

Unilateral vibrissa contact: changes in amplitude but not timing of rhythmic whisking

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Abstract

Electromyographic recordings from the mystacial pad of rats were used to assess the effect of unilateral vibrissa contact on the bilateral movement of the vibrissae. A first group of animals was trained to whisk freely in air and served to establish the baseline variability in bilateral symmetry. We observed that the electromyogram (EMG) activity across the two mystacial pads was rhythmic and synchronous to within 2 ms on a whisk-by-whisk basis; this value is small in comparison with the ~50 ms required for protraction during the whisk cycle. A second group of animals was trained to use their vibrissae to contact a sensor that was located on one side of the head. The average EMG activity across the two pads was synchronous at the time of vibrissa contact, albeit with higher variability than for the case of free whisking. In contrast, the average amplitude of the activity on the contact vs noncontact side of the face was transiently greater, by 25% or ~10°, at the time of contact. These data show that the amplitude of the vibrissae on the two sides of the face can be controlled independently, while the timing of vibrissa movement is largely synchronous.

Key words: electromyogram, rat, synchrony, touch

A multitude of muscles in animals operate with coordinated bilateral symmetry. In mammals, the facial muscles that are used for chewing, smiling and suckling are one such set. In rodents, the facial muscles are specialized for the movement of the macrovibrissae (Dorfl, 1982; Wineski, 1983, 1985); long sensory hairs that the animal uses for touch. The vibrissae are used to guide locomotion, discriminate between surfaces, and to judge the distance to objects (Vincent, 1912, 1913; Welker, 1964; Hutson and Masterton, 1986; Guic-Robles *et al.*, 1989, 1992; Carvell and Simons, 1990, 1995; Brecht *et al.*, 1997). Qualitative (Welker, 1964; Semba and Komisaruk, 1984; Carvell and Simons, 1990) and quantitative (Gao *et al.*, 2001) observations suggest that these behavioral tasks are performed with bilaterally symmetric movements of the vibrissa.

Here we ask if whisking maintains bilateral symmetry in the face of an intrinsically asymmetric task. We use a paradigm in which a food reward serves to reinforce movement of the vibrissae so they reliably contact an object placed on one side of the face. To the extent that the correct decision depends on contact with only one set of vibrissae, the asymmetric nature of this task is likely to maximize any potential differences in muscular control of the opposing mystacial pads. Our goal is to determine if such unilateral contact leads to asymmetry in

movement. We distinguish between two possibilities. First, that the movement of vibrissae on the two sides remains fully coordinated, as may be expected if the central control of whisking has bilateral symmetry. Second, that the movement on the two sides of the face is controlled independently, so that the animal may move the vibrissae on one side more than the other side as it achieves contact.

Two sets of experiments were performed. The first involved a precise measurement of the baseline symmetry of whisking. Free ranging animals were trained to whisk in air for extended periods (Fig. 1B). Previous analyses of freely moving rats established that such whisking is highly rhythmic (Fee *et al.*, 1997; O'Connor *et al.*, 2002; Berg and Kleinfeld, 2003), which facilitates the use of correlation techniques to calculate potential timing differences (Loeb *et al.*, 1987). The second set of experiments involved the use of animals that were trained to use their vibrissae to contact a sensor (Bermejo and Zeigler, 2000) that was placed on one side of the face (Fig. 1C and D). The head was fixed in one position to insure that only the vibrissae moved (Ono *et al.*, 1986; Bermejo *et al.*, 1996). This restraint prevented the rat from making contact without moving its vibrissae and insured that the same vibrissae made contact with the sensor on successive trials. In all cases, the rectified electromyogram (EMG) of

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mystacial muscles was used as a surrogate of vibrissa position (Berg and Kleinfeld, 2003).

Methods

Fifteen adult Long Evans rats, 250–350 g in mass, were used as subjects. Rats were gentled and acclimatized to the experimental environment over a period of 1–2 weeks prior to surgical implanting of the EMG electrodes. Eleven of these animals were trained to whisk in air, as described previously (Fee *et al.*, 1997; O'Connor *et al.*, 2002; Berg and Kleinfeld, 2003), and used as controls to measure the degree of bilateral synchrony in EMG activity during rhythmic movement of the vibrissae in air (Fig. 1B). The experimental sequence is summarized as

Training → EMG surgery → Recording EMG.

Four of the 15 animals were used in a head-fixed preparation, as described previously (Sachdev *et al.*, 2000, 2002), in which animals were trained to whisk with their head held rigidly in place. We recorded the bilateral EMG, a contact signal, and video images of the vibrissae as the animal contacted an object. The progression for these animals is summarized as

Training → Headpost surgery → Retraining →
EMG surgery → Recording EMG.

The care and all aspects of the experimental manipulation of our animals were in strict accord with guidelines from the National Institutes of Health (1985) and have been reviewed, approved, and observed by members of the local Institutional Animal Care and Use Committees at Vanderbilt University and at UCSD.

Surgery

Animals were anesthetized with ketamine (90 mg per kg rat mass) and xylazine (10 mg per kg rat mass). For the case of head-fixed animals only, a first surgery involved the placement of a stainless steel post over the cerebellum. The post was fastened by placing

00–90 self-tapping screws in the skull and bridging the screws to the base of the post with dental acrylic. The post was attached to a clamp that held the trained animals as they were restrained in a body tube.

The mystacial pads of all animals were implanted with Teflon-coated tungsten microwires to serve as recording electrodes for the EMG. We used 0.002" diameter wire with 1 mm of insulation stripped off the end and threaded the wires through the mystacial musculature. Up to three wires were placed in each pad. A reference wire was threaded under the skin of the nose.

Behavioral training: whisking in air

After a 5-day recovery from surgery, rats were deprived of solid food and trained to explore a figure-of-eight maze as a means to gain access to liquid food (50% (w/v); LD-100; PMI Feeds Newco Distributors Rancho Cucamongo, CA). Small objects were occasionally introduced to the maze to encourage exploratory whisking. Food was presented through a hand-held syringe that was placed at different locations. Each recording session lasted about 1 h and a total of 10 ml of liquid food was typically imbibed in a session. Recording was repeated daily for 3–7 days.

Behavioral training: whisking for contact

Animals were trained to drink chocolate flavored whole milk while restrained in a tube that restricted movements of their limbs. After a 5-day recovery from surgery to implant the headpost, the animals were subsequently head restrained and trained to move their whiskers to obtain the milk as a reward. The vibrissae were trimmed in a manner that allowed only the caudal D2 or D1 vibrissae to make contact with a sensor (Fig. 1c). Trimming also made it possible to reliably follow the position of a particular vibrissa with videography. With continued training, the sensor was positioned further from the vibrissae so that vigorous whisking became the norm.

Electronics and recording

The EMG wires were buffered at the head of the animal with a field effect transistor (SST4118; Vishay Siliconix, Santa Clara,

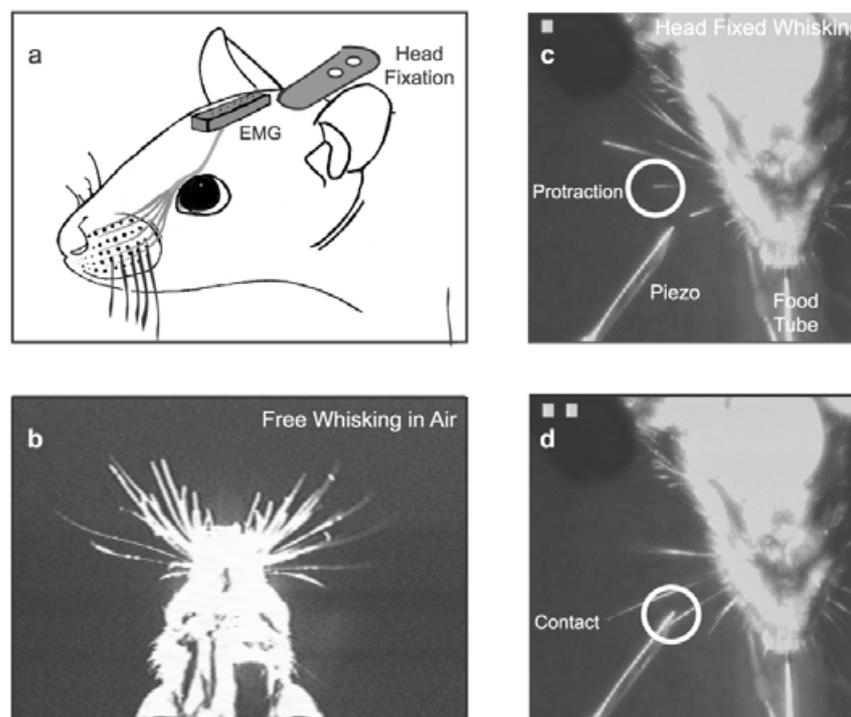


Figure 1. Overview of the experimental procedures. (a) Schematic of the mystacial pad of the rat. Microwire electrodes were placed in each of the pads as a means to record the electromyogram (EMG) on both sides of the face; the wires exited through a connector mounted on the head of the animal. For the contact experiments, the head of the animal was fixed by attachment to a fixation post. (b) Video image of the rat as it whisks freely in air. Data from such free roaming animals were used to record the bilateral symmetry of whisking. (c and d) Selected frames from a sequence taken 12 ms before and upon a single contact of the D2 vibrissa with a piezoelectric sensor. The circle highlights the D2 vibrissa. Note the food tube in the foreground.

CA) in a common-source configuration and recorded differentially with respect to the reference in the nose. We filtered the fast motor unit activity on the EMG wires between 200 Hz and 10 kHz. The signal was subsequently full-wave rectified, low-pass filtered at 90 Hz, and subsampled at $t_s = 500$ Hz. Vibrissa contact was determined with a piezoelectric film element (LDT0-028K; Measurement Specialties, Inc., Wayne, PA), whose voltage output was shunted across a 20 k Ω resistance to improve the temporal response of the device. The output was amplified and sampled at $t_s = 500$ Hz. It was further used to trigger a solenoid that gated the flow of chocolate milk in a food tube to be contingent on contact. There was an approximately 10 ms delay between contact and the onset of the flow of the milk reward.

In addition to EMG activity, vibrissa movement in the head-fixed animals was directly recorded with videography at a rate of 250 frames per second (Motion Scope, Redlake Inc., San Diego, CA) for periods extending at least 100 ms before and after contact (Fig. 1C and D). The video images were used to estimate the absolute angle of vibrissae movement during whisking for the head-fixed animals.

Analysis

Our primary tool was crosscorrelation analysis. We denote the EMG signals on the right and left side of the face by $E_R(t)$ and $E_L(t)$, respectively. The time-varying components are given by $\delta E_R(t) \equiv E_R(t) - \bar{E}_R$ and $\delta E_L(t) \equiv E_L(t) - \bar{E}_L$, respectively, where the time average is defined by

$$\bar{E} = \frac{1}{N_T} \sum_1^{N_T} E(t)$$

where N_T is the number of time points so that $N_T t_s$ is the temporal window of the correlation. The crosscorrelation, denoted $C(\tau)$, is a normalized measure that is defined by

$$C(\tau) = \frac{\sum_{t=1}^{N_T} \delta E_R(t) \delta E_L(t+\tau)}{\sqrt{\sum_{t=1}^{N_T} \delta E_R^2(t) \cdot \sum_{t=1}^{N_T} \delta E_L^2(t)}}$$

The parameter τ is the lead or lag time of one signal with respect to the other. The crosscorrelation can have multiple maxima and minima, but will have a single absolute maximum. The value of the lead/lag time at the absolute maximum is designated τ_{lead} .

Results

Our trained animals tended to whisk robustly for epochs that ranged from 1 s to nearly 10 s (Fig. 2A). Qualitatively, there was a high degree of synchrony between the right and left sides. We quantified the fidelity of the bilateral symmetry in terms of the crosscorrelation of the EMG on the two sides of the face for temporal windows of 1.0 s. For the particular example shown in Figure 2A, the crosscorrelation peaks at $\tau_{\text{lead}} = 5.5$ ms (Fig. 2B; in this example the vibrissae on the right side are slightly ahead of those on the left. A histogram across all whisking epochs with this animal shows that the responses are distributed in a narrow range (Fig. 2C), with a mean correlation time of $\langle \tau_{\text{lead}} \rangle = 2.1$ ms and a standard deviation (SD) of 5.2 ms.

As a control for bias in our instruments, we measured the crosscorrelation between a pair of electrodes in the same mystacial pad. With three EMG electrodes on each side of the face, there are six possible crosscorrelations on one side. For all possibilities, we observed that the correlation was narrowly distributed and centered around equal time, i.e., $\langle \tau_{\text{lead}} \rangle = 0.0$ ms. The results for a particular pair are illustrated in Figure 2D.

The mean correlation time, denoted $\langle \tau_{\text{lead}} \rangle$, was calculated across all epochs for each of our animals (Fig. 2E; 6,997 1 s epochs across 11 animals). With a single exception, the value of $\langle \tau_{\text{lead}} \rangle$ was within 1 SD of zero. On the other hand, there was a systematic shift of the mean value across all epochs toward leading with the right side. This bias was statistically significant, with an average over all animals of

$$\langle \langle \tau_{\text{lead}} \rangle \rangle = 1.6 \pm 0.7 \text{ ms (mean} \pm \text{SEM)}.$$

The average SD of $\langle \langle \tau_{\text{lead}} \rangle \rangle$, which defines the range of normal variability in the bilateral symmetry of whisking, was 6.1 ms. Thus while the value of τ_{lead} is biased in the sense of a population average, this bias is not discernible on a whisk-by-whisk basis.

We now consider whisking during the unilateral contact task (Fig. 3). Compared with the case of whisking in air, there was considerable variability in the movement of the vibrissae between different experimental trials and within a given trial. The typical situation is that contact occurred near the start of the whisking epoch and that the EMG signals from the two sides of the face remained largely synchronized (Fig. 3A). The amplitudes of the two EMG signals differed, particularly at the time of contact (Fig. 3A). Lastly, and interestingly, the animals continued to whisk for periods well over 1 s after contact, although food appeared well within one whisk cycle after contact.

As for the case of whisking in air, we quantified the fidelity of the bilateral symmetry in terms of the crosscorrelation of the EMG on the two sides of the face. With respect to the above example, the crosscorrelation provided a means to quantify the time-lead during, as well as before and after, contact (Fig. 3B; the correlation has a window of 0.67 s). As a means to quantify the change in the crosscorrelation across our sample, we extracted the time-lead from calculations of the crosscorrelation as a function of the time relative to contact; we chose a window of 0.25 s and analyzed only those trials for which whisking extended for at least 1.0 s ($n = 58$ trials across four animals). Only trials with a single contact event were included in the analysis. We observe that, on average, the timing of activity on the two sides was not disrupted by contact. The average time-lead over all animals was given by (Fig. 3C)

$$\langle \langle \tau_{\text{lead}} \rangle \rangle = 7 \pm 12 \text{ ms (mean} \pm \text{SEM)}.$$

The above result shows that unilateral contact does not disrupt the bilateral symmetry of whisking with respect to the timing of the motion across the two sides of the face. The symmetry is maintained as the animal whisks in air for up to ~ 1 s after contact. The large variability in comparison with the case for whisking in air reflects the smaller sample size with the head-fixed animals and the greater irregularity in whisking with this population.

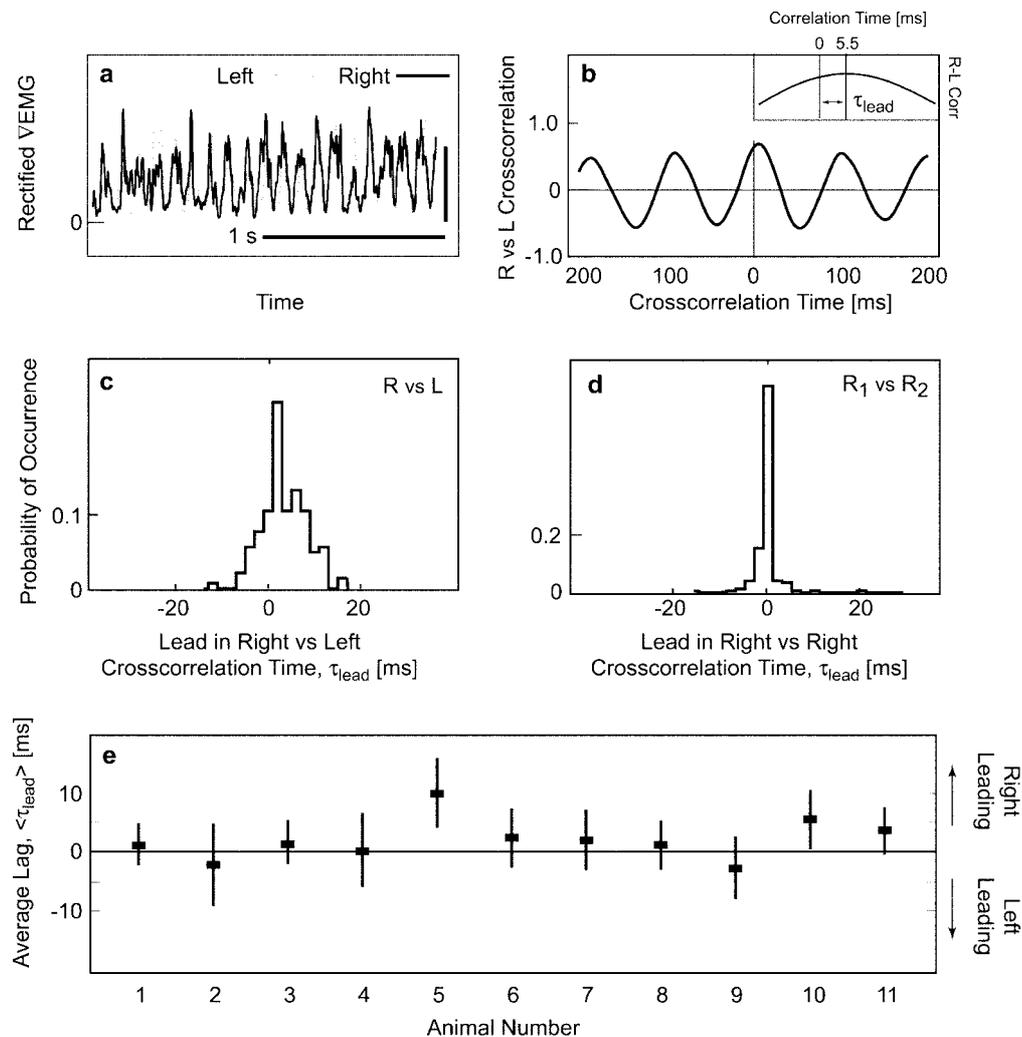


Figure 2. Symmetry of the right vs left EMG during whisking in air. (a) A representative rectified and low-pass filtered EMG trace during an epoch of whisking. Notice that EMG from the right side of the face is slightly advanced compared with that from the left side. Vertical bar is $100 \mu\text{V}$. (b) The crosscorrelation for the 1 s interval depicted by the temporal scale bar in part (a). The inset is an expansion around equal time and highlights a small asymmetry, denoted τ_{lead} ; the positive sign implies that activation of the musculature on the right side leads that on the left. (c and d) The probability distribution of τ_{lead} determined for an ensemble of whisking epochs with a representative animal. The mean is $\langle \tau_{\text{lead}} \rangle = 2.1 \text{ ms}$ and variability is $\text{SD} = 5.2 \text{ ms}$ ($n = 149$). The control data in part (d) were obtained by computing the distribution for the EMG from a pair of wires on the same side of the face ($n = 149$). The mean is $\langle \tau_{\text{lead}} \rangle = 0 \text{ ms}$. (e) The mean values and SDs of τ_{lead} measured across all 11 animals.

A second aspect of whisking is the amplitude, or angular displacement, of the vibrissae movement. In principle, the motion of the two sides can follow the same time course, or frequency for rhythmic whisking, yet have different amplitude. We calculated the amplitudes of the rectified EMG on the contact vs noncontact side of the face, denoted A_{contact} and $A_{\text{noncontact}}$, respectively, as a function of the time relative to contact. We observed that the amplitude of the vibrissae movement was nearly equal except at the time of contact (Fig. 3D) for which

$$\frac{A_{\text{contact}} - A_{\text{noncontact}}}{A_{\text{noncontact}}} = 0.25 \pm 0.09 \text{ (mean} \pm \text{SEM)}.$$

This difference corresponds, on average, to $10 \pm 4 \text{ deg}$ of difference in the absolute amplitude of vibrissa angular displacement; see, e.g., the initial whisk cycle in Figure 3A.

The above result shows that the amplitude of whisking is transiently modulated by unilateral

contact. Subsequent to contact, the rats whisk with essentially equal amplitude, as in the case of whisking in air for up to $\sim 1 \text{ s}$ after contact.

Discussion

We have shown that, on average, the vibrissae maintain bilateral synchrony while they whisk to contact a salient object on a single side of the face (Fig. 3E). This finding parallels the synchrony observed when animals whisk in air, as analyzed here (Fig. 2E) and in previous work (Gao *et al.*, 2001). Our novel finding is that the amplitude of the vibrissa movement on the two sides can transiently decouple, so that movements on the side that makes contact have significantly larger amplitude (Fig. 3D).

When vibrissae touch on only one side because they contact edges or objects that are present only on one side, the vibrissae on the two sides might be expected to move in different ways. In this study,

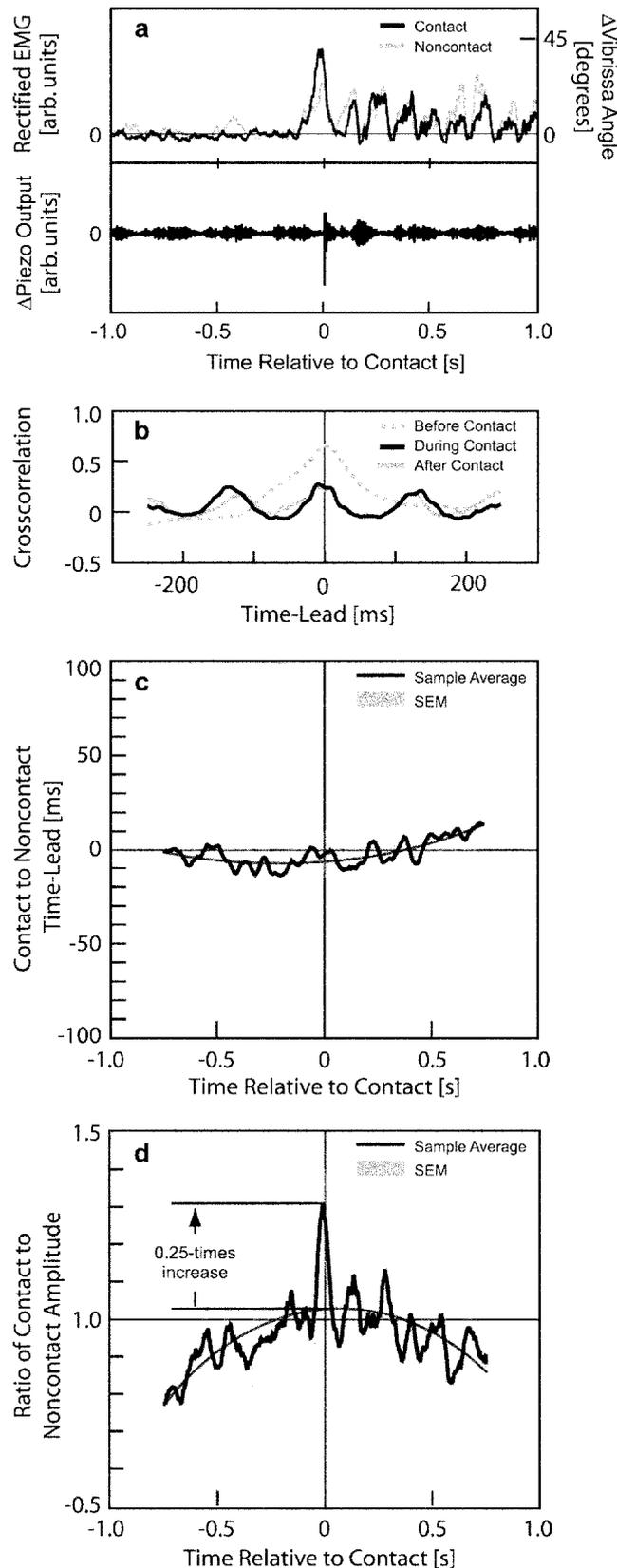


Figure 3. Symmetry of the right (contact side) vs left (noncontact side) EMG during vibrissa contact in return for a liquid reward. (a) Activity of the mystacial muscular, as reflected in the rectified and low-pass filtered EMG activity on the two sides, as a head-fixed animal whisks. Note that the animal makes a single whisk prior to contact with the piezoelectric sensor and continues whisking after contact. Videography was used to calibrate the EMG scale. The contact signal was derived from the piezoelectric sensor (Fig. 1C). (b) Crosscorrelation of the EMG activity for the records in part (a). The windows were centered 0.5 s prior to contact, at contact, and 0.5 s after contact, respectively, and the integration window was 0.5 s. Note that all of the correlations have a peak close to equal time. (c) Average time-lead as a function of the amplitude on the noncontact side. The integration window was 0.5 s. (d) The ratio of the amplitude of the EMG on the contact vs the amplitude on the noncontact side.

we maximized the possibility of observing different movement on the two sides by training animals to move their vibrissae into contact with a sensor placed on only the left side of the face. Though we find that the movement on the two sides of the face is not perfectly coherent on a whisk-by-whisk basis, which leads to a large variability in the crosscorrelation in the contact task (Fig. 3C), on average movements on the two sides of the face occur synchronously.

Bilateral symmetry during free whisking

The rhythmic movements that form exploratory whisking in air occur essentially at a constant frequency (Berg and Kleinfeld, 2003). This allowed us to determine the timing between movements on the right and left sides of the rat with high precision (Fig. 2C). We found that, as a population, there is a bias of 1.6 ms for the vibrissae on the right to lead those on the left (Fig. 2E). The value of the bias is small compared with the approximately 50 ms period for protraction of the vibrissae (Gao *et al.*, 2001; Sachdev *et al.*, 2002), yet it is significant on the time-scale of timing differences that are relevant for the induction of plasticity (Bi and Poo, 1998; Feldman, 2000). One may thus conjecture that slight behavior asymmetries play a role in the learning of sensory tasks. Interestingly, the same direction of bias has been observed when rats use their vibrissae to forage (LaMendola and Bever, 1997).

Mechanisms for asymmetric whisking

Our results suggest that the control of the timing of rhythmic vibrissae motion can be decoupled from the control of the amplitude of whisking. This suggests that the timing of vibrissa movement is controlled largely in a symmetric fashion. Neuroanatomical substrates exist for bilateral communication of motor control at the level of the brainstem (Li *et al.*, 1993a, b). In contrast to the bilateral coupling of the timing of vibrissa motion our data suggest that the amplitude of vibrissa motion may be individually controlled on each side of the animal's face. One aspect of this control may involve contact-initiated feedback via ipsilateral and contralateral projections from the trigeminal nuclei to the vibrissa motoneurons in the facial nucleus (Erzurumlu and Killackey, 1979; Isokawa-Akesson and Komisaruk, 1987; Li *et al.*, 1997; Kleinfeld *et al.*, 1989).

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References

- BERG, R.W., and D. KLEINFELD (2003) Rhythmic whisking by rat: retraction as well as protraction of the vibrissae is under active muscular control. *J Neurophysiol* **89**: 104–117.
- BERMEJO, R., D. HOUBEN, and H.P. ZEIGLER (1996) Conditioned whisking in the rat. *Somatosens Mot Res* **13**: 225–234.
- BERMEJO, R., and H.P. ZEIGLER (2000) “Real-time” monitoring of vibrissa contacts during rodent whisking. *Somatosens Mot Res* **17**: 373–377.
- BI, G.Q., and M.-M. POO (1998) Synaptic modifications in cultured hippocampal neurons. Dependence on spike timing, synaptic strength, and postsynaptic cell type. *J Neurosci* **18**: 10464–10472.
- BRECHT, M., B. PREILOWSKI, and M.M. MERZENICH (1997) Functional architecture of the mystacial vibrissae. *Behav Brain Res* **84**: 81–97.
- CARVELL, G.E., and D.J. SIMONS (1990) Biometric analyses of vibrissal tactile discrimination in the rat. *J Neurosci* **10**: 2638–2648.
- CARVELL, G.E., and D.J. SIMONS (1995) Task- and subject-related differences in sensorimotor behavior during active touch. *Somatosens Mot Res* **12**: 1–9.
- DORFL, J. (1982) The musculature of the mystacial vibrissae of the white mouse. *J Anat* **135**: 147–154.
- ERZURUMLU, R.S., and H.P. KILLACKEY (1979) Efferent connections of the brainstem trigeminal complex with the facial nucleus of the rat. *J Comp Neurol* **188**: 75–86.
- FEE, M.S., P.P. MITRA, and D. KLEINFELD (1997) Central versus peripheral determinates of patterned spike activity in rat vibrissa cortex during whisking. *J Neurophysiol* **78**: 1144–1149.
- FELDMAN, D.E. (2000) Timing-based LTP and LTD at vertical inputs to layer II/III pyramidal cells in rat barrel cortex. *Neuron* **27**: 45–56.
- GAO, P., R. BERMEJO, and H.P. ZEIGLER (2001) Vibrissa deafferentation and rodent whisking patterns: behavioral evidence for a central pattern generator. *J Neurosci* **21**: 5374–5380.
- GUIC-ROBLES, E., W.M. JENKINS, and H. BRAVO (1992) Vibrissal roughness discrimination is barrel cortex-dependent. *Behav Brain Res* **48**: 145–152.
- GUIC-ROBLES, E., C. VALDIVIESO, and G. GUAJARDO (1989) Rats can learn a roughness discrimination using only their vibrissal system. *Behav Brain Res* **31**: 285–289.
- HUTSON, K.A., and R.B. MASTERTON (1986) The sensory contribution of a single vibrissa's cortical barrel. *J Neurophysiol* **56**: 1196–1223.
- ISOKAWA-AKESSON, M., and B.R. KOMISARUK (1987) Difference in projections to the lateral and medial facial nucleus: anatomically separate pathways for rhythmical vibrissa movement in rats. *Exp Brain Res* **65**: 385–398.
- KLEINFELD, D., BERG, R.W., and O'CONNOR, S.M. (1999) Anatomical loops and their electrical dynamics in relation to whisking in rat. *Somatosens Mot Res* **16**: 69–88.
- LAMENDOLA, N.P., and T.G. BEVER (1997) Peripheral and cerebral asymmetries in the rat. *Science* **278**: 483–486.
- LI, Y.-Q., M. TAKADA, and N. MIZUNO (1993a) Identification of premotor interneurons which project bilaterally to the trigeminal motor, facial or hypoglossal nuclei: a fluorescent retrograde double-labeling study in the rat. *Brain Res* **611**: 160–164.
- LI, Y.-Q., M. TAKADA, and N. MIZUNO (1993b) Premotor neurons projecting simultaneously to two orofacial motor nuclei by sending their branched axons. A study with a fluorescent retrograde double-labeling technique in the rat. *Neurosci Lett* **152**: 29–32.
- LI, Y.G., M. TAKADA, T. KENOKO, and N. MIZUNO (1997) Distribution of GABAergic and glycinergic premotor neurons projecting to the facial and hypoglossal nuclei in the rat. *J Comp Neurol* **378**: 283–294.
- LOEB, G.E., W.J. YEE, C.A. PRATT, C.M. CHANAUD, and F.J. RICHMOND (1987) Cross-correlation of EMG reveals widespread synchronization of motor units during some slow movements in intact cats. *J Neurosci Meth* **21**: 239–249.
- NATIONAL INSTITUTES OF HEALTH (1985) *Guide for the Care and Use of Laboratory Animals*, NIH Publication 85-23, Bethesda.
- O'CONNOR, S.M., R.W. BERG, and D. KLEINFELD (2002) Coherent electrical activity along vibrissa sensorimotor loops during free whisking in rat. *J Neurophysiol* **87**: 2137–2148.
- ONO, T., K. NAKAMURA, H. NISHIJO, and M. FUKUDA (1986) Hypothalamic neuron involvement in integration of reward, aversion and cue signals. *J Neurophysiol* **56**: 63–79.

- SACHDEV, R.N., T. SATO, and F.F. EBNER (2002) Divergent movement of adjacent whiskers. *J Neurophysiol* **87**: 1440–1448.
- SACHDEV, R.N., H. SELLIEN, and F.F. EBNER (2000) Direct inhibition evoked by whisker stimulation in somatic sensory (S1) barrel field cortex of the awake rat. *J Neurophysiol* **84**: 1497–1504.
- SEMBA, K., and B.R. KOMISARUK (1984) Neural substrates of two different rhythmical vibrissal movements in the rat. *Neuroscience* **12**: 761–774.
- VINCENT, S.B. (1912) The function of the vibrissae in the behavior of the white rat. *Behav Mon* **1**: 7–81.
- VINCENT, S.B. (1913) The tactile hair of the white rat. *J Comp Neurol* **23**: 1–23.
- WELKER, W.I. (1964) Analysis of sniffing of the albino rat. *Behaviour* **12**: 223–244.
- WINESKI, L.E. (1983) Movements of the cranial vibrissae in the golden hamster (*Mesocricetus auratus*). *J Zool (Lond)* **200**: 261–280.
- WINESKI, L.E. (1985) Facial morphology and vibrissal movement in the golden hamster. *J Morphol* **183**: 199–217.