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BRAIN RESEARCH

Research Report

Adaptive rescaling of central sensorimotor signals is preserved after unilateral vestibular damage

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ABSTRACT

Adaptive rescaling is a widespread phenomenon that dynamically adjusts the input–output relationship of a sensory system in response to changes in the ambient stimulus conditions. Rescaling has been described in the central vestibular neurons of normal cats. After recovery from unilateral vestibular damage, the vestibulo-ocular reflex (VOR) remains nonlinear for rotation toward the damaged side. Therefore, rescaling in the VOR pathway may be especially important after damage. Here, we demonstrate that central vestibular neurons adjust their input–output relationships depending on the input velocity range, suggesting that adaptive rescaling is preserved after vestibular damage and can contribute to the performance of the VOR. We recorded from isolated vestibular neurons in alert cats that had recovered from unilateral vestibular damage. The peak velocity of 1-Hz sinusoidal rotation was varied from 10 to 120°/s and the sensitivities and dynamic ranges of vestibular neurons were measured. Most neuronal responses showed significant nonlinearities even at the lowest peak velocity that we tested. Significant rescaling was seen in the responses of neurons both ipsilateral and contralateral to chronic unilateral damage. On the average, when the peak rotational velocity increased by a factor of 8, the average sensitivity to rotation decreased by roughly a factor of 2. Rescaling did not depend on eye movement signals. Our results suggest that the dynamic ranges of central neurons are extended by rescaling and that, after vestibular damage, adaptive rescaling may act to reduce nonlinearities in the response of the VOR to rotation at high speeds.

1. Introduction

In normal individuals, the vestibulo-ocular reflex (VOR) stabilizes gaze during head rotation over a wide range of velocities (Maioli et al., 1983; Paige, 1983a). After unilateral labyrinthectomy (UL) or unilateral plugging of the semicircular canals, compensation occurs, but the range of velocities over which the VOR can stabilize gaze remains subnormal (Maioli et al., 1983; Fetter and Zee, 1988; Paige, 1983b; Lasker et al., 1999, 2000). This restriction on the compensated VOR may be due to the limited linear ranges of central vestibular neurons. Because of the rapid and direct reflex output of the VOR, it is desirable that vestibular sensory signals should provide linear functions that can be used as motor commands. However,

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Abbreviations: EM, eye movement; MSE, mean square error; RI, rescaling index; $SD_{H=0}$, zero-velocity spike density; s.e.m., standard error of the mean; UVD, unilateral vestibular damage; UL, unilateral labyrinthectomy; V-only, vestibular-only

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many secondary vestibular neurons display cutoff responses (i.e., are silenced during rotation in their off-directions), even at low speeds (Melvill Jones and Milsum, 1970; Newlands and Perachio, 1990a; Escudero et al., 1992; Chen-Huang and McCrea, 1999; Broussard et al., 2004). In awake cats, most central vestibular neurons consistently have asymmetric responses to sinusoidal rotation (Broussard et al., 2004). Primary afferents from the semicircular canal endorgans also are not purely linear in their response characteristics, and irregularly-firing afferents can be silenced during contralateral rotation (Dickman and Correia, 1989; Hullar et al., 2005).

In spite of the nonlinear responses of its neurons, the normal VOR can generate an overall linear response, presumably because it is based on inputs from the two labyrinths which complement each other. But after unilateral labyrinthectomy, neurectomy or plugging of the horizontal canal, the head velocity signal arising from the damaged side is lost, and the VOR's response has a reduced linear range (Maioli et al., 1983; Paige, 1983b; Fetter and Zee, 1988; Tusa et al., 1996; Foster et al., 1997; Lasker et al., 2000). Thus after unilateral vestibular damage (UVD), the VOR begins to express some of the nonlinear features of its neurons. A mechanism for extension of the dynamic ranges of neuronal responses might therefore improve gaze stability after UVD.

Adaptive rescaling refers to an adjustment in the sensitivities of sensory neurons that accompanies a change in the expected dynamic range of the sensory signal and increases the efficiency of coding (Brenner et al., 2000). Flexible sensitivities, adjusted to the expected range of sensory inputs, can optimize information transmission by neurons (McLaughlin, 1967). During high-amplitude inputs, sensitivity is minimized so that the dynamic ranges of neurons are exceeded less often; this would be especially useful in the vestibular system because of the requirement for linearity. During small inputs, sensitivity is maximized, improving the accuracy of coding. Most adaptation in sensory systems is adaptive rescaling, rather than an inability of the receptor to respond to continuing stimuli. One exception is the adaptation to ongoing rotation at a constant velocity by the vestibular system, which we will call peripheral adaptation and which is a consequence of hydrodynamics and of peripheral inhibition (Rabbitt et al., 2005). In addition to peripheral adaptation, central vestibular neurons demonstrate adaptive rescaling. When the peak velocity of sinusoidal rotation is increased, central neurons in normal cats reduce their sensitivities (Melvill Jones and Milsum, 1970). In this report, we will describe adaptive rescaling after recovery from unilateral vestibular damage.

2. Results

We recorded the responses of 52 isolated cells in the medial and ventral lateral vestibular nuclei of 3 cats, during rotation at peak velocities of 10–80°/s; a subset of neurons were also tested at 120°/s. Neuronal responses were recorded under two different chronic lesion conditions, a unilateral labyrinthectomy (UL) and a unilateral horizontal semicircular canal plug. All of the cells reported here were tested at 10, 20, 40 and 80°/s peak velocities. Although some of the final samples were quite small, it was nevertheless clear that rescaling was not exclusive for a particular lesion type or for either side of the brainstem with respect to the lesion.

Cells were classified according to the polarity of their responses as types I, II or III (see Experimental procedure). The breakdown of our sample according to lesion type, side and response type is shown in Table 1. All neurons had non-zero resting discharge rates. In the ipsilesional vestibular nuclei, the largest subgroup of cells responding to rotation showed type II responses (54%). On the contralesional side, only 17% were type II and 75% were type I. The prevalence of type II responses ipsilateral to UVD was expected based on earlier studies (Shimazu and Precht, 1966; Smith and Curthoys, 1988b; Newlands and Perachio, 1990a,b). The observation that type I neurons were prevalent contralateral to UVD also agreed with earlier reports (Shimazu and Precht, 1966; Smith and Curthoys, 1988a; Newlands and Perachio, 1990a,b).

Neuronal sensitivities to rotation were measured as illustrated in Fig. 1. Spike density was plotted against head velocity; any phase lead or lag was removed. To determine the linear range for sensitivity measurements, a best fit of two lines was used (Fig. 1). If the slopes were significantly different, a breakpoint was defined as the head velocity at the intersection of the fitted lines; otherwise the response was said to be linear (Fig. 1C). For cutoff responses, the sensitivity was the slope of the response function above the breakpoint (arrow in Fig. 1) and for saturation-type responses, the sensitivity was the slope below the breakpoint. Further details are given under Experimental procedure.

Table 1 – Neuronal types and lesion conditions

Side	Lesion	Cat(s)	Cell type	Sample sizes	Total for type (*n*)	Total for side	% of type
Ipsi	UL	O	I	4	–	–	–
Ipsi	UL	O	II	12	–	–	–
Ipsi	UL	O	III	5	–	–	–
Ipsi	CP	J	I	1	–	–	–
Ipsi	CP	J	II	1	–	–	–
Ipsi	CP	J	III	1	–	–	–
Ipsi	**Either**	**O, J**	**I**	–	**5**	**24**	**21**
Ipsi	**Either**	**O, J**	**II**	–	**13**	**24**	**54**
Ipsi	**Either**	**O, J**	**III**	–	**6**	**24**	**25**
Contra	UL	O	I	1	–	–	–
Contra	UL	O	II	1	–	–	–
Contra	UL	O	III	0	–	–	–
Contra	CP	C	I	20	–	–	–
Contra	CP	C	II	4	–	–	–
Contra	CP	C	III	2	–	–	–
Contra	**Either**	**O, C**	**I**	–	**21**	**28**	**75**
Contra	**Either**	**O, C**	**II**	–	**5**	**28**	**17**
Contra	**Either**	**O, C**	**III**	–	**2**	**28**	**7**

This table shows the samples, subdivided according to neuronal type, that were obtained from each side of the brain in each cat. The rows in boldface type summarize the samples of cells from each side of the brain.