Oscillatory Activity in the Cerebellar Hemispheres of Unrestrained Rats

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Hartmann, Mitra J. and James M. Bower. Oscillatory activity in the cerebellar hemispheres of unrestrained rats. *J. Neurophysiol.* 80: 1598–1604, 1998. We recorded multiunit neural activity in the granule cell layer of cerebellar folium Crus IIa in unrestrained rats. Seven- to 8-Hz oscillatory activity was seen during behavioral states in which the animal was immobile; any movement the animal made coincided with termination of the oscillations. However, nearly one-third of oscillatory episodes appeared to cease spontaneously, in the absence of any observable sensory input or movement. Oscillations were synchronized both within and between cerebellar hemispheres, demonstrating precise temporal coordination among multiple, bilateral levels of the somatosensory system. We interpret these data in the context of similar oscillations observed in other brain structures and suggest that the oscillations are an underlying dynamic property of the entire somatosensory network.

INTRODUCTION

In the awake rat, 7- to 12-Hz synchronous activity has been seen at multiple levels of the sensory trigeminal system, including the spinal trigeminal nucleus (SpV), ventrobasal thalamus (VB), and primary somatosensory (S1) cortex (Buzsáki 1991; Kandel and Buzsáki 1993, 1997; Nicolelis et al. 1995; Semba et al. 1980, 1984). In addition, it is well established that 7- to 12-Hz spindle oscillations occur in many neocortical areas during the early stages of drowsiness and sleep (Contreras et al. 1997; Hammond et al. 1979; Kandel and Buzsáki 1993, 1997; Steriade and Deschenes 1984; Steriade and Llinás 1988). In this study, we examined oscillations in tactile regions of the granule cell layer (GCL) of the lateral cerebellar hemispheres (Crus IIa) in unrestrained rats. This cerebellar folium receives projections from S1 via the pontine nuclei (Bower and Woolston 1983; Brodal 1983; Mihailoff et al. 1981) as well as direct tactile input from the trigeminal sensory nuclei (Huerta et al. 1983; Watson and Switzer 1978; Woolston et al. 1981, 1982). Our results demonstrate clear 7- to 8-Hz field potential oscillations in the GCL of Crus IIa, synchronized both within and between cerebellar hemispheres. Oscillations were present only during periods of immobility, and any movement invariably disrupted the oscillatory activity. However, a significant percentage of oscillatory episodes ceased spontaneously, in the absence of observable movement or sensory input. We therefore propose that the oscillations reflect the baseline dynamic state of the entire tactile sensory system; although they can be interrupted by sensory input or movement, they do not under natural conditions appear to anticipate such interruption.

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METHODS

Five female albino Sprague-Dawley rats, aged 4–10 mo, were implanted with microwire electrode arrays, either in left Crus IIa ($n = 3$) or in both right and left Crus IIa ($n = 2$). During implantation animals were anesthetized with xylazine/ketamine-hydrochloride delivered intramuscularly (70 mg/kg ketamine, 3.5 mg/kg xylazine, 0.7 mg/kg acepromazine) and pentobarbital sodium delivered intraperitoneally (20 mg/kg). During the surgery five or six stainless steel screws were placed over neocortical areas and covered with dental acrylic to form a stable base. Next, Crus IIa was exposed and the grid of wire electrodes (either 18-μm-diam platinum-iridium or 50-μm-diam stainless steel) was fixed with acrylic above the exposure. The electrodes were lowered and fixed in position, and the receptive field at each recording site was determined. During implantation surgery, we confirmed that the responses were physiologically characteristic of the Crus IIa GCL. The reference electrode was a stainless steel (76-μm diam) wire laid flat over the entire length of Crus IIa. All animal procedures were approved by Caltech's Animal Use Committee.

Field potentials and multiunit activity were recorded from the most superficial GCL of Crus IIa as in previous experiments (Bower and Kassel 1990). Maximum amplitude responses were found between 400 and 700 μm below the pial surface. A high-input-impedance preamplifier (Microprobe, CFP-1020) mounted directly on the animal's head carried neural signals to a custom-built amplifying system with a minimum of mechanical and electrical artifact. Signals were amplified and filtered in analog between 1 Hz and 5 kHz and collected at a $\geq$10-kHz sampling rate. Neural data were synchronized with behavioral data in real time with the use of a custom-built video mixer (Rasnow et al. 1997). During subsequent computer analysis, data were digitally filtered either between 1 and 300 Hz (field potential activity) or between 300 and 3,000 Hz (multiunit burst activity). To detect and quantify periods of oscillation, continuous neural recordings were divided into 1-s trials and processed through a standard fast Fourier transform (FFT; Matlab v5.0.0 1996, the MathWorks). The power spectrum was taken to be the square of the absolute value of the FFT. Any individual trial was considered to include oscillatory activity if any peak in the power spectrum accounted for >8% of the total power.

We refer to our multiunit recordings as GCL activity rather than as the activity of granule cells because we did not isolate action potentials from single granule cells. This issue has been discussed extensively in previous publications (cf. Bower and Kassel 1990), but in brief, the small size (5–6 μm) of granule cells precludes single-cell isolation in awake behaving animals. It is very likely, however, that some component of the multiunit activity reflects the activation of granule cells because these same signals have been shown to precede and predict short-latency simple spike re-

sponses in overlying Purkinje cells (Bower and Woolston 1983; Jaeger and Bower 1994).

Electrode placement in the GCL was guided by physiological responses. The GCL in the rat hemispheres has very strong and distinct responses to tactile stimulation of perioral regions, as confirmed in numerous physiological studies (Bower and Kassel 1990; Huang et al. 1991; Jaeger and Bower 1994; Joseph et al. 1978; Morissette and Bower 1996; Shambes et al. 1978; Welker 1987). Depth profiles in anesthetized animals have demonstrated that these type of responses are not found in the Purkinje cell or molecular layers and that GCL responses are well isolated with the use of either 20- or 50-μm wires. We confirmed that neural responses were localized to the GCL at three different stages during experiments: first, during the implantation surgery; second, during recording sessions after recovery from the surgery; and, third, in several rats, immediately before euthanasia.

As additional confirmation that our recordings were located in the GCL, we histologically verified the positions of electrode tips with the use of standard procedures (Shambes et al. 1978). Prior to euthanasia, the animal was anesthetized and electrolytic lesions (-5.0 μA, 10 s) were made at recording sites. The animal was then perfused with phosphate buffer solution and a 4% formaldehyde solution. The cerebellum was extracted, the hemispheres sectioned parasagitally, and the slices stained either with neutral red or cresyl violet. Lesion sites were centered in the middle of the GCL.

RESULTS

We recorded oscillatory activity in Crus IIa from all five implanted rats. Figure 1*A* shows simultaneous recordings from three electrodes in left Crus IIa of an awake animal during an oscillatory episode. The three electrodes were arranged in a mediolateral line and spaced ~500 μm apart. As shown in the enlarged timescale in Fig. 1*B*, each oscillation in the local field potential was accompanied by a burst of multiunit activity. Each oscillatory peak usually had two or more smaller subsidiary peaks (arrowheads).

Figure 2*A* provides an analysis of the frequency of the recorded oscillations. Peaks in the power spectrum that met our criteria for oscillations (described in METHODS) were centered between 1 and 2 Hz, 7 and 8 Hz, and 14 and 16 Hz. In single 1-s trials, activity between 7 and 8 Hz was found to be responsible for up to 28% of the total power in the signal. As shown in the amplitude spectrum in Fig. 2*A*, all three peaks were consistent enough to be averaged across all rats, over a total of 205 1-s trials. Finally, in 7% of the trials, a 21- to 23-Hz component also accompanied the 7- to 8-Hz oscillations (e.g., *rat 5*).

To examine whether the oscillatory activity could be the result of oscillatory peripheral input or motor activity, we examined GCL activity during small-amplitude (10–20°) whisker movements associated with exploratory behavior. Unlike the extremely consistent 7- to 8-Hz oscillations seen during immobility, whisking could occur over a much wider frequency range, usually between 6 and 12 Hz. Rhythmic whisker movements, even those near 7 or 8 Hz, generated periodic signals in the GCL quite different in appearance from the oscillations seen during immobility. The *top graph* of Fig. 2*B* compares GCL activity during active whisking (*bottom trace*) with the oscillatory activity seen during immobility (*top trace*). Both recordings were from *rat 1* on the same day. Active whisking occurred at ~7 Hz, with an amplitude of ~10°, as measured by video analysis. During the period of immobility no whisker movements were visible. The *bottom graph* of Fig. 2*B* compares the periodic GCL activity seen during more generalized exploratory activity (*bottom trace*) with the oscillations seen during immobility (*top trace*). Both recordings were from *rat 3* on the same day. In this example exploratory activity consisted of walking and whisking along the wall of a cage, and it was therefore impossible to observe movements of individual whisk-

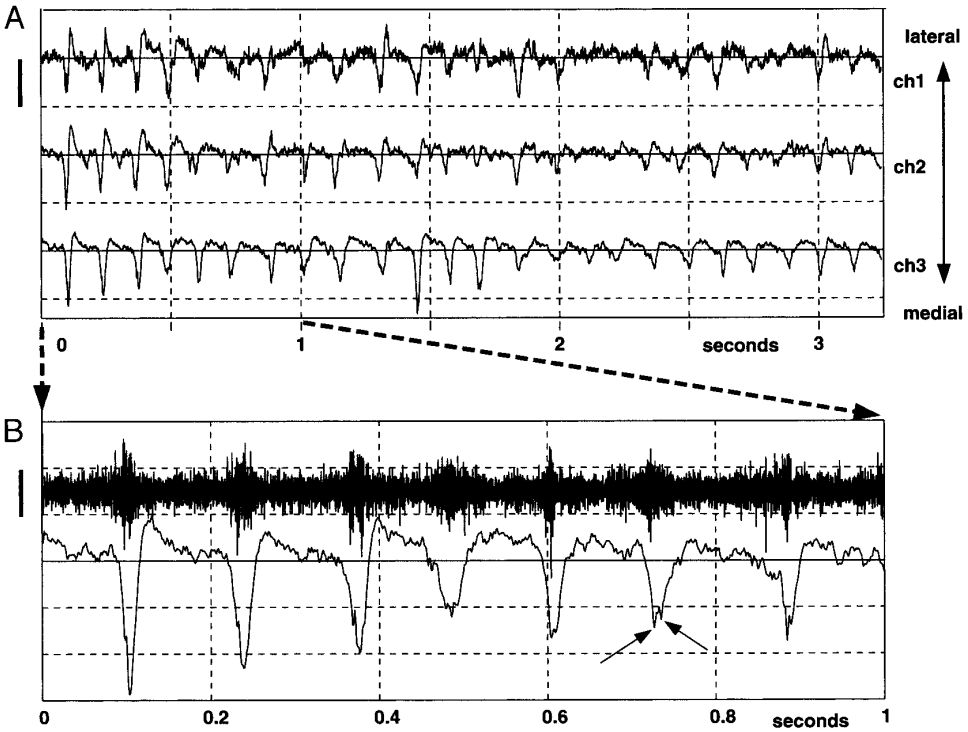

FIG. 1. Oscillatory activity seen in left Crus IIa during awake immobility. Positive potentials (relative to ground) are upward in this and all subsequent figures. *A*: 3 s of typical oscillatory activity recorded from 3 electrodes spaced ~500 μm apart mediolaterally. Data were filtered between 1 and 300 Hz. Scale bar: 250 μV *top trace*, 500 μV *bottom 2 traces*. *B*: expanded timescale of the data from the most medial electrode in *A*. Each field potential oscillation (*bottom trace*, filtered 1–300 Hz) was accompanied by a burst of multiunit activity (*top trace*, filtered 300–3,000 Hz). Most oscillatory peaks were found to contain two or more subsidiary peaks (→). Scale bar: 50 μV *top trace*, 200 μV *bottom trace*.

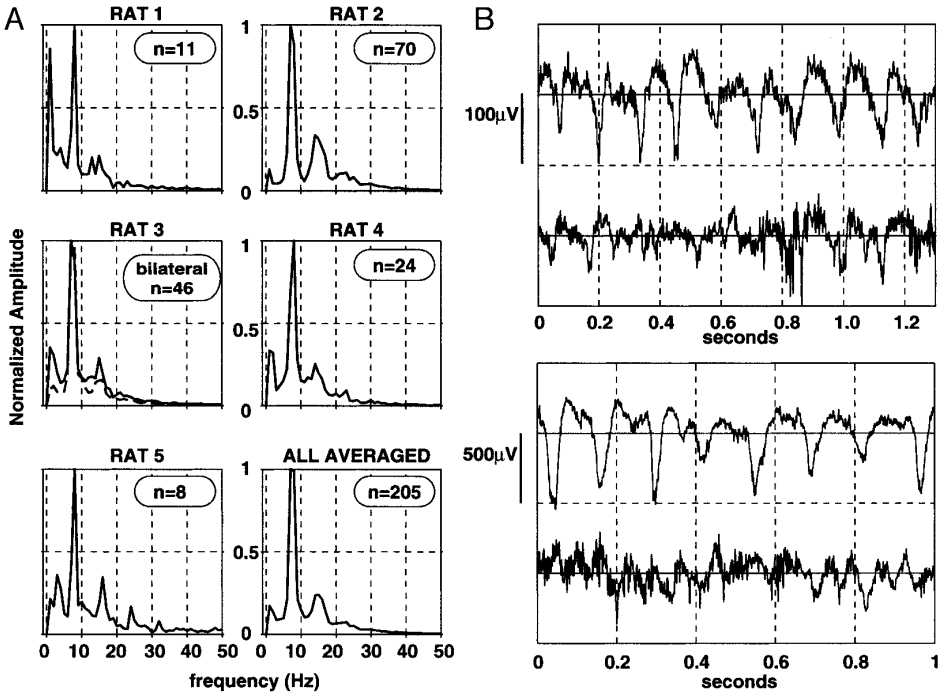

FIG. 2. *A*: oscillation frequency compared among all rats. For each rat, we recorded episodes of oscillatory activity over several days, then divided these episodes into *n* 1-s trials and averaged the Fourier spectra of these trials. Because field potential amplitude depends on many factors, including electrode impedance, each average spectrum was normalized such that the amplitude of the central (8 Hz) peak exactly equals 1. Oscillatory activity in all rats exhibited a central peak ~8 Hz, with subsidiary peaks near 1.2 and 15.0 Hz. *Rat 3* shows the frequency spectra from electrodes implanted bilaterally (——, left Crus IIa; – – –, right Crus IIa). *B*: examples of granule cell layer (GCL) activity from 2 different rats comparing the oscillations observed during immobility (*top trace* in each graph) with the periodic activity seen during active whisker movements (*bottom trace* in each graph). See text for details.

ers to determine the exact whisking frequency. During the period of immobility (*top trace*) no whisker movements were visible.

Periodic GCL activity during whisker movements is apparent in both examples of Fig. 2*B*; in the *top graph* the dominant frequency is near 7 Hz (the whisking frequency), whereas in the *bottom graph* it is in the 15-Hz range. Despite this rhythmicity, however, GCL activity during whisking and general exploration is different from the oscillations observed during immobility. Four differences are immediately apparent: the variability in the dominant frequency is larger, the signal amplitude is smaller, the peaks are less well defined, and the waveform shape is no longer stereotyped.

For all rats, oscillatory activity was always synchronized within Crus IIa (Fig. 1*A*). Oscillations were also found to be synchronized between right and left Crus IIa when electrodes were placed in GCL locations responding to stimulation of the ipsilateral upper lip (left hemisphere, left upper lip; right hemisphere, right upper lip). Figure 3*A* shows 8 continuous seconds of recordings made simultaneously from right and left Crus IIa. In this example, the first episode of oscillatory activity was interrupted when the rat twitched its nose, whereas the second oscillatory episode terminated with a head movement. On an expanded scale (Fig. 3*B*) the oscillatory activity is clearly seen to be synchronized between hemispheres. Figure 3*C* shows the interhemispheric correlation for these data during the periods of nonoscillatory (– – –) and oscillatory (——) activity. Both cross-correlations were normalized by the variance in the autocorrelation of each signal alone, demonstrating a doubling of the correlation coefficient from 0.35 to 0.70. The increase in synchrony during oscillatory episodes was found to hold uniformly throughout trials taken over several days. Over a span of 13 1-s trials from one rat, the average correlation coefficient between hemispheres during nonoscillatory periods was 0.31 ± 0.16, whereas during oscillatory periods it increased to 0.60 ± 0.09 (Student's *t*-test significance level $< 1 \times 10^{-5}$).

Analysis of videotaped behavioral sequences synchronized with ongoing neural activity revealed that oscillations occurred during periods when the animal was immobile and its mouth was not in direct contact with any object. The majority of oscillations occurred after the rat had been recently active (eating, drinking, grooming, or exploring) but then sat quietly for 1–15 min. However, oscillations sometimes also occurred during brief (5–60 s) pauses in activity, a behavioral state sometimes called ''attentive resting'' (Nicolelis et al. 1995). Finally, oscillations at the same frequencies were observed during the early stages of sleep and drowsiness, during recording sessions in the middle of the afternoon (when the rat would normally be asleep). During these sessions the room lights were fully on, the rat was curled into a small motionless ball, and respiration dropped to ~1–1.5 breaths/s. The time course and frequency of oscillations were essentially identical in each of the three behavioral states. During the later stages of sleep we also observed bursts of large, irregular 7- to 12-Hz waves, but these were not included in this analysis.

Detailed analysis of videotape records indicated that the cerebellar oscillations were not related in a consistent way to any overt behavior. Occasionally low-amplitude ($<2°$) tremor of the facial musculature and vibrissae occurred during oscillatory periods, but oscillations also occurred when such tremor was not observable. Table 1 shows the frequency with which different movements coincided with the termination of oscillations and the average duration of oscillatory episodes. Movements that coincided with the termination of oscillatory episodes were defined as follows. *1*) Nose twitch: the nostrils flared and contracted one to five times. *2*) Vibrissal twitch: the vibrissae deflected once, back and forth, never more than 5° in amplitude. We never observed sustained whisking activity to coincide with the termination of oscilla-

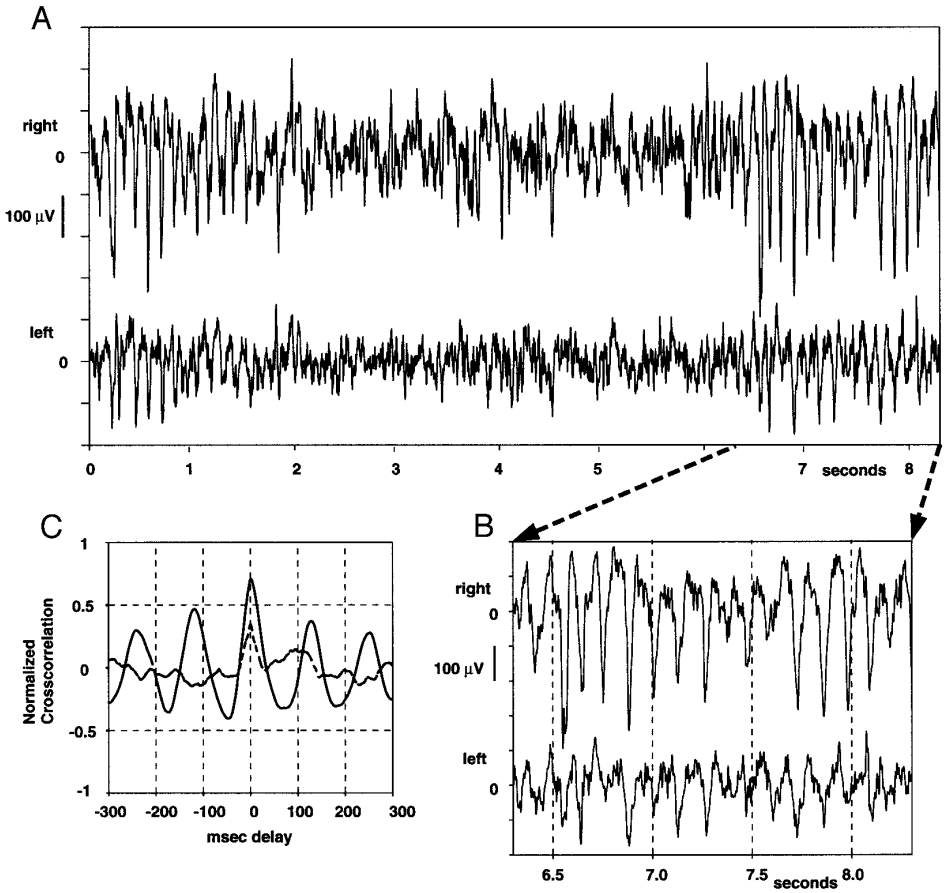

FIG. 3. Interhemispheric synchronization during oscillatory episodes and bilateral interruption of oscillatory activity. *A*: 8 s of continuous recording from right and left cerebellar hemispheres of a bilaterally implanted rat. The 1st episode of oscillatory activity was interrupted when the rat twitched its nose, and the 2nd oscillatory episode terminated with a head movement. *B*: expanding the timescale of the oscillations in the last 2 s of *A* shows clearly that the 2 hemispheres are oscillating in phase. *C*: cross-correlations of the data shown in *A*, comparing periods of oscillatory and nonoscillatory activity. All correlations were normalized by the autocorrelations of each of the two signals alone. ——, average cross-correlation for the data between 1–2 and 6.3–8.3 s (periods of oscillation). – – –, cross-correlation for the data from 2 to 6 s (period of nonoscillatory activity). Correlation coefficient during oscillatory periods = 0.70; during nonoscillatory period = 0.35.

tory activity. *3*) Lip smack: the mouth opened and closed, sometimes accompanied by licking. *4*) Head movement: the head moved, at the level of the neck, while the rest of the body remained immobile. *5*) Body movement: both the head and other body structures (usually the forepaw) moved. These five types of movement were always associated with immediate cessation of oscillatory activity. However, the presence of oscillations did not predict whether a movement would occur: ~32% of the time oscillations ceased spontaneously, without observable sensory input or movement. The duration of oscillatory episodes was highly variable and did not predict whether the oscillations would terminate with a movement or spontaneously cease. Finally, the average duration of oscillatory episodes was not related to the type of movement that coincided with termination. The average duration of oscillatory episodes was not statistically different between any of the behavioral conditions that coincided with oscillation termination, including spontaneous cessation (all Student's *t*-test values >0.1).

TABLE 1. *Frequency of behaviors coinciding with termination of oscillatory activity*

Behavioral Termination	Number of Episodes	Duration, s
Nose twitch	20	3.6 ± 1.6
Vibrissal twitch	9	3.4 ± 1.4
Lip smack	12	3.6 ± 1.8
Head movement	22	4.1 ± 2.7
Body movement	2	3.8 ± 3.6
Spontaneous cessation	30	3.7 ± 2.3
Total	95	3.7 ± 2.1

Duration values are means ± SD. Behaviors are defined in RESULTS.

DISCUSSION

We report for the first time the presence of 7- to 8-Hz oscillatory activity in the GCL of the rat lateral cerebellar hemispheres. These oscillations are similar in frequency to oscillations previously described in rat S1, VB, and SpV (Buzsáki 1991; Kandel and Buzsáki 1993, 1997; Nicolelis et al. 1995; Semba et al. 1980, 1984). In addition, the cerebellar oscillations occur during the same behavioral states as in these earlier studies, including both immobile ''crouching'' or ''attentive resting'' (Nicolelis et al. 1995; Semba et al. 1980, 1984) and drowsiness (Coenen et al. 1991, 1995; Drinkenburg et al. 1991 1993; Steriade and Llinás 1988; Steriade et al. 1993). The majority of oscillatory episodes, however, occurred during behavioral states between these two extremes that could not be satisfactorily classified as alert or drowsy. Under these conditions, the animal had usually been sitting quietly for 1–15 min. Oscillations occurred only when the animal was immobile and the perioral regions represented in Crus IIa (Bower and Kassel 1990) were not being stimulated. Oscillations immediately ceased on any movement but also (in 32% of trials) appeared to cease spontaneously in the absence of observable movement or sensory input.

Since these type of oscillations were first observed in rodent neocortex (Vanderwolf 1975), there has been considerable debate concerning both their origin and functional significance (reviewed in Kaplan 1985). Researchers studying thalamus and neocortex generally proposed that they originate in bursting thalamic cells and thalamocortical loops (Buzsáki 1991; Inoue et al. 1993; Steriade et al. 1985; Steriade and Llinás 1988). The discovery of similar patterns in SpV (Nicolelis et al. 1995) and now the cerebellum suggests that a much larger network of somatosensory structures is involved in this oscillatory activity. Because Crus IIa receives projections from both the trigeminal nuclei (Huerta et al. 1983; Woolston et al. 1981, 1982) and S1 (Bower and Woolston 1983; Morissette and Bower 1996), the coherence seen in the cerebellar oscillations implies a coordination in timing throughout different levels of the somatosensory pathway. It is possible that the subsidiary peaks noted within each larger oscillatory peak reflect coordinated activity between these two pathways. In addition, the high degree of bilateral synchrony observed during oscillatory episodes again suggests widespread involvement of the entire somatosensory system. That the oscillations are so precisely timed, over multiple, bilateral levels of the somatosensory system, makes it unlikely that they emanate from a single brain structure and more likely that they have multiple sources and/or are an emergent property of the somatosensory network. Recent work in culture and computer modeling indeed suggested that the cerebellar GCL itself may participate in the generation of oscillations near these frequencies (Maex and DeSchutter 1998; Nuñez et al. 1996).

Because these type of oscillations occur at a frequency similar to that of whisker movements (Carvell and Simons 1990; Welker 1964), several authors have speculated that they may represent an internal model for whisking or a mechanism to increase sensory reception during whisking (Nicolelis et al. 1995; Semba et al. 1980, 1984). Consistent with these studies, we did on occasion observe whisker tremor ($<2°$) during some oscillatory episodes, but the majority of oscillations occurred without visible tremor. Furthermore, oscillatory activity did not predict the onset or occurrence of any particular type of movement, including that of the whiskers. Movements that resulted in the termination of oscillations included nose and vibrissae twitches, lip smacks, and head and body movements. Vibrissal twitches, defined as a single back-and-forth deflection ($<5°$) of the large vibrissae, coincided with only 10% of oscillation terminations. In no instance did sustained whisking activity coincide with the termination of an oscillatory episode.

An alternative possibility is that instead of predicting whisker movements, the observed oscillatory activity actually *results* from vibrissal movements so small as to be unobservable in video recordings. The most sensitive cells in the trigeminal ganglion respond to vibrissal deflections of $<0.1°$, although the median threshold for the population of trigeminal ganglion cells is about 1.0° (Gibson and Welker 1983). Movements of 0.1° would not be observable in standard video recordings, but there are three reasons why the oscillations are highly unlikely to be the result of rhythmic peripheral input or motor activity. First, the oscillations were not present when the animal was sniffing the air rhythmically, even when the sniffing was accompanied by whisker tremor or whisker movements. Second, as shown in Fig. 2*B*, the periodic GCL activity during low-amplitude whisker movements is different from the GCL oscillations associated with immobility, even when the whisker movements occur in the same frequency range as the oscillations. Finally, previous studies have established that these type of oscillations occur in central sensorimotor structures in the absence of oscillatory activity in more peripheral structures. Semba et al. (1980) showed that 7- to 8-Hz cortical and thalamic oscillatory activity can occur without oscillations in the vibrissal EMG. Nicolelis et al. (1995) demonstrated that this type of synchronous activity occurs in the SpV, VB thalamus, and S1 without oscillatory activity in either the trigeminal ganglion or the principal trigeminal nucleus.

It appears unlikely, then, that the oscillations described here either predict or result from whisker movements, and we must expand our search for possible functional significance. To this end, it is instructive to compare these oscillations with those recently discovered in the lateral cerebellum of awake monkeys performing reaching movements (Pellerin and Lamarre 1997). Consistent with this work, we found GCL oscillations to occur only during immobility and to terminate immediately with any movement. However, unlike the reaching monkeys, our rats were not engaged in a timed behavioral task; rather, they were unrestrained and freely moving. While this paradigm limits our ability to time the oscillations relative to an invariant sensory or motor event, it also puts us in a much better position to examine the correlations of these oscillations with natural behavior. It is clear from both studies that movement or sensory input always disrupt the oscillations, but it is important to distinguish between the following two possibilities. *1*) Are the oscillations ''anticipatory of'' the sensory input or movement that coincides with their termination? *2*) Does sensory input or movement simply *interrupt* a continuous baseline of oscillatory activity that might otherwise cease spontaneously? Our data are more consistent with the latter hypothesis; we found that oscillations were associated with a wide range of behavioral states, and the presence of oscillations did not predict imminent movement or sensory input. Oscillatory episodes had highly variable durations, and the durations did not predict whether, or which type of, movement was to follow. In fact, a large percentage of oscillatory episodes ceased spontaneously, in the absence of any observable movement or sensory input.

Thus, although we consider it quite likely that the oscillations may be modulated by subtle fluctuations in arousal state (see below), we do not believe that the oscillations preferentially occur when the animal is waiting for sensory input or that the oscillations are specifically antecedent to movement. Instead, we propose they are related to the overall dynamical state of the sensorimotor system. In some sense this interpretation is consistent with earlier associations of these oscillations with systemic cortical epileptiform activity (Buzsáki et al. 1990; Coenen 1995; Coenen et al. 1991; Drinkenburg et al. 1991, 1993; Robinson and Gilmore 1980; Vergnes et al. 1987). However, it is our view that the tendency of the rat somatosensory system to oscillate at these frequencies does not reflect a pathological state as in the case of epilepsy, but is rather a fundamental and important property of the system as a whole.

Specifically, we propose that in analogy to the θ (4–12 Hz) frequency of the olfactory system, the oscillations described here reflect a baseline clocking activity of the entire somatosensory system, important for the temporal segmentation of incoming data. We previously proposed such a function for theta oscillations based on our computer models of the olfactory cerebral cortex (Bower 1996; Wilson and Bower 1992). These models suggest that θ oscillations in olfactory cortex emerge from network properties of the cortex itself and that the olfactory cortex is tuned to oscillate at the frequencies of input it naturally receives (Wilson and Bower 1992). In awake rats θ oscillations are coincident with sniffing behavior, and this oscillatory activity thus reflects the way in which the olfactory system segments its sensory data stream.

Similarly, we propose that the oscillations now seen throughout the somatosensory system also reflect an underlying system resonance. Several studies in anesthetized animals have already demonstrated that somatosensory cortex segments incoming stimuli at ~10 Hz (Agmon and Connors 1991; Morissette and Bower 1996; Simons 1978; Simons and Carvell 1989). The current study shows that oscillatory activity near 10 Hz arises in the somatosensory system of awake animals specifically in the *absence* of movement and tactile sensory input. We suggest that these oscillations, observed during periods of immobility, directly reflect the mechanism for the ~10-Hz segmentation, and further that this segmentation is an inherent part of computation within cerebral-cortically related systems. As resonant modes of physical systems are often most obvious in the absence of forcing functions, so the baseline oscillations of neural circuits may be most apparent when the network is not under barrage by sensory data. This hypothesis leads to the prediction that there must exist inhibitory feedback loops to prevent uncontrolled oscillations; the epileptic activity observed in some inbred strains of rats may result from deficiencies in this feedback regulation.

This hypothesis also leads to the prediction that the underlying resonance, always found between 7 and 8 Hz, could interact in complex ways with the periodic signals resulting from whisking movements, which, although rhythmic, are not stereotyped. Whisking movements can vary substantially in velocity and amplitude and encompass a large frequency range (Carvell and Simons 1990). Whisker movements frequency matched to the resonance might result in enhanced signal amplitude, processing speed, and efficiency, but whisking frequencies unmatched to the resonance may result in more complicated functions, as suggested especially by the *bottom traces* of both graphs in Fig. 2*B*. Thus, although our hypothesis is consistent with the earlier suggestion that the oscillations might serve to increase sensory reception at the 7- to 8-Hz whisking frequency, the oscillations may be more precisely said to reflect the temporal structure inherent to cortical information processing. In other words, thalamocorticocerebellar loops may serve to ensure that incoming data are processed near 10 Hz, independent of the frequency of the incoming data: the oscillations are simply what we observe when recording the baseline state of this resonant system. That the oscillations do not occur at all times when the rat is immobile suggests that they may be additionally modulated by internal variables without externally observable behavioral correlates, such as subtle fluctuations in arousal.

With respect to the cerebellum, 7- to 12-Hz oscillations have more usually been associated with the inferior olivary nucleus and its climbing fiber projections (Llinás 1988; Llinás and Yarom 1986; Sasaki et al. 1989) than with the GCL. For example, it was recently suggested that oscillatory activity within the inferior olivary nucleus is the source of periodic timing information controlling motor coordination (Welsh et al. 1995). In our view, however, the tendency for the inferior olive to oscillate near 10 Hz may simply reflect the tendency for a much larger network of cerebral-cortically related structures to oscillate at these frequencies. In this study we have suggested that these underlying dynamics are most apparent in the absence of sensory input or motor behavior; consistent with our data, Keating and Thach (1997) recently reported that climbing fibers do not exhibit oscillatory activity while monkeys are actively performing arm movements. It may very well be, then, that olivary oscillations, like the GCL oscillations described here, are not as apparent when the sensorimotor system is actively receiving input or generating output.

Understanding the computational consequences of the 7- to 8-Hz resonant state of the inferior olive and the somatosensory system as a whole will require additional experiments as well as more sophisticated computational models. However, we regard the data presented here as further evidence that the cerebellar hemispheres are closely tied to the somatosensory system. We recently proposed, in fact, that these regions of the cerebellum are more concerned with sensory data than with motor output (Bower 1997). The results presented here are consistent with this idea.

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