

# SWITCH BETWEEN PROCESSING OF ACTIVE AND PASSIVE TOUCH IN RAT BARREL CORTEX IS CONTROLLED BY A CENTRAL MOVEMENT RELATED SIGNAL

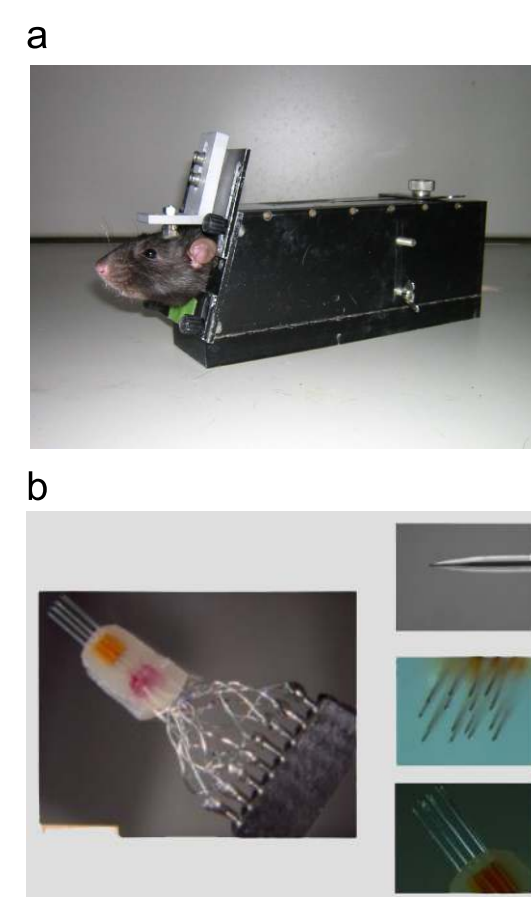
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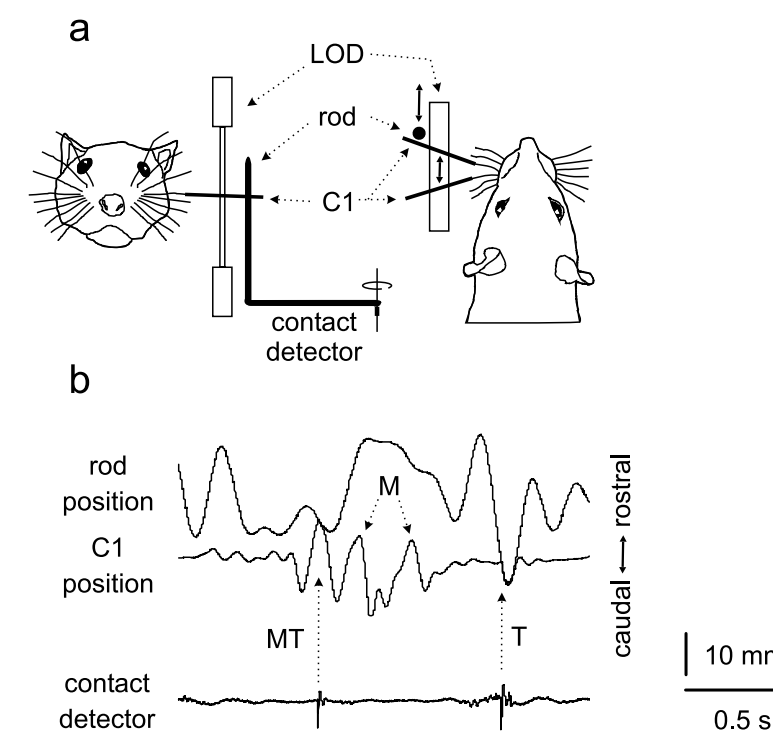
## Introduction

Palpatory movements contribute specifically to the accomplishment of a somatosensory percept and, thus, are an integral part of sensing. Here, we investigated how a specific palpatory motor act - muscle-propelled whisker movement in rats - altered neuronal responses to a tactile stimulus (contact with an object) in barrel cortex.

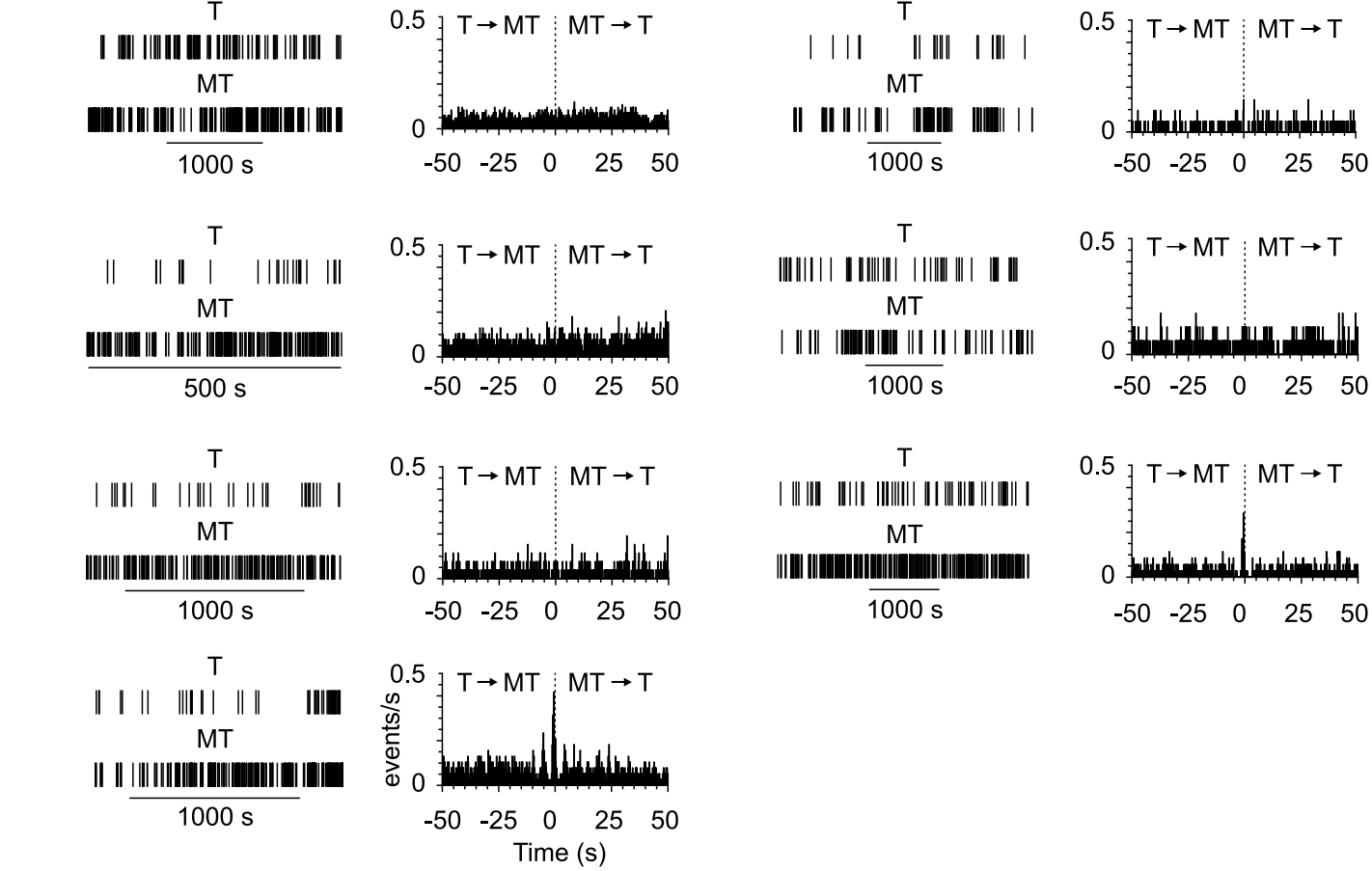
## Methods



**Head-fixed rats and multielectrode electrophysiology were used to assess LFP and spike response in barrel cortex during active and passive touch.** **a.** Head restrained rat outside the experimental set up. **b.** Custom made array of the type used in this study (shown is a 4x4 array). In this study nine pulled and ground glass coated platinum tungsten electrodes (80  $\mu$ m shank diameter, 23  $\mu$ m diameter of the metal core, free tip length ca. 8  $\mu$ m, impedance >1 MW) were mounted inside a 1x9 array of polyimide tubing setting distance between tips to about 450  $\mu$ m. The free ends of the electrodes were soldered to teflon insulated silver wires which in turn connected to a microplug. The electrodes were permanently implanted into the posteromedial barrel subfield (barrel cortex) at a depth of 1200-1400  $\mu$ m below the surface. The electrode array covered the barrel corresponding to whisker C1 in all cases as verified by receptive field properties. Surface potentials were recorded from a steel ring (O.D. 5 mm) placed on the pia embracing the site of electrode penetration.

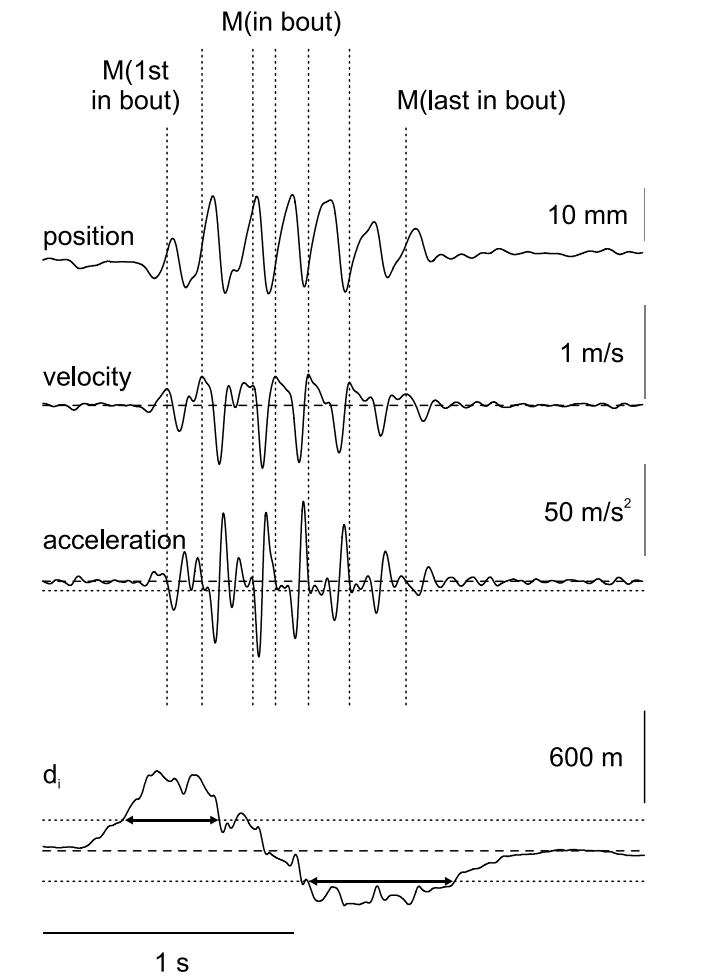


**Dissection of sensorimotor behavior.** **a.** Trajectory of elongated whisker C1 was measured in the rostro-caudal plane with a laser-optical device (LOD). Whisker contacted a randomly moving glass rod mounted on a magnetic cartridge to detect minute concussions. Licking movements were detected by the tongue intersecting a light beam and triggered a water reward through a spout in front of the rat's snout (not shown). **b.** Classifications of contacts. T: touch only; MT: movement and touch. M: movement only.

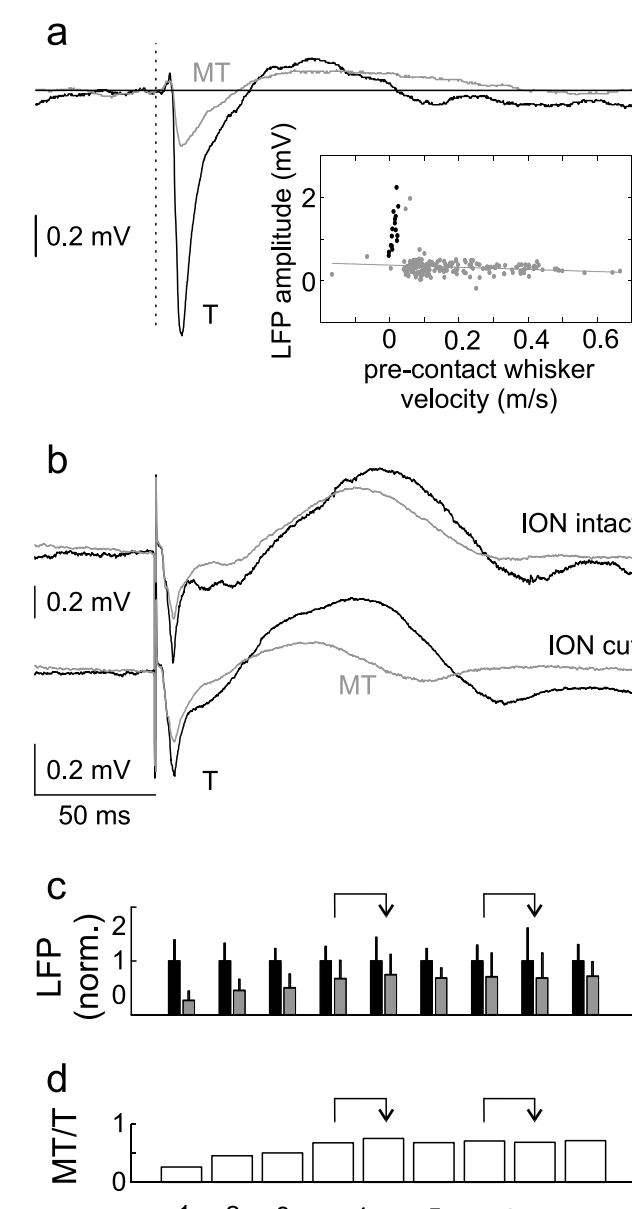


**T and MT events were well intermingled** (sample of 7 animals/sessions). Left columns: Single raster of T and MT events during the entire session. Right columns: Cross correlograms of T and MT events from the same sessions (bin width 0.1s).

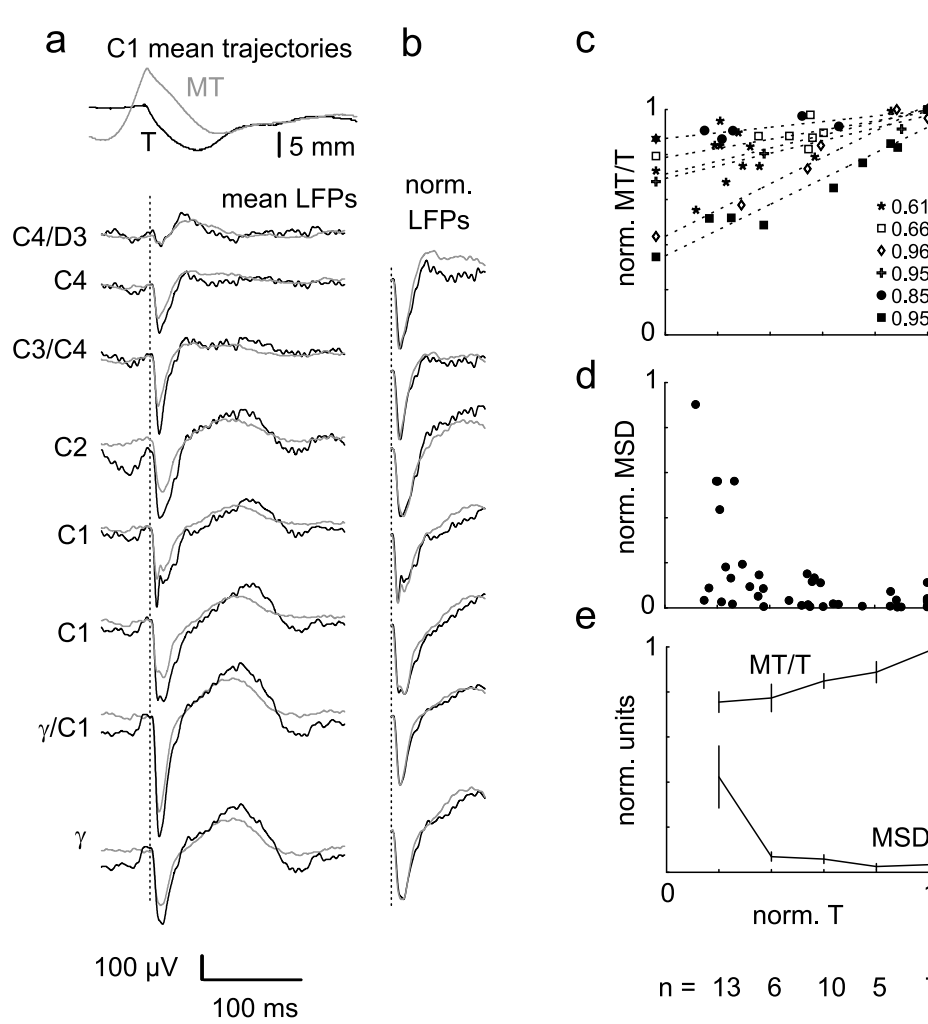
**Detection of M events.** **d.** is the difference of the integral obtained from the rectified velocity trace in a window 300 ms before and after each point in time. Three thresholds were adjusted individually for each rat (positive and negative thresholds for **d**, symmetric around zero and a negative threshold for acceleration; all indicated by dotted lines; dashed lines indicate zero). Intervals in which **d** stayed above the positive or below the negative threshold for at least 100 ms (indicated by double arrows) were used to search for the first and the last whisker stroke in the bout, respectively. All M events were aligned to points in time in which the acceleration was zero and velocity assumed a local maximum. If intervals of less than 75 ms were obtained the second event was purged from the data. Also, contacts with the rod in a window [-150 150] around a M event led to its elimination.



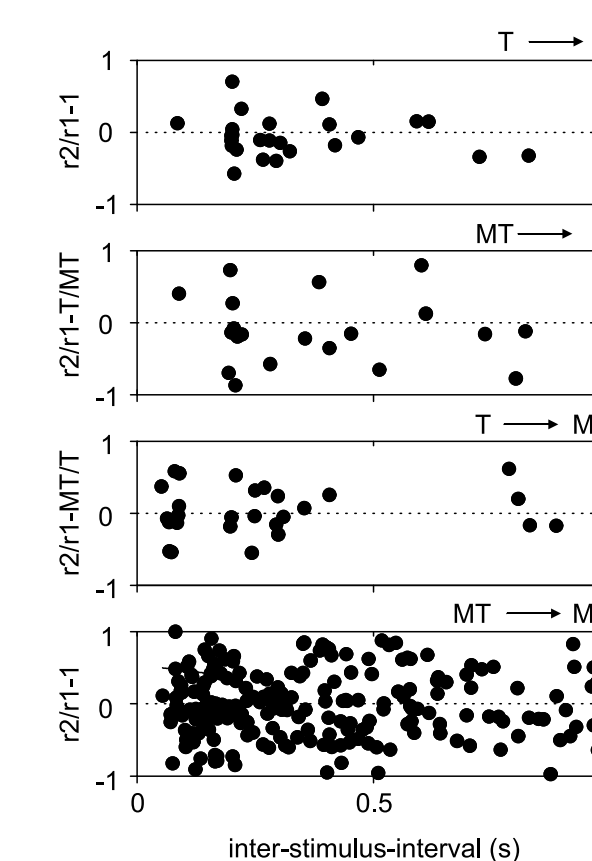
**A central signal attenuates evoked LFP responses in a switch like manner for active touch.** **a.** Mean LFP response during resting whisker (black trace), and during whisker movement (gray trace) (MT/T ratio 0.23). Inset, black dots: amplitudes to T events, gray dots: MT events. **b.** Mean responses from a different rat that received contact-triggered stimulation via a cuff electrode at the contralateral infraorbital nerve (ION, note the stimulus artifacts). Signal attenuation in the active case is smaller than in a (MT/T ratio 0.68) and was virtually unchanged after cutting the nerves bilaterally (MT/T ratio 0.71). **c.** Population data of means and standard deviation of evoked LFP amplitudes normalized to the response obtained with T events (T: black, MT: gray). Rats # 1,2,3,5, and 7 received mechanical stimulation and rats #4 and 6 received electrical stimulation (the arrows point to the results obtained after the nerve was cut). **d.** corresponding MT/T ratios obtained in the 9 sessions depicted in c.



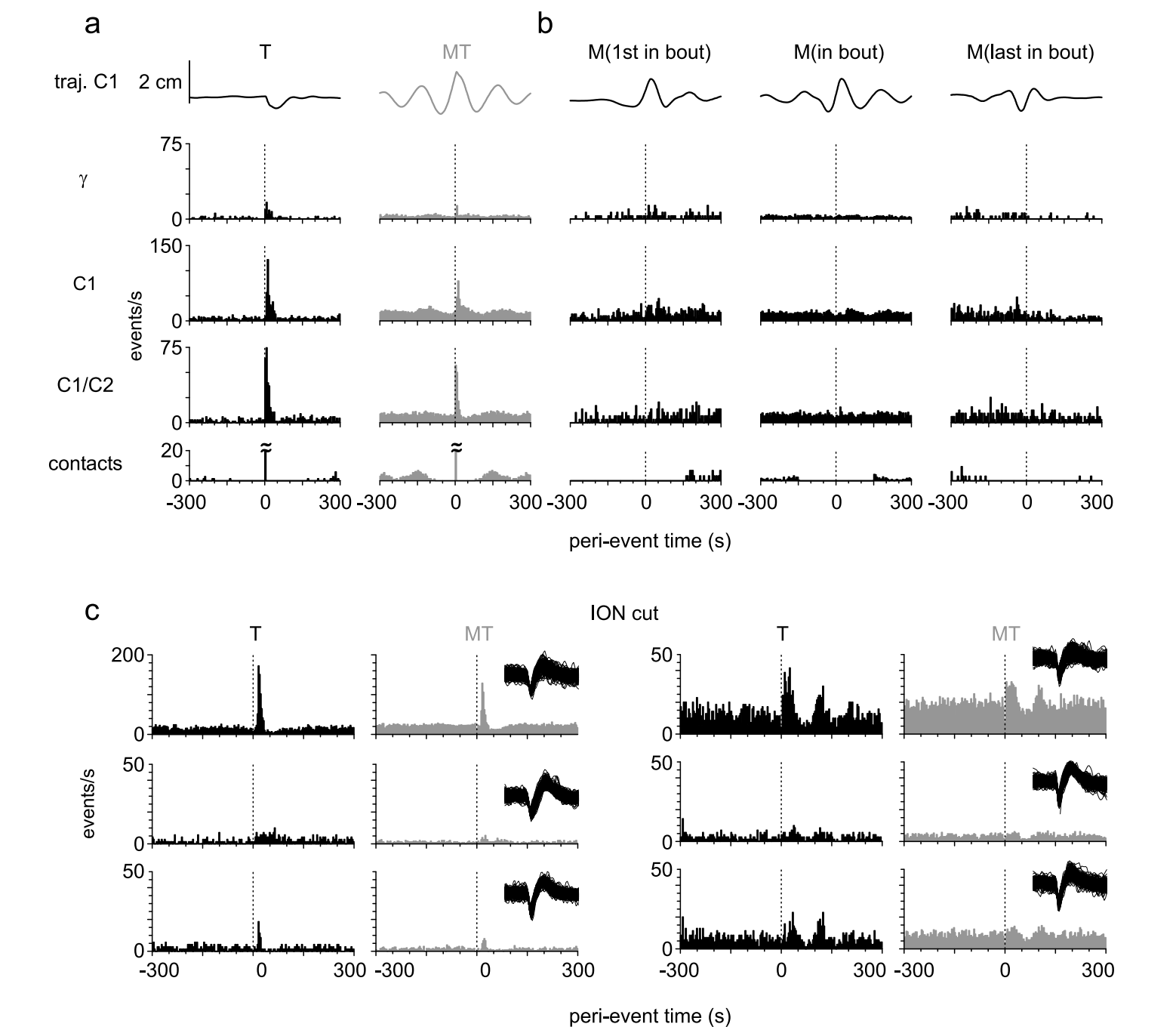
**Response attenuation is a decrement in gain and is smallest in the main barrel.** **a.** Mean whisker trajectories (upper graph) and eLFPs from all electrodes (lower graphs) of one animal. Peak responses differed between the contact classes (MT/T ratio 0.71 at  $\gamma$ /C1). **b.** Same data as in a but peak-normalized. **c.** MT/T ratios from all electrodes in 6 animals (coded by the symbols). The MT/T ratio for LFP recordings from each electrode normalized to the one found in the barrel C1 is plotted against the mean T response amplitude normalized to the one found in barrel C1. The numbers are correlation coefficients obtained for each rat (4 coefficients were significant at  $p < 0.05$ ; data from rats symbolized by asterisks ( $p = 0.10$ ) and crosses ( $p = 0.19$ ) failed significance). **d.** Mean squared distance (MSD) of peak-normalized T and MT eLFPs in post-contact interval of 100 ms. **e.** Mean and standard deviations of the data shown in c and d in bins of width 0.2. Scale on ordinates in c,d are the same as in e.



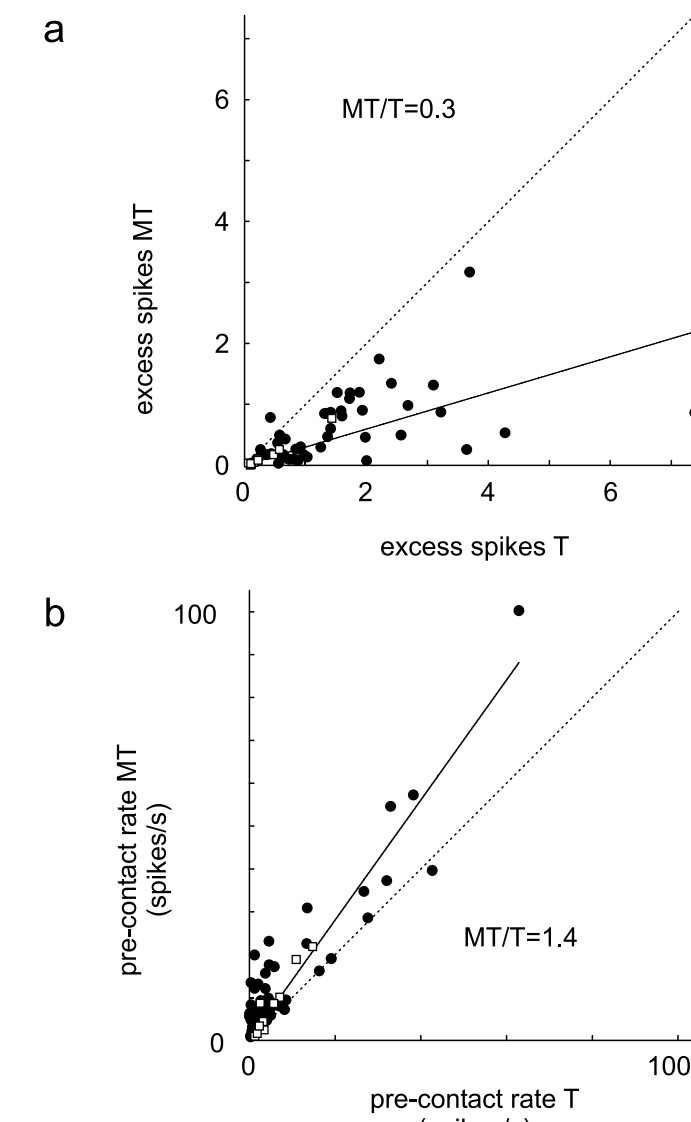
**Switching between active and passive touch is fast.** Data from pairs of contacts subdivided in four groups comprising T-T, MT-T, T-MT, and MT-MT combinations and isolated by at least 1 second from any previous contact. Ratios of LFP amplitudes found in a pair were subtracted by the ratio of the mean responses in the respective contact classes in each animal (1, MT/T or T/MT). The response ratios were scattered around zero, indicating that ISIs (larger than 75 ms) did not influence the gain switch between neuronal responses.



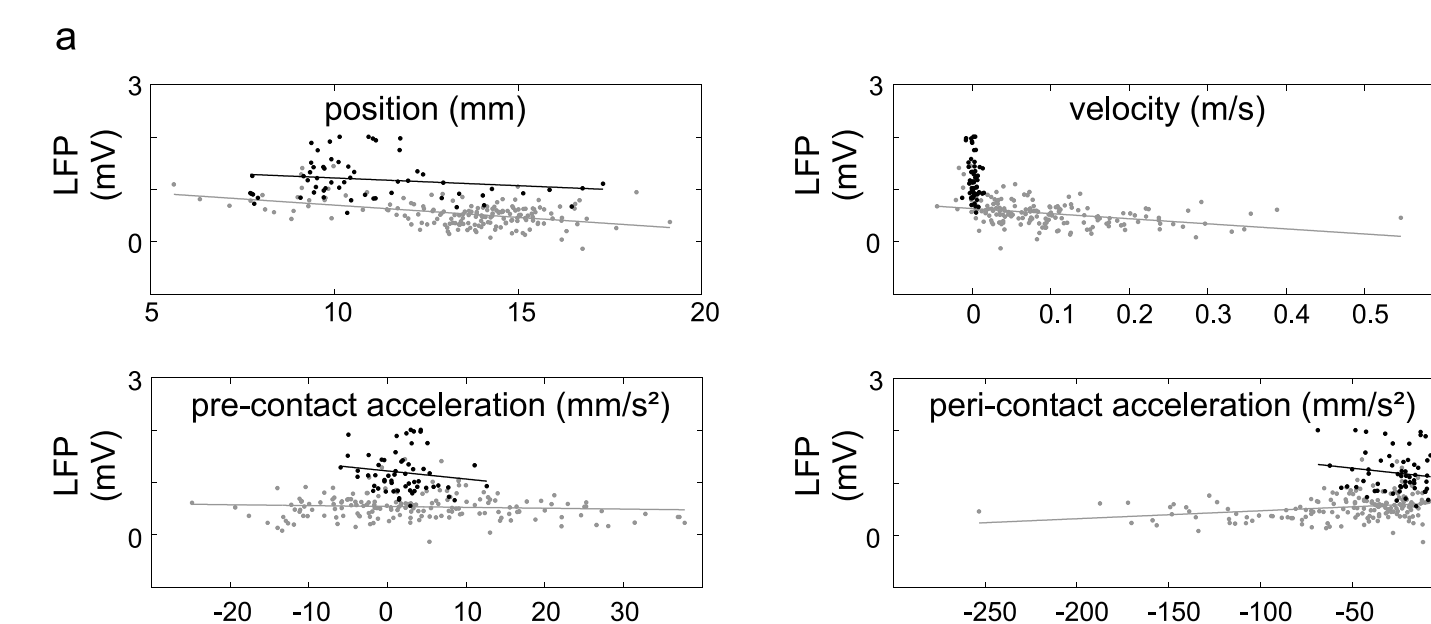
**Action potential responses reveal increased background firing before active touch.** **a and b,** mean trajectories and PSTHs of three multi-unit spike trains recorded from one electrode in the barrel column C1 and two neighboring electrodes in one animal. Bottom row: contacts (peak at time zero truncated). **a.** PSTHs triggered on T (black) and MT (dark gray) contacts. **b.** PSTHs triggered on M events. **c.** Action potential responses to electrical stimulation via a cuff electrode at the infraorbital nerve after the nerve was transected. PSTHs from 6 spike trains that showed a significant response to T contacts in one animal. Insets show spike waveforms of multi units (3 ms duration). Bin width of all PSTHs 3 ms.



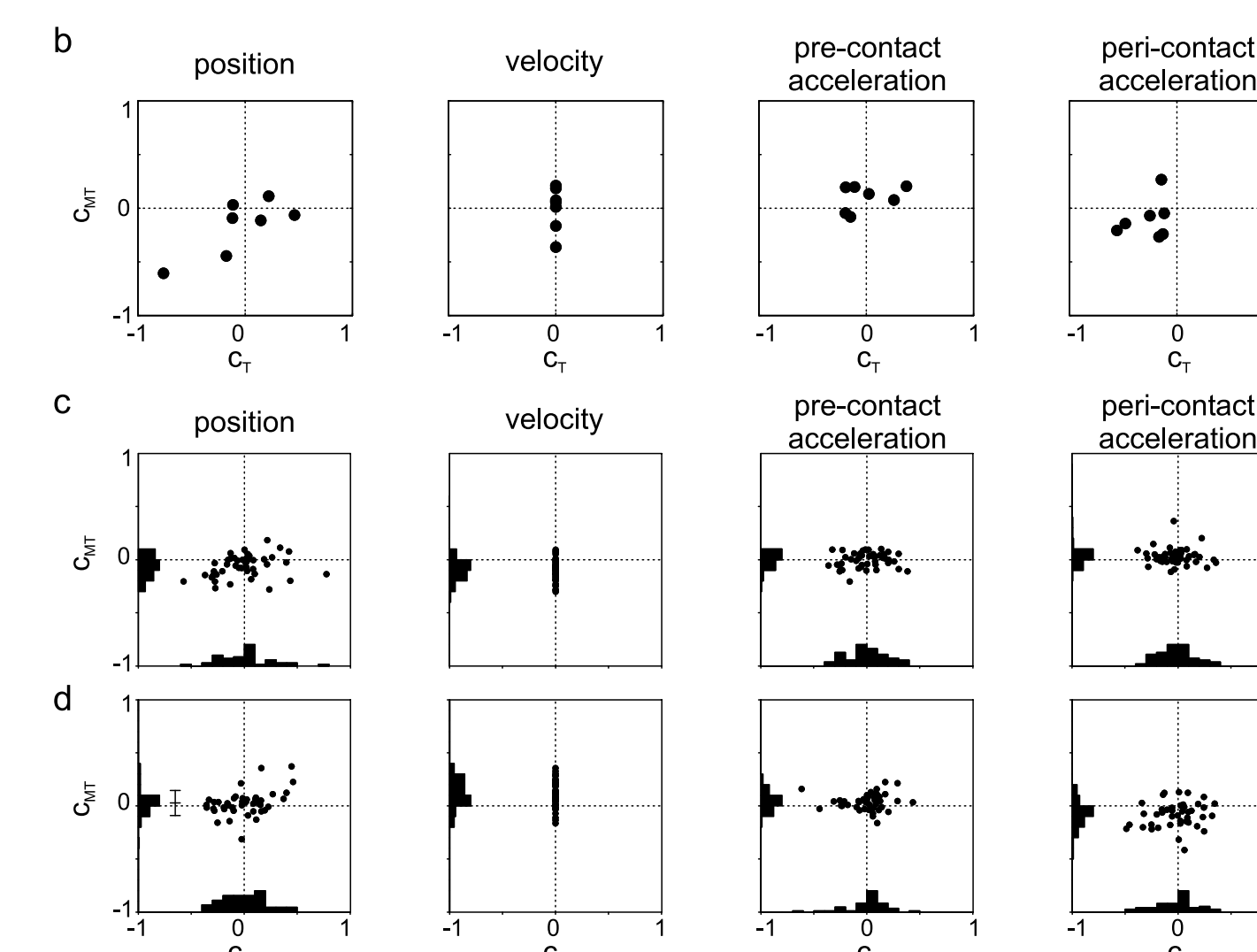
**The footprint of active touch is an increased background firing combined with reduced spike response.** **a.** contact-elicited excess spikes. **b.** pre-contact rates. The sample encompasses 50 responding multi-unit spike trains (out of 84, black dots) obtained from 7 animals (7 sessions with intact infraorbital nerve; 5 using mechanical and 2 using electrical stimulation) and 12 (out of 34) spike trains (open squares; from 2 animals/sessions after transection of infraorbital nerve). Dotted lines indicate a ratio of 1. Solid lines indicate best linear fits to the data.



**The switching signal (as assessed in this study using LFP amplitude, excess spikes and background firing rate) does not code for (cyclically varied) kinematic parameters.** Relationship of neuronal responses with whisker kinematics (position, velocity and pre-contact acceleration) and 'strength of contact' (peri-contact acceleration). **a.** scatter plots showing LFP amplitudes obtained in barrel C1 of rat #2. T: black dots, MT: gray dots. Lines indicate best linear fits. **b.** Correlation coefficients obtained for the whole population ( $n=7$  rats). Coefficients for T ( $c_T$ ) and MT ( $c_{MT}$ ) events of each animal are plotted against each other. **c.** Correlation coefficients of action potential responses. The trial by trial excess spikes for each spike train ( $n=50$ ) were calculated by subtracting the background rate assessed in the interval 100 ms before the event from the response rate assessed in the interval 50 ms after the event. The result was then correlated with kinematic parameters and the strength of contact as in a, and plotted as in b. **d.** Correlation coefficients of background firing. Response parameters associated to T events were not analyzed with respect to whisker velocity as T events by definition occur only at a narrow range of velocities close to zero ( $C_T$  was set to zero in the respective plots in b,c, and d).



## Results



## Summary

- Contact-elicited neuronal responses due to whisker movements were markedly smaller than responses elicited by a moving object contacting the whisker at rest.
- This modulation of response gain had a switch-like characteristic: maximal responses were observed only with pre-contact whisker velocities close to zero.
- The modulation of response gain switched as fast as within 75 ms, and was of central origin because it resisted transection of the infraorbital nerve.
- The switching signal is non-rhythmic and is most likely reflected by elevated activity in barrel cortex during whisker movements.