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COMPLEX PODOKINETIC (PK) RESPONSE TO POST-ROTATIONAL VESTIBULAR STIMULATION

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INTRODUCTION

Recent studies have explored the dynamic characteristics of a "Podokinetic" (PK) system involved in sensing and controlling spatial orientation by referencing body orientation to the space-stable stance foot on the ground (Gordon et al, 1995; Mergner et al, 1993, 1998; Weber et al 1998). An interesting feature of this system is that, unlike the more familiar open-ended vestibulo-ocular response, a vestibular-PK response that turns the body around relative to space would presumably generate a dependent mechanical response in the semicircular canals, thus modifying the vestibular-PK drive through a mechanically-coupled feedback loop between the two systems. Due to widely different dynamics in its two primary components (Vestibular τ = 15 sec, phase lead; Podokinetic τ = 300 sec, phase lag; see Weber et al., 1998 e Figure 2) one could expect a complex response pattern from such a closed loop system.

The present study addresses this prediction by asking blindfolded subjects to try and "step-in-place" (ie without turning relative to space) after exposing them to a unidirectional post-rotational vestibular stimulus.

METHODS

In the present preliminary phase of these experiments, four male and five female subjects have been examined over an age range of 28-75 years. None of these had a relevant clinical history and all gave their informed consent to the experiments. After blindfolding, they each stood on the centre of a servo-controlled rotating platform while holding onto a low friction, concentric wheel fixed to the ceiling directly above their head. This wheel served both to provide a safety postural support and to record angular position of the body relative to space through a rotary potentiometer with linear output over 360 degrees. Turntable angular position was separately recorded from an internal potentiometer. Labview (National Instruments) software was employed for both turntable control and data acquisition and processing.

The turntable and subject were slowly accelerated at 0.75 deg/sec/sec for 60 sec to reach a final angular velocity of 45 deg/sec, which was then maintained constant for a further 60 sec (dashed lines, Figure 3). Due to the inherent highpass filtering characteristic of the semi-circular canal system (eg Wilson & Melvill Jones, 1979) there should be no rotational vestibular signal remaining at the end of this manoeuvre. Hence sudden cessation of rotation would normally stimulate a transient vestibular response equivalent to 45 deg/sec in the opposite direction (i.e. a post-rotational vestibular stimulus).

RESULTS

Immediately after sensing the post rotational stimulus, the blindfolded subjects were required to "step-in-place" on the now stationary disc, without turning themselves relative to space. However, when trying to do so the predominant tendency was to start by vigorously rotating themselves in the same direction as the preceding turntable rotation, but *notably without sensing their rotation.*

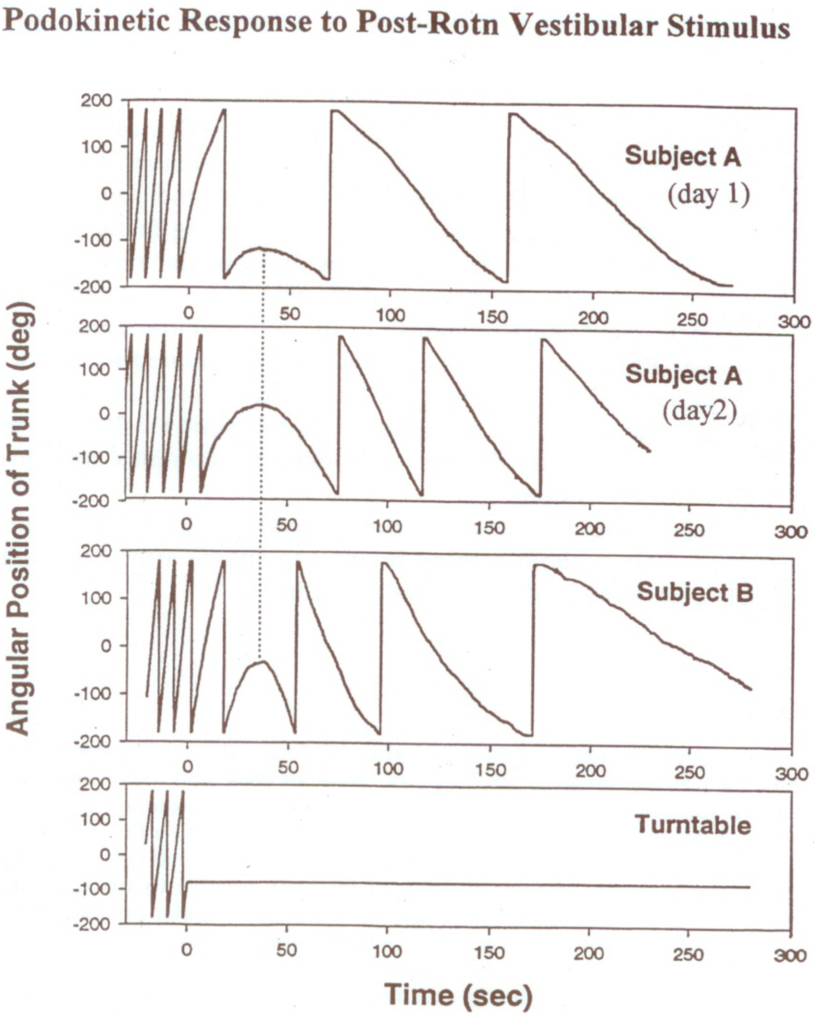

Fig. 1. - *Podokinetic response to post-rotational vestibular stimulation.*

Note the consistency of response between subjects A and B, and between the two responses of subject A obtained on different days separated by more than a week. The vertical dotted line indicates the approximate time of direction reversal for all three records.

Figure 1 illustrates the typical pattern of this podokinetically generated self-rotation, obtained from two of the six subjects who responded consistently to the post-rotational vestibular stimulus. The apparent saw-tooth nature of the traces is due to the overhead recording wheel being connected to the ceiling through a single turn potentiometer which conveniently re-sets the trace of angular position once per turn. Note that prior to stopping, the turntable and subject records are necessarily identical. The moment initiating the post-rotational vestibular stimulus is indicated by cessation of turntable rotation in the bottom trace of the figure.

At this moment both subjects started rotating themselves at around 30 deg/sec on the now stationary platform, turning in the same direction as the preceding turntable rotation. Thereafter, the rate of body rotation progressively declined to reach zero velocity after some 30-35 sec (vertical dotted line in Figure 1). The direction of rotation then reversed, first accelerating over the next 30-50 sec and then slowly decaying over the next 4-5 minutes. The robustness of this complex response pattern is reflected both in the similarity between the two subjects A & B, and the repeatability of subject A's response on two different days separated by more than a week. Six of the nine subjects responded in this characteristic fashion. The remaining three produced no recognizable pattern of response, accompanying their endeavours with comments such as "I don't seem to know what I'm supposed to be doing".

A preliminary index of pattern consistency within the six systematically responding subjects is seen in Table 1. It gives the time in seconds between start of the podokinetically generated rotation and the reversal of direction, as tested after clockwise and counter clockwise directions of prior turntable rotation. Mean values of 32 (SE 5.1) and 34 (SE 8.8) sec for clockwise and counter clockwise directions emerge. Lumping these two data sets, but bearing in mind the limited number of samples as yet available from these preliminary experiments, an overall mean of 33 (SE 4.8) sec emerges for this characteristic duration.

Table 1. - Time in seconds from stimulus initiation to reversal of podokinetic rotation (dotted line in Figure 1), obtained from the six subjects who produced a consistent response pattern. CW and CCW represent clockwise and counter clockwise rotation of the turntable prior to post rotational stimulation.

	TIME TO REVERSAL	
Subject #	CW	CCW
1	22	22
2	33	—
3	29	13
4	54	36
5	36	65
6	20	34
Mean	32	34
SE	5.1	8.8
Overall Mean	33	± 4.8

SIMULATION STUDIES

To gain insight into the complex nature of these response patterns, we formulated a simple mathematical model of the closed loop interaction between vestibular and podokinetic systems, as shown in Figure 2. For this we have to ascribe transfer functions for the two systems. The literature abounds with descriptions of first order dynamics for the vestibular rotation-sensing system (reviewed in Wilson and Melvill Jones, 1979). We chose a first order lead with time constant 15 sec, as indicated in the upper (canal) box of the figure. For an estimate of Podokinetic dynamics we drew on data from our previous investigation of adaptive characteristics in the podokinetic system (Weber et al., 1998). As indicated in the bottom (PK) box, we chose a first order lag with time constant 300 sec. The implied presumption is that the post-rotational vestibulo-spinal signal will cause the stepping subject to rotate and that this rotation feeds back into the vestibular system as noted above.

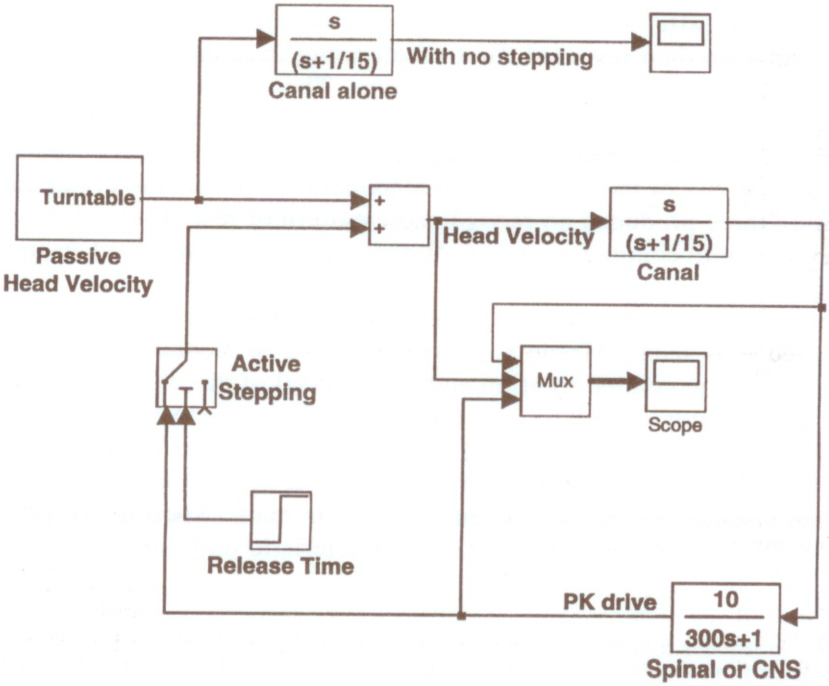

Fig. 2. - *Mathematical model simulating podokinetic and vestibular interactions in response to a post rotational vestibular stimulus.*

Figure 3 shows the outcome of feeding our turntable rotation profile into the system. The first 120 sec in the diagrams serve to set up the initial conditions, with the simulated response of the whole system to cessation of rotation commencing

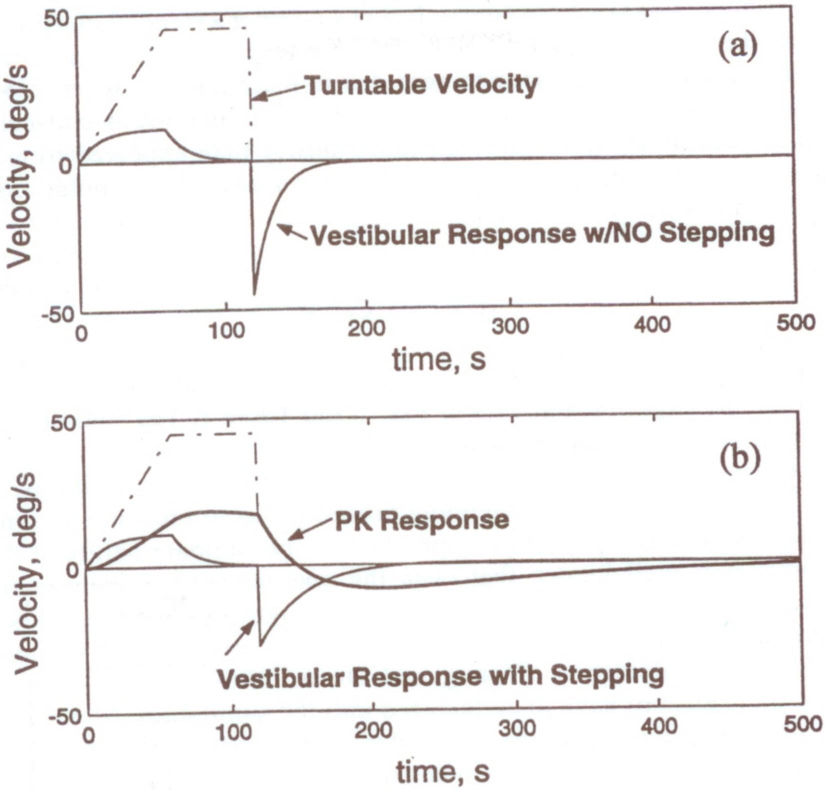

Fig. 3. - *Simulation of response to a post rotational stimulus of 45 deg/sec.*

a) The purely vestibular response in a subject standing still after the post rotational stimulus. b) The interactive vestibular and podokinetic responses of the closed loop system in Figure 2, to the same post rotational stimulus. In both figures the first 120 sec on the abcissa represents the setting up of initial conditions with passive turntable control, after which the post-rotational simulation begins. Note that in Figure 3b the initial vestibular signal is reduced in magnitude compared to that of Figure 3a by exactly the magnitude of the PK response, since the latter represents real rotation relative to space. Also, in the closed loop system the vestibular signal declines more slowly than that of the purely vestibular response in Figure 3a.

after this point. Note that whereas in Figure 1 the ordinate is expressed in terms of angular position, the simulated data are presented in terms of angular velocity. As in the experiments, cessation of turntable rotation generates the intended reversed vestibular response (Fig. 3a). However this immediately activates the podokinetic system which in turn reduces the vestibular signal by the magnitude of the PK-induced velocity of body rotation relative to space (Fig. 3b). Thereafter, analogous to the experimental results of Figure 1, podokinetic rotational velocity progressively declines, passing through zero about 30 sec later, then increasing in the opposite direction over the next 40 sec and finally declining slowly to zero velocity over the next 4 to 5 minutes.

The vestibular signal's time course follows a rather extended quasi-exponential decline, all the while being modified by the changing PK-induced angular velocity of the body, but finally decaying to zero due to its inherently short "decay" time constant. An interesting feature is that while the vestibular-PK loop remains active, it causes the vestibular trace to decay more slowly than expected from the canal dynamics alone, as shown by comparing the curves of vestibular response in Figures 3a and 3b.

DISCUSSION

The interesting feature of these simulated results is the closeness with which they emulate the experimental data of Fig. 1 and Table 1. The finding encourages the view that vestibular and podokinetic systems do in fact interact in a closed loop fashion, at least in the circumstances of these experimental conditions, when the subject is required to adjust the stepping process so as to prevent any sensation of turning. It is however important to appreciate the preliminary nature of these data. For example it is well known that even the open-ended vestibulo-ocular reflex demonstrates a post-post response somewhat analogous to that of the PK signal in the simulations, due to a long-time constant (~ 80 sec) 'adaptive' term in the vestibular sensory dynamics (Young and Oman, 1969; Malcolm and Melvill Jones, 1970). This will have to be factored into the simulation. Also, the phenomenon of adaptive plasticity in the vestibular neural system (Reviewed in Berthoz and Melvill Jones, 1985) will have to be taken into account. Nevertheless, reversal of the PK signal in Fig. 3 clearly cannot be due to "post-post" reversal of the vestibular signal, since this would occur much later than the time of PK reversal; and plastic neural adaptation in the vestibular system would presumably require much more time to produce any major effects.

In conclusion we infer that even at this preliminary phase of the experiments, the results imply a functionally closed-loop interaction between vestibular and podokinetic systems, a conclusion supported by additional evidence of their functional interaction briefly reported elsewhere (Weber et al., 1996; 1997).

SUMMARY

Recent studies identified an adaptive "Podokinetic" (PK) sensory motor system involved in sensing and controlling spatial orientation during locomotion, by referencing body orientation to the space-stable stance foot. This paper investigates the interaction of vestibular and PK systems by asking blindfolded subjects to 'step-in-place' (ie without turning) after exposing them to a unidirectional post-rotational vestibular stimulus. Six of the nine subjects consistently began by vigorously propelling themselves round in the direction of preceding turntable rotation, but notably without any sensation of turning. In all these subjects the speed of this PK-induced rotation progressively declined to zero over about the next 30 sec and then reversed direction with increasing speed for about 50 sec. Thereafter the speed of rotation declined slowly to zero over the next 4 to 5 minutes. Since the PK-generated body rotation presumably feeds back into the vestibular-PK drive, we formulated a closed loop model of the combined system to investigate the complex nature of the behavioral response. The simulated response of this model closely resembled the experimental data, suggesting that there is indeed a functionally closed loop operating between the vestibular and podokinetic systems in natural life.

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