Scher, 1969; Rademaker and Ter Braak, 1935).

Figure 2 shows the measured head roll position projected onto a plane normal to the roll axis. Head position is shown beginning at -90° due to the inverted starting position, and progressing through zero to a final position of $+40^\circ$. The total head angle trajectory was only 130° , because the head did not achieve a fully upright position of $+90^\circ$ during the

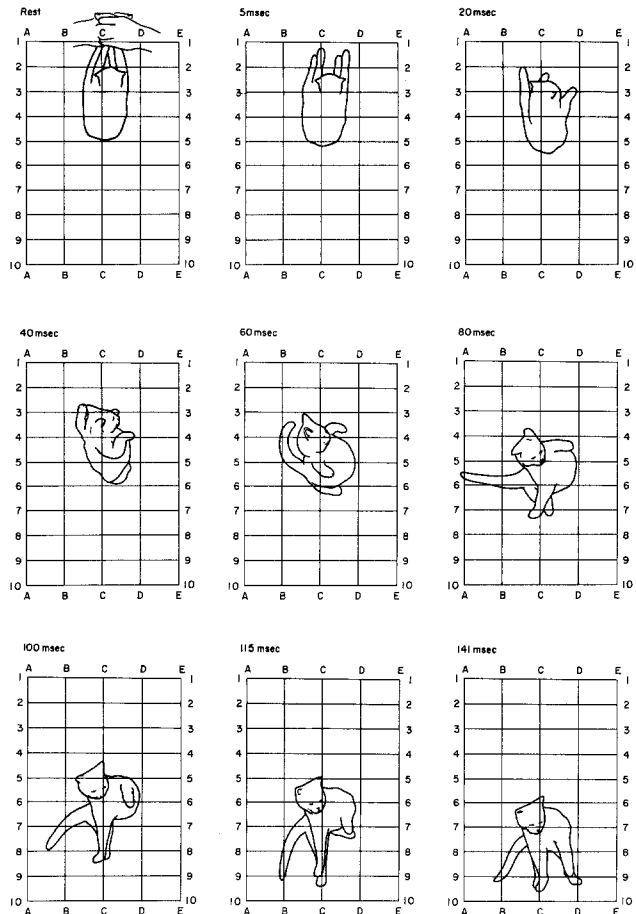


Fig. 1. Schematic drawings of the freely falling cat at rest (upper left) and at post-release times indicated in ms above each panel. Each drawing was made from a printed photograph of selected individual pictures from a high-speed film taken at 1000 pictures per second. The lattice grids were traced from those superimposed by the camera onto each film frame. Dimensions of each grid division are: horizontal, 17.6 cm; vertical 11.5 cm. First landing contact of the tail and one rear foot occurred at 115 ms. All four feet contacted the table at 160 ms

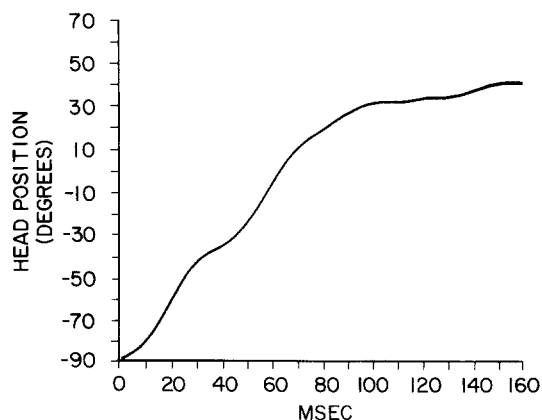


Fig. 2. Trajectory of head roll axis angular position vs. time during the fall

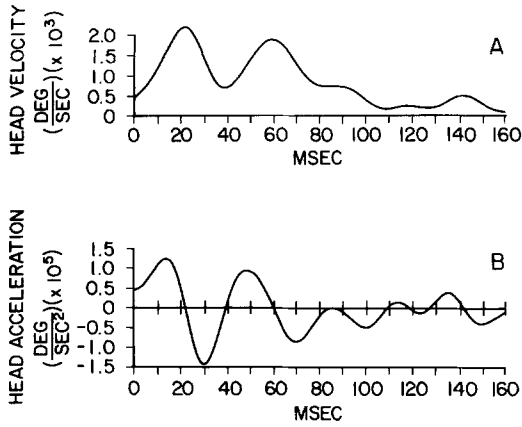


Fig. 3. A Trajectories of head roll axis rotational velocity and B rotational acceleration vs. time during the fall

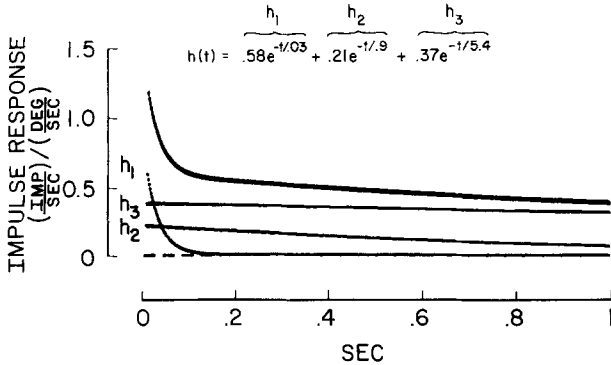


Fig. 4. Unit impulse response (UIR) (upper trace) of a cat semi-circular canal afferent response, from (5) and (8), shown plotted over a one-second time epoch. Components of the UIR are labeled h_1 , h_2 , and h_3 , respectively

filmed epoch. The head position trajectory did not increase linearly with time, but showed inflection points, implying that head motion proceeded at a nonuniform rate. We controlled for the possibility that the inflection points were artifacts introduced through projection distortion of the reference marker as it became less centrally located in the projected image. Using overlapping film segments, we digitized other centrally located markers and showed that they followed the same inflection trajectories as the original markers.

Figure 3A shows head roll velocity plotted vs. time. The head accelerated during the first 22 ms to a peak velocity of about 2200 deg/s, followed by deceleration during the next 18 ms to about 750 deg/s. The rotational angle trajectory was about 50° during this time. This periodic pattern was repeated with a reduced peak velocity of about 1800 deg/s. The two successive periods approximated cosines with periods of about 38 msec. They were followed by a negative "slow down" epoch during the landing approach and contact with one foot.

Figure 3B shows head roll acceleration as computed by low-pass filtering and first differencing the velocity data. The resulting acceleration trajectory resembles a damped sinusoidal oscillation during the initial 80 ms epoch. Peak-to-peak acceleration during the first period approximated 265,000 deg/s² with positive and negative peak amplitudes of 125,000 and -140,000 deg/s² at 14 and 30 ms, respectively. These peak values are about three orders of magnitude larger than the accelerations usually used experimentally in mammalian vestibular studies (e.g., Bizzi et al., 1972; Tomko et al., 1981). But they were necessary to complete the righting maneuver during the relatively brief fall time.

The periodicities in Fig. 3 had the effect of permitting the cat's trunk to "catch up" with the head at certain times during the maneuver. The head led the body at the beginning of the roll trajectory, followed by "catch up" epochs during the maneuver. This can be seen in the position sequence of Fig. 1, and also by observing the slow motion films.

Predicted Horizontal Canal Afferent Responses

Three afferent cells, which are representative of response types from this receptor, were used to determine afferent response profiles that would be predicted from the falling cat acceleration of Fig. 3B. The cells' experimental responses to pseudorandom rotational stimuli were fitted with transfer functions, and the latter were Laplace transformed into time domain unit impulse responses. The transfer functions were described by Tomko et al. (1981) [their Eqs. (4)–(6) with an additional adaptation term] in units of (imp/s)/(deg/s²) as:

$$H_A(s) = \frac{1.5(2.9s + 1)}{(7.3s + 1)(1.8s + 1)}, \quad (4)$$

$$H_B(s) = \frac{2.2(1.3s + 1)(0.059s + 1)}{(5.4s + 1)(0.90s + 1)(0.03s + 1)}, \quad (5)$$

$$H_C(s) = \frac{1.7(1.3s + 1)(0.059s + 1)}{(14s + 1)(1.7s + 1)(0.025s + 1)}, \quad (6)$$

by applying Laplace transformations to (4)–(6), the respective unit impulse responses are, in units of (imp/s)/(deg/s):

$$h_A(t) = 0.164 \exp(-t/7.3) + 0.167 \exp(-t/1.8), \quad (7)$$

$$h_B(t) = 0.367 \exp(-t/5.4) + 0.210 \exp(-t/0.9) + 0.578 \exp(-t/0.03), \quad (8)$$

$$h_C(t) = 0.125 \exp(-t/14.0) - 0.032 \exp(-t/1.7) + 0.126 \exp(-t/0.25). \quad (9)$$

Figure 4 shows a plot of the initial 1 s epoch of the impulse response from (8), and also its three exponential components. Note that component h_1 , with a time constant of 30 ms, dominates the impulse response contour during the 160 ms epoch corresponding to the trajectory of the righting cat. This result was found to be typical of other canal afferents which exhibited three-component impulse responses (Tomko et al., 1981).

Linear predictions of afferent response profiles to the head acceleration trajectory of Fig. 3B were obtained by a discrete linear convolution of a data file containing acceleration points spaced at uniform sample times of 1 ms with the unit impulse responses of (7)–(9), respectively. The resulting predicted afferent response profiles for the three afferents are shown over an epoch of 149 ms in Fig. 5.

The predicted peak spike rates in Fig. 5 range from 280 to 1550 spikes/s. These are necessarily “instantaneous” spike rates, in the sense that they represent spike rates at one instant of time. Their relatively large predicted magnitudes are a result of the gain (i.e. sensitivity) factors of the individual cells, in combination with the large magnitudes of head acceleration that occurred over short epochs during the fall. Such fast spike rates are not possible in single vestibular afferents due to refractory periods. However, they could well represent population responses of groups of neurons (c.f. Discussion) and earlier transduction stages, such as receptor potentials. It is therefore useful to compare their characteristics.

The spike rate contours of Fig. 5 each resemble approximately the velocity trajectory of Fig. 3A. But there are subtle differences among them. 1) The peak response rate of Fig. 5B occurred about 5 ms earlier than the peak rate of Fig. 5A. 2) The peak-to-peak modulation varied considerably from 400 spikes/s in Fig. 5A to more than 1500 spikes/s in Fig. 5B. 3) Figure 5B shows periodicities which are unipolar in an excitatory direction, and fully modulated, in the sense of returning to the zero, or spontaneous, level. In contrast, the periodicities in Fig. 5A do not return to the zero level, thus showing less than full modulation. 4) Figure 5B goes below the zero baseline at 72 ms, whereas this occurs at the later time of 92 ms in Fig. 5A. 5) Figure 5B shows a greater slope during the early epoch from 5 to 15 ms than the slope of Fig. 5A, which indicates significant differences in the high frequency sensitivities of these cells. 6) Figure 5C shows earlier peaks, but also lower predicted response rates, than either Fig. 5A or 5B.

In summary, our results show periodic head velocity and acceleration trajectories during the falling cat righting maneuver. The periodicities were reproduced in simulated predictions of horizontal canal

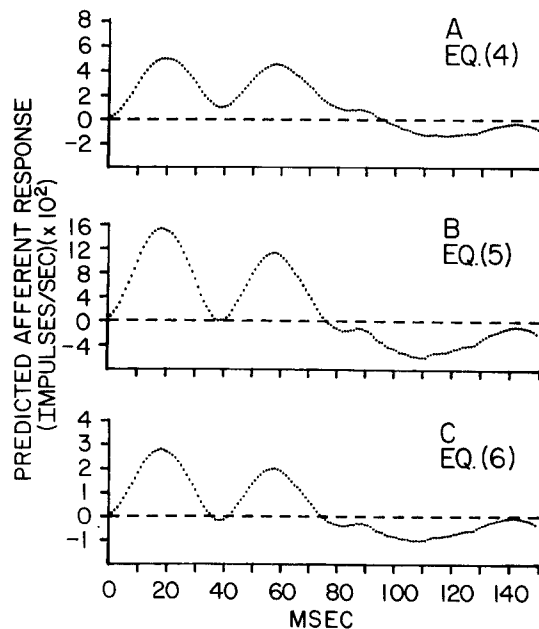


Fig. 5A–C. Predicted horizontal canal afferent responses to the falling cat trajectory from three different afferents. Transfer functions of the afferents are shown in the text as A Eq. (4), B Eq. (5), and C Eq. (6)

afferent responses to this stimulus. The predicted afferent response rates exceeded the magnitudes expected from single vestibular afferents. This implies that the afferent response dynamics include components with sufficient frequency and sensitivity requirements to respond to the rapid head accelerations of the falling cat.

Discussion

This study is a computer simulation, based on both experimental data and linear system theory, of fast head movement processing in the semicircular canal. The falling cat righting maneuver provided a rapid, intense physiological acceleration trajectory with which to examine simulated afferent responses.

It was apparent from afferent response transfer functions determined in a pseudorandom rotational study by Tomko et al. (1981) that higher-frequency afferent response components were present. However, it was still necessary to verify that head accelerations at the higher frequencies would be large enough to stimulate those afferent components, with their particular sensitivity characteristics. Our results in this study show that falling cat head accelerations were indeed sufficient in amplitude to result in large-magnitude predicted afferent responses.

An unexpected result was the periodicity of the velocity and acceleration trajectories, and the damped

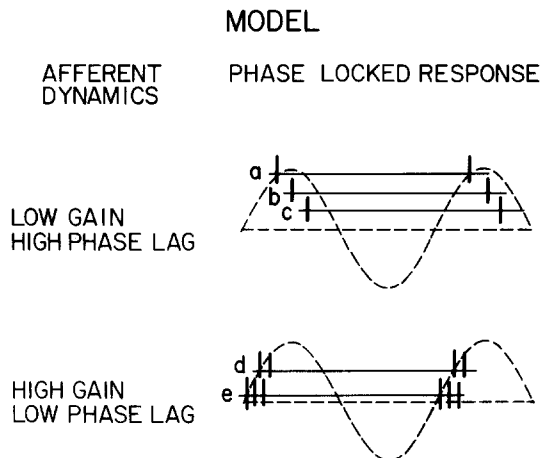


Fig. 6. Model of predicted semicircular canal afferent response patterns during phase locking to a periodic high-frequency head movement. The periodic stimulus is shown schematically as the dashed sinusoid. Responses of a population of five different afferents, labeled *a–e*, are shown as phase-locked vertical spikes spaced along a time axis. Each afferent is shown responding with one or more spikes over a different epoch of the periodic stimulus. From previous studies of afferent dynamic characteristics, cells with high gains and low phase lags would respond with multiple spikes early in the stimulus period, whereas afferents with low gains and high phase lags would respond with only one spike later in the stimulus period

oscillation contour shown by the latter. The cat's head executed two successive cycles of positive-negative torque, with each peak showing a characteristic decrease in magnitude to result in an apparent damped oscillation. Such periodicities have been described in certain other motor responses. For example, Bahill and Stark (1975) described human eye saccadic velocity trajectories, during execution of overlapping saccades, which appeared to be two saccades spaced close together. Damping could be an important control variable in such systems. Note that the cat's apparent precision in controlling slowing down and landing was at least as impressive as its ability to generate and control the large initial torque.

The periodicity and damping of head acceleration was shown to be reproduced accurately in the predicted afferent responses. The stimulus and response periodicities were 38 ms. The experimental study of cat afferent response dynamics by Tomko et al. (1981) described a mean high-frequency time constant for their total afferent population to be 51 ± 42 ms, and their most sensitive subset to be 44 ± 23 ms. This suggests that the fastest components of afferent responses are closely matched to the fastest physiological head movements in the sense that the afferents have "corner frequencies" (or reciprocal time constants) that are close to that of the cat head acceleration periodicity. Thus, the fastest afferent components could detect and process such fast stimulus information.

Encoding Hypothesis: Phase-Locking in Neuronal Population Ensembles

We suggest that such fast information is in fact encoded by *ensembles* of neurons, with individual ensemble members exhibiting phase locking over different epochs of each periodicity. A similar form of periodic phase locking of individual afferents has been suggested in other sensory systems. For example, the "volley theory" of audition is based upon the hypothesis that phase locking of auditory neuronal ensembles serves as the basis for high frequency hearing (Galambos and Davis, 1943; Rose et al., 1971). But does phase locking occur in the vestibular system?

Phase locking of semicircular canal afferents has been studied experimentally by applying high frequency sinusoidal rotations in fish. O'Leary and Wall (1979) stimulated isolated guitarfish labyrinths with combinations of pseudorandom noise and single-frequency sinusoids in the range 10–100 Hz. Different neurons were observed to phase lock over different epochs of the stimulus period. One or more spikes per period were observed as a function of the intensity of the stimulus. Hartmann and Klinke (1980) stimulated semicircular canal afferents of locally anesthetized goldfish with rotational frequencies ranging up to 63 Hz. In agreement with the guitarfish results, Hartmann and Klinke (1980) showed phase locking that was functionally dependent on the stimulus frequency and amplitude, in addition to the sensitivity of individual units. These authors proposed a model of their semicircular canal afferent data in which equivalent filter characteristics of receptor potential, afferent synapse and EPSP's were cascaded with assumed hydromechanical characteristics (Hartmann and Klinke, 1980, Fig. 6).

If the stimulus frequency and amplitude are fixed, the experimental and modeling results described above imply that a unit's sensitivity at that frequency would determine its phase-locked response characteristics. The cat's head acceleration profile, shown in Fig. 3B, approximated a sinusoid with a frequency of 26 Hz and large peak amplitudes. Therefore, the wide variation in cat afferent sensitivities and dynamic characteristics would be instrumental in ensemble encoding of this stimulus. For example, consider the predicted responses shown in Fig. 5 from three afferent units with different sensitivities. The instantaneous firing frequencies shown on the ordinate varied over a wide range among these cells, suggesting that each cell would fire one or more spikes over different epochs of the head movement stimulus. This is shown schematically in Fig. 6. Semicircular canal afferents show a wide diversity in higher frequency phase values. Thus, phase locking to a periodic stimulus would vary among cells

according to their relative gain and phase relationships. Cells with low values of phase lag and high gain would phase lock early in the stimulus cycle, whereas cells with low gain and large phase lags would phase lock later in the cycle, as represented in Fig. 6. Sensitivity (gain) characteristics of individual cells influence the number of spikes per period produced by each (Hartmann and Klinke, 1980). Information over the entire stimulus period would therefore be distributed over a population ensemble of afferents, with relatively wide dispersions in phase.

The above hypothetical model of ensemble encoding of fast head movements is functionally dependent on the wide variation of sensitivities and dynamic phase characteristics that has been observed in studies on the cat and other species. It provides also a rationale for this variation. The model predicts that a rapid, intense stimulus would result in a bilateral barrage of first-order afferent activity that was an ordered time series of spike events, occurring over specific epochs of the stimulus. Presumably higher-order "receiver" neurons could decode this time series by utilizing information as to "labeled-line" anatomical projection patterns, in addition to other meaningful coding parameters.

Hypothetical Considerations of Central Programming and Peripheral Feedback

Eye-head coordination during horizontal rotations of the head about a vertical axis imposes certain constraints on the temporal characteristics of eye and neck muscle coactivation during different types of movements. In particular, head movements in monkeys made in anticipation of a *predicted* visual stimulus were shown to have different motor output characteristics from eye-head movements which were *triggered* by a visual stimulus (Bizzi et al., 1972). Whether such results apply to cats during the righting maneuver is unclear. However, cats are known to use visual information to assist in righting in the light, particularly after a bilateral labyrinthectomy (Muller and Weed, 1916). Righting in the dark occurs without visual information, and is apparently dependent primarily on vestibular information (Muller and Weed, 1916).

Results from the present computer simulation suggest that horizontal canal neurons could provide peripheral feedback channels, via vestibular processing from phase-locked ensemble populations, in addition to those channels that carry vision and proprioception information. Within this hypothesis, the gravity receptors could first signal the cat's starting position (Brindley, 1965), and the semicircular canals could

then contribute the dynamic feedback information necessary for fine adjustments during the righting maneuver.

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