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Research note

Cortical barrel field ablation and unconditioned whisking kinematics

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Abstract

The effects of "barrel cortex" ablation upon the biometrics of "exploratory" whisking were examined in three head-fixed rats which had previously sustained unilateral ablation of the left cortical "barrel field" under electrophysiological control. Unconditioned movements of a pair of bilaterally homologous whiskers (C-1, Right, Left) were monitored, optoelectronically, with other whiskers present. Whisking movements on the intact and ablated side were analyzed with respect to kinematics (protraction amplitude and velocity) whisking frequency and phase relationships between whisking movement on the two sides of the face. Histological analysis confirmed complete removal of S-1 "barrel cortex". In normal animals whisking movements have a characteristic rhythm (6–9 Hz), and protractions on the two sides of the face tend to be both synchronous and of very similar amplitudes. In the lesioned animals, whisking frequency was unchanged and whisking movements remained bilaterally synchronous. However, there was a significant difference between the amplitude of Right and Left whisker movements which was evident many months postoperatively. Our results suggest that the deficits in vibrissa-mediated tactile discrimination reported after "barrel" field ablation may reflect an impairment in the animal's ability to modulate whisking parameters on the two sides of the face to meet the functional requirements of a discriminative whisking task. The effects upon whisking amplitude seen after unilateral barrel field ablation are consistent with a model in which the activity of a whisking Central Pattern Generator is modulated by descending inputs to achieve sensorimotor control of whisking movement parameters.

Keywords:*somatosensory cortex, barrel field, vibrissa, whisking, patterns*

Introduction

The rat's mystacial vibrissae function as sensorimotor elements in an "active touch" system. During *exploratory* behaviors the rat emits bursts of "whisking"—a rhythmic pattern of alternating protraction and retraction movements of the mystacial vibrissae (Welker, 1964). Recent analyses of whisking biometrics have established that these movements have a characteristic rhythm (6–9 Hz), and that protractions on the two sides of the face tend to be both synchronous, and of very similar amplitudes (Carvell and Simons, 1990; Bermejo *et al.*, 1998; Gao *et al.*, 2001a). Whisker contact with object surfaces generates patterns of somatosensory input which contribute to *discriminative* behavior by resolving spatial properties of objects into spatio-temporal patterns of neural activity. Identification of the neural substrates mediating the generation and modulation of whisking behavior is an important problem for the analysis of vibrissal sensorimotor function.

Anatomical, physiological and behavioral evidence suggests a possible role for the whisker "barrel field", which occupies a substantial proportion of the rat's somatosensory cortex (Woolsey *et al.*, 1974). In addition to their isomorphic representation of the whiskers, this region possesses reciprocal, topographically organized connections with ipsilateral vibrissal motor cortex (Miyashita *et al.*, 1994; Izraeli and Porter, 1995), forming a *sensorimotor* feedback circuit for the recurrent control of vibrissa movements. Previous studies have shown that "exploratory" whisking remains intact after extensive cortical lesions (Welker, 1964; Semba and Komisaruk, 1984). However, we have no data on the effects of cortical "barrel field" lesions upon the biometrics of "exploratory" whisking.

To provide such data we examined the effects of unilateral "barrel field" ablation upon the kinematics of unconditioned whisking movements, ipsilateral and contralateral to the ablated area. Because contact with object surfaces affects both whisking amplitude and frequency (Carvell and Simons, 1990) our data were obtained from head-fixed animals, restricted to whisking in air, i.e., isolated from *ex*-afferent inputs. We used a high-resolution optoelectronic system to record whisking trajectories in a pair of identified, bilaterally homologous whiskers on the two sides of the face, with all the remaining whiskers present. Unilateral ablation of the cortical

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"barrel" field does not effect whisking frequency but is followed by a significant imbalance in the amplitude of whisking movements on the two sides of the face which is evident many months postoperatively.

Materials and methods

Subjects and surgical procedures

Three Long–Evans rats served as subjects. Animals were anesthetized with Nembutal (50 mg/kg), with supplements (tenth of original dose) given as necessary. A craniotomy was made above S1 cortex and carbon fiber electrodes were advanced into layer IV of cortex (~550 μm). Multi-unit responses evoked by vibrissal-stimulation were monitored on an audio-monitor. A rough map of the "barrel field" was made by determining the receptive field of neurons encountered in each penetration. The location of each electrode placement with respect to bregma was mapped on a diagram showing the blood vessel pattern overlying the "barrel field". Using this information, the left "barrel field" was delineated and removed by subpial aspiration. The cavity was filled with gelfoam, the scalp replaced over the ablated area, and a dental cement crown with an embedded mounting screw was constructed to allow head fixation. Data on whisking in normal animals were obtained from several rats, previously anesthetized and fitted with head mounts for use in another study.

Behavioral testing

For about a month postoperatively, the lesioned subjects were used in an experiment in which they were reinforced with water for lever pressing on a Variable Interval schedule, but no discrimination training was given, and whisker movements were never reinforced. Approximately 8 months postoperatively, the movement trajectories of a pair of bilaterally homologous whiskers (C-1 Right, Left) were monitored (under head-fixation and body restraint conditions) in three successive 30 min daily test sessions during which the rats were whisking in air. To reduce stress, water was delivered at random intervals during the session but water delivery was independent of the occurrence of whisking, i.e., subjects were never reinforced for whisking movements. Each session involved 30 "trials" whose termination was defined by the occurrence of 2 s periods during which the house light was turned off and data were saved to disc.

Methods for characterizing whisking kinematics have been described in detail elsewhere (Bermejo *et al.*, 1998). Briefly, an optoelectronic system (laser emitters and detectors) was used to monitor individual whisker movements along a plane that includes the rostro-caudal axis. Movements of the whisker generated a voltage shift in the detector and the location of that shift is linearly related to whisker position. An emitter–detector pair was positioned on each side of the face, perpendicular to the axis of movement, and whisking movement trajectories were determined *separately* for each side (Harvey *et al.*, 2001, Fig. 1). Movement trajectories were transformed to angular coordinates and displayed on a computer monitor as a plot of whisker position against time (Fig. 2). A cursor-driven program was used to scan this plot and select episodes of whisking for analysis. Individual whisks were selected on the basis of their general shape (i.e., a protraction followed by a retraction). Once selected, a specially written algorithm found the beginning, peak and end of the whisk—the peak being defined simply as the maximum forward position attained prior to retraction—and calculated the values for specific kinematic parameters (e.g., peak amplitude, velocity and rise time). The data were then downloaded to a spreadsheet program for statistical and graphic manipulations. Time series data were analyzed using a finite Fourier analysis (FFT) of the whisking waveforms. The bilateral synchrony of whisker movements on the two sides of the rat face was assessed using cross-correlation analysis.

Histological analysis

Animals were killed with an overdose of Nembutal, perfused with heparinized 0.1 M phosphate buffer, followed by 4% paraformaldehyde. The brain was removed, post-fixed over night and sectioned. Coronal sections were stained for cytochrome c-oxidase (Wong-Riley, 1979) and the extent of the lesion was determined.

Results

Figure 1 presents coronal sections at the level of the lesion in each of the three animals. There is some inter-animal variability in the depth of the ablation, which extends into the internal capsule in two of the three animals. In all three rats, the cortical damage was restricted to the posterior-medial barrel field and includes all of the S1 barrel cortex, covering an area of 3–5 mm medio-laterally and nearly 6 mm rostro-caudally.

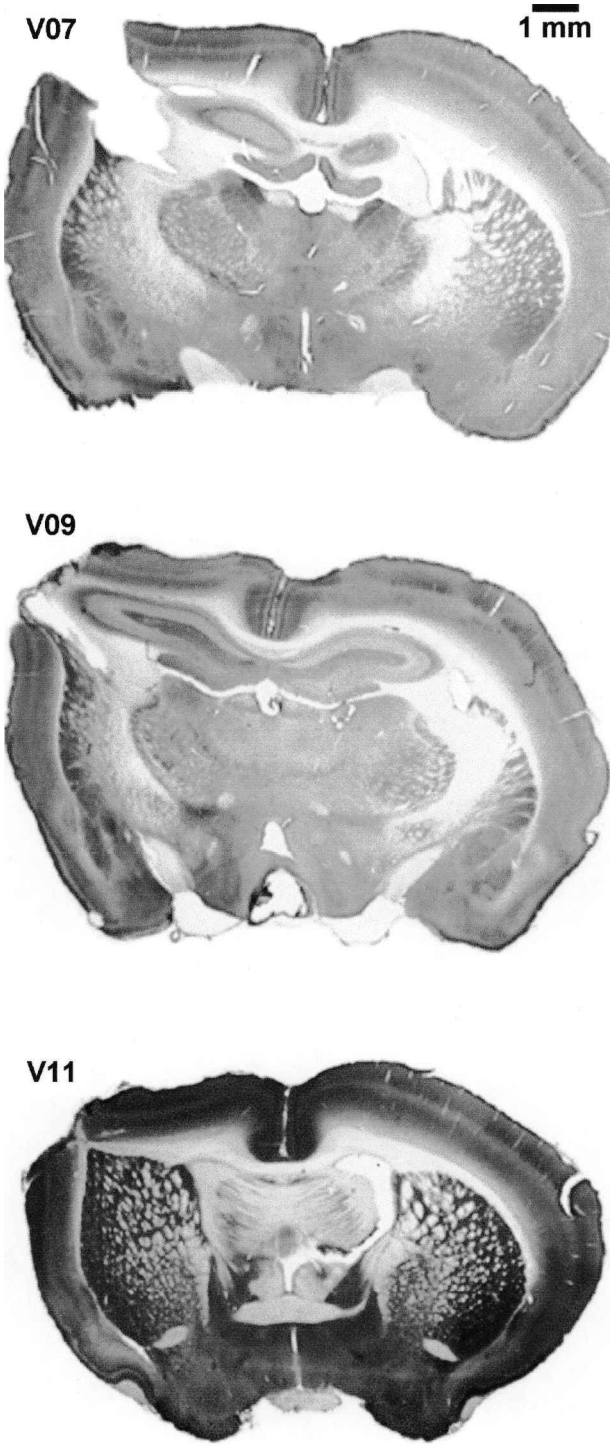

FIGURE 1. Cytochrome-oxidase stained, coronal sections through the middle of the cortical barrel field, at the level of the lesion in each of the three experimental animals.

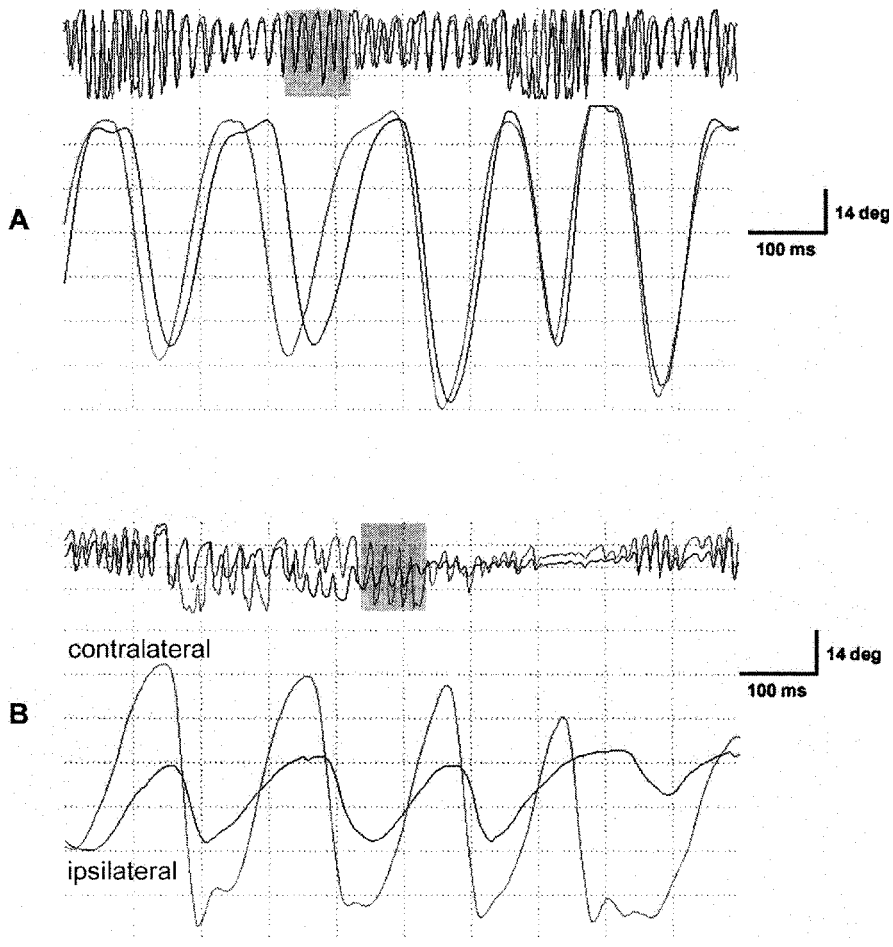

FIGURE 2. Optoelectronic monitoring of whisking movements made by the Right and Left C-1 whiskers in a normal animal (top panel) and a lesioned animal (bottom panel). The top trace in each panel is plotted at low resolution and in the bottom trace the shaded portion of the top record is replotted at high resolution. Upward movements are protractions; downward movements are retractions. The scale bars are relevant only to the high-resolution plots.

Kinematic analysis

Figure 2 illustrates the basic finding of the study. The top panel presents low- and high-resolution plots of the movement trajectories of the Right and Left C-1 whiskers in a normal animal, head-fixed and whisking in air. The bottom panel presents similar data for a rat with a lesion of the left cortical barrel field. In the normal animal (top panel), whisking movement trajectories on the two sides have very similar amplitudes. In the lesioned animal there are obvious differences in amplitude between the movements of the whisker ipsilateral and contralateral to the lesion which, though variable, are evident throughout the record. Figure 3 plots the mean amplitude of whisking movements recorded from the Right and Left C-1 whiskers of the three lesioned animals. In all three rats, the amplitudes of whisking movements on the two sides of the animal were significantly different.

No other aspect of whisking kinematics was affected by the lesion. Despite the differences in whisking amplitudes on the two sides of the face, amplitude scaling functions for the whiskers ipsilateral and contralateral to the (left) ablated cortical barrel field were similar (Fig. 4). A Fourier analysis of whisking frequencies showed no significant differences between power spectra on the two sides of the

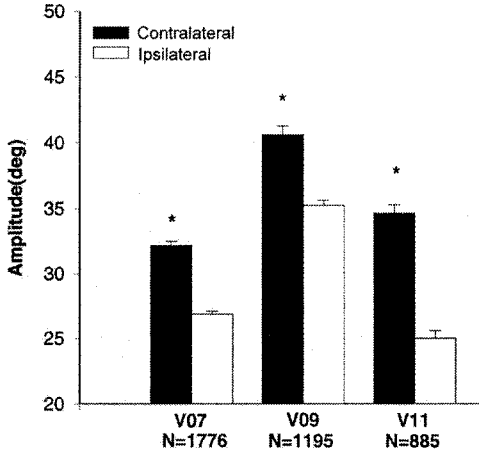

FIGURE 3. Mean whisking amplitudes for the Right and Left C-1 whiskers in three animals with a lesion of the *left* barrel field. Values of *N* refer to the number of whisking movement pairs measured for each animal; the variability measure shown is the standard error of the mean, and an * indicates that the amplitude difference on the two sides is significant at or beyond the 5% confidence level.

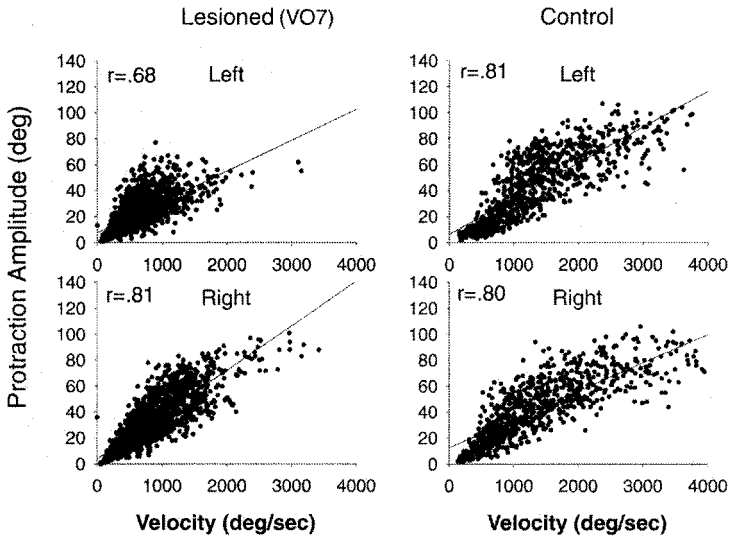

FIGURE 4. Amplitude scaling functions in a lesion and a control animal. (Left panels) Scaling functions for the left and right whiskers in one of the lesioned animals. (Right panels) Scaling functions for the right and left whiskers in a control animal. The regression line and correlation coefficient are shown. Although the range of protraction amplitudes emitted differs on the two sides of the lesioned animals, the correlation between peak protraction velocity and peak protraction amplitude is highly significant for both.

same animal. Cross-correlation analysis of phase relationships between whisking movements on the two sides of the face indicated that whisking remained bilaterally synchronous. The cross-correlograms had their main peaks centered about zero and correlation values were highly significant ($r = +0.5$ to $+0.65$; $p < 0.001$).

Discussion

In normal rats whisking in air, whisker movements on the two sides of the face exhibit similar frequencies, tend to be bilaterally synchronous and have very similar protraction amplitudes. Following ablation of the cortical "barrel field", whisking frequency and amplitude scaling functions are unchanged and whisking movements remain bilaterally synchronous. However, the mean *amplitudes* of whisking movements on the two sides of the face are significantly different, and the effect is present many months postoperatively. In normal animals, amplitude scaling of whisking movements involves primarily control of protraction velocity, an observation consistent with a "pulse-height" motor control strategy (Gordon and Ghez, 1987). Since the lesion produces a unilateral shift in amplitude, it is important to note that there is no difference in the basic amplitude/velocity scaling function for whisking movements on either side, between the treated and untreated sides.

(Note: There was some incidental involvement of internal capsule and more dorsal regions of basal ganglia). We consider it unlikely that such collateral damage contributed to the reported effects for the following reasons. First, representation of oral regions in the rat striatum lies in the most ventral part of the lateral striatum (Cho and West, 1997). Second, even very large unilateral striatal lesions, while they may disrupt performance of a sensory-cued motor task (Aldridge *et al.*, 1997), do not produce substantial or persistent effects upon simple movements (Villablanca *et al.*, 1976). Third, there is no relation between the extent of basal ganglia involvement and the change in whisking amplitude. Finally, a recent study of the effects of unilateral ablation of vibrissal motor cortex, in which there was no basal ganglia involvement, found changes in whisking amplitude on the side contralateral to the lesion (Gao *et al.*, 2001).

Unfortunately, the absence of preoperative data on whisking kinematics makes it impossible to specify the *direction* of the amplitude shift produced by the lesion in the present study. Nevertheless, the observation that barrel cortex lesions produce an imbalance in the amplitude of whisking responses may have implications for previous studies which have shown that such lesions disrupt whisker-mediated tactile discrimination (Guic-Robles *et al.*, 1992). During the acquisition of a tactile discrimination, the rat refines its whisking pattern by modulating vibrissa movement parameters. Indeed, improved discrimination performance is correlated with control of whisking amplitude (Carvell and Simons, 1995). Moreover, whiskers on the two sides of the face move synchronously as they palpate the discriminanda (Carvell and Simons, 1990). Thus, sensory processing during discriminative whisking is dependent upon a significant degree of sensorimotor control of the whiskers on both sides of the face. Ablation of the cortical "barrel" field may disrupt the coordinated control of whisking amplitude required to meet the demands of the discriminative task and such a disruption could account for the deficits in "active touch" reported after barrel field ablations. This conclusion is consistent with previous reports

showing that "barrel field" ablation has no effect upon tactile detection or discrimination tasks involving *passive touch*, but does disrupt performance on tasks requiring control of whisker movements, e.g., gap-detection, texture discrimination (Hutson and Masterton, 1986; Guic-Robles *et al.*, 1992).

The effects of unilateral "barrel field" ablation upon whisking amplitude are also consistent with the hypothesis of a whisking Central Pattern Generator, which is modulated by descending inputs from cortical sensorimotor structures (Carvell *et al.*, 1996; Kleinfeld *et al.*, 1999; Gao *et al.*, 2001). S1 vibrissa cortex, in addition to its callosal connections, possesses topographically organized reciprocal connection with vibrissal motor cortex (Miyashita *et al.*, 1994; Izraeli and Porter, 1995), which, in turn, projects upon brainstem premotor circuits implicated in the organization of such a putative "whisking" CPG (Hattox *et al.*, 2000). Because input from the "barrel fields" makes a substantial contribution to the activity of vibrissal motor cortex, its *unilateral* removal might produce an imbalance in modulatory cortical input to the CPG, accounting for the differential amplitudes of whisker movements on the two sides of the face.

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