Central Signals Rapidly Switch Tactile Processing in Rat Barrel Cortex during Whisker Movements

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Palpatory movements (‘active’ touch) are an integral part of tactile sensing. It is known that tactile signals can be modulated in certain behavioral contexts, but it is still unresolved to what degree this modulation is related to movement kinematics and whether it stems from tactile receptors or from central sources. Using awake, head-fixed rats, trained to contact an object, we measured trajectories of muscle-propelled whisker movement precisely and compared tactile responses to contacts thus accomplished with ‘passive’ contacts (motionless whisker contacted by object). Multielectrode extracellular recordings in deep layers of barrel cortex revealed that when the animals moved their whiskers actively, tactile processing switched from high response amplitudes, wide cortical representation and low background firing, to low response amplitudes, narrow spatial representation and elevated background firing. Switching was fast (<100 ms) and unrelated to the degree of alertness as assessed by spectral analysis of pre-contact field potentials. Switching persisted when information about whisker kinematics was interrupted by transection of the infraorbital nerve and contacts were mimicked by peripheral electrical stimulation. Taken together, these characteristics render central signals derived from the motor system a likely contributor to the processing of active touch.

Keywords: active sensing, neural coding, primary somatosensory cortex, sensorimotor integration, vibrissae, whisking

Introduction

‘Active’ touch is characterized by a movement of tactile sensors. While humans move their fingertips for tactile sensing (Gibson, 1962; Lederman and Klatzky, 1987; Gainzu and Ahissar, 2001), rodents rely on the mobile set of mystacial vibrissae (whiskers) arranged in five horizontal rows along the flanks of the snout (Welker, 1964). In the whisker system, sensory signals project through brainstem and thalamus to corresponding ‘barrel columns’ in the primary somatosensory cortex, so named for the morphological appearance of distinct neuronal clusters in layer 4 (Woolsey and Van der Loos, 1970). In exploring their environment, rats sweep their array of whiskers across surfaces using various strategies adapted for the discrimination of different spatial frequencies (Carvell and Simons, 1995). Such goal-specific variation of whisking suggests that movement-related information is used in tactile perception. Therefore, an important question is whether and how neuronal signals from movement interact with tactile signals accomplished by contact with an object. Initial studies addressing this question delivered electrical stimuli to the infraorbital nerve of rats, which carries this tactile information, in behavioral states labeled ‘quiet’ and ‘active’ or ‘activated’ (Fanselow and Nicolelis, 1999; Castro-Alamancos, 2004a). These reports clearly indicate that processing of vibrissal tactile information at the thalamo-cortical level is susceptible to modulatory influences. Specifically, the ‘active’ state, characterized by or including exploratory movements of the body and/or whisking movements, depressed response amplitudes. The origin and functional aspects of modulatory signals, however, are unresolved issues at present. One extreme in the range of possibilities would be central modulatory signals from brainstem centers, which can reduce tactile response amplitudes (Castro-Alamancos and Oldford, 2002). At the other end of the spectrum is a movement-related activation of sensory receptors (Fee et al., 1997; Szwed et al., 2003) which, however, has not yet been shown to interact with contact-related signals. Finally, motor commands may interfere with somatosensory processing. There is strong evidence for the latter scheme in the case of non-palpatory movements in primates (Seki et al., 2003). In rats performing a tactile discrimination task, the finding that tactile sensory signals in barrel cortex were preceded by neuronal activity entering via the infragranular layers (Krupa et al., 2004) could be interpreted along the same lines, although kinematic detail of whisker movements was not provided. Taken together, the presumptive modulatory signals discussed at this time are diverse in nature and origin but not necessarily mutually exclusive. We aimed to clarify two decisive issues needed to determine the functional role of modulatory signals: their origin (peripheral versus central) and their detailed relationship to whisker trajectories. By combining precise measurement of whisker movements with multielectrode electrophysiology in the deep layers of barrel cortex of head-fixed rats, the present study shows that modulation of tactile processing occurs in exact temporal relation to individual palpatory movements and provides strong evidence that a central modulatory signal exists.

Materials and Methods

Behavioral Training and Surgery

All animal experiments were carried out in accordance with the policy on the use of animals in neuroscience research of the Society for Neuroscience and German law. Surgery was performed under anesthesia with isoflurane (1.5–3%, dose adjusted to keep pain reflexes subthreshold). Body temperature was measured and kept at 35°C. The rats (Long Evans, five male, two female, 3–4 months of age) were placed in a stereotaxic apparatus, the skin incised, the connective tissue removed, and the skull trepanated over barrel cortex. Barrel C1 was located by probing the cortex with a single electrode and recording spike responses to light touch on the whiskers, using a cotton swab. The electrode array was implanted (tips at a depth of 1200–1400 μm) such that barrel C1 was included in the recordings. The array and connected wires and plugs were covered with light curing dental cement (Flowline, Heraeus Kulzer, Hanau, Germany) and anchored to skull screws. The open skin was sutured and carefully attached to the implant. After surgery the animals were kept warm and provided with...
Electrophysiology

Multielectrode arrays were custom made in our laboratory. Nine pulled and ground glass-coated platinum tungsten electrodes (80 μm shank diameter, 23 μm diameter of the metal core, free tip length ~8 μm, impedance >1 MΩ; Thomas Recording, Giessen, Germany) were mounted inside a 1 × 9 array of polyimide tubing, with distance between tips set to ~450 μm (HV Technologies, Trenton, GA). The free ends of the electrodes were soldered to Teflon-insulated silver wires (Science Products, Hofheim, Germany), which in turn connected to a microplug (Bürklin, Munich, Germany). The electrodes were permanently implanted in the postero-inferior barrel subfield (barrel cortex) at a depth of 1200-1400 μm below the surface. The electrode array covered the barrel column corresponding to whisker C1 in all cases, as verified by receptive field properties. Surface potentials were recorded from a steel ring (OD: 5 mm) placed on the pia surrounding the site of electrode penetration.

The signal from each electrode was split and fed into two preamplifiers, which recorded the voltage trace with respect to different reference potentials. For unit recordings the reference was one of the nine electrodes lowered in impedance to prevent the recording of action potentials. Together with shielding, this arrangement effectively reduced interference from muscle activity (e.g. licking). Local field potentials (LFP) and the surface potential were recorded with respect to a skull screw over the cerebellum (Bregma -12 to -13). All recordings were performed using a multichannel extracellular amplifier (Multi-ChannelSystems, Reutlingen, Germany, gain ×5000, sampling frequency 20 kHz, band pass 1-5000 Hz). Voltage traces were band-pass filtered offline with digital filters, at 5-500 Hz to yield LFPs and the surface potential, and at 200-5000 Hz to extract multi-unit activity.

Kinematic Data

Whisker position traces were digitally lowpass filtered (<3 dB cutoff frequency 200 Hz). Whisker position, velocity and acceleration were determined in short time windows (Fig. 2b). The strength of contact between whisker and rod was expressed in terms of the peak negative acceleration (relative backward movement) of the whisker. Due to mass inertia and flexibility of the whisker, the peak of deceleration occurred ~2–4 ms post-contact. Due to this lag between contact and peak negative acceleration, the time windows were asymmetrical with respect to the time of contact, which was defined as t = 0. They were [−10 0] ms for peri-contact kinematic parameters (Fig. 2a, upper panels) and [0.5 5] ms for peri-contact acceleration (strength of contact, Fig. 2b, bottom panel). Rod position and velocity, which were unaffected by contacts, were calculated within [-2 2] ms.

Definition of Neural Response

The offset of the base line during the interval [-2 2] ms was subtracted from each LFP trace. The absolute value of the negative peak of the field potential during the interval [2 15] ms was measured as response amplitude. The spike renewal function, indicating firing rate across peri-stimulus time, was calculated at a resolution of 1 ms from the unit data (Abeles, 1982) and plotted as peri-stimulus time histograms (PSTHs). The statistical significance of single PSTH bins was derived by assuming an underlying Poisson process, the mean rate of which was set to the average pre-stimulus frequency of the unit (within an interval of [-100 0] ms), and calculating the 99% confidence interval. Spike data were classified as responding, if they showed an elevation of firing rate across the confidence limit within 20 ms after the contact. Excess spikes were calculated as the integral of the spike renewal function above the pre-stimulus average rate.

Whisker Contacts: Criteria and Classification

First, an interval of [-30 70] around a contact had to be devoid of licking movements. Second, the inter-contact-interval (ISI) to the previous contact had to be at least 75 ms. Third, the EEG recording from the steel ring above barrel cortex had to be free of high frequency noise, typical of artifacts generated by large scale muscular activity (root mean square of field potential = 30 μV). Fourth, whisker ‘switching’ periods characterized by high amplitude rhythmic signals at 7–14 Hz (Semba et al., 1980; Fanselow and Nicolelis, 1999), which occurred rarely in the present data set, were purged from the data before analysis.
Contacts were classified as 'passive' and 'active' according to two whisker motion-based criteria. A slight adaptation of the criteria from animal to animal was necessary because rats showed different 'whisking personalities' (i.e. there was some interindividual variability: first, in the amount of spurious whisker movement at rest induced by face movements, and second, in the abruptness and definition of transitions from whisking to rest and the reverse). (i) The first criterion was based on a threshold derived from the bimodal distribution of the pre-contact velocities (Fig. 2a). For each session, the narrow, zero-centered peak was fit by a Gaussian (gray area in Fig. 2a). Abscissa values corresponding to double the Gaussian’s half-width were taken as the threshold (0.015-0.04 m/s). (ii) Since this definition did not exclude whisker movements which had their apex (velocities close to zero) in the short window before a contact, an additional criterion was included: the root mean square (RMS) of the whisker velocity during the 75 ms before the contact had to be below a threshold value of 0.02-0.04 m/s for a contact to be considered 'passive'.

Whisker movements were searched automatically using the following strategy (Supplementary Fig. 2): the whisker trajectory was lowpass filtered using an edge frequency of 30 Hz, then differentiated to obtain the traces for velocity and again for acceleration. The whisker velocity was rectified and integrated within an interval of 300 ms before \( (L_r) \) and 300 ms after \( (L_l) \) for each sampled point. At each point in time, the difference of these two integrals \( (d_t = L_r - L_l) \) is a time-varying variable that can be interpreted as the 'dynamics of whisking activity': during rest \( d_t \) is zero, reaching positive values at the start of a whisking bout, relaxing back to zero during rhythmic whisking, and assuming negative values at the end of a whisking bout. The intervals to search for the start and end of whisking bouts were defined by the periods in which \( d_t \) stayed above a positive threshold and below a negative threshold, respectively (symmetric to the positive one with respect to zero; double arrow in Supplementary Fig. 2). To determine movement time stamps (‘M events’), the first local minima of whisker acceleration falling below a threshold were determined. The zero crossing of the acceleration before such a local minimum (i.e. the point in time at which maximal protraction velocity was reached) was then taken as the time stamp of a whisking cycle. In a final step, M time stamps of <75 ms following the last one, related to negative velocities, and <150 ms from a contact were purged.

Results

Switch between Active and Passive Touch and its Relation to Whisker Kinematics

We trained head-fixed rats to touch a non-stationary rod with one of their whiskers (C1) to receive a water reward (Fig. 1a). By measuring the position of the whisker (Bermejo et al., 1998) and controlling the trajectory of the rod we were able to experimentally dissect a sensorimotor act into its sensory and motor components (Fig. 1b). Whisker movement that was followed by a contact with the object constituted the full sensorimotor act and was labeled ‘active’ touch (abbreviation A). The sensory component, a ‘passive’ touch, consisted of a contact caused by the rod moving towards and touching the whisker at rest (abbreviation P), while the motor component was represented by a whisker movement alone which did not result in object contact (abbreviation M, indicated by asterisks in Fig. 1b; for details, see Fig. 3d and Supplementary Fig. 2).

Figure 2 explains our rationale for the binary differentiation of contacts into active and passive classes. The basic criterion was the velocity of the whisker, calculated from a small window immediately preceding contact (Fig. 2b, center panels). The distribution of this pre-contact whisker velocity was bimodal, with a narrow, zero-centered peak on top of a much wider backdrop of higher velocities (Fig. 2a). The wide distribution clearly corresponds to whiskers actively moved to touch. In contrast, the narrow peak was interpreted as the whisker being 'at rest' (passive); the small non-zero velocities contained in this peak, bounded by values of ~0.03 m/s, were due to small movements of the face and snout, even when the hairs were not moved against the whisker pad (see methods for details).
Figure 2. Classification of active versus passive contacts. (a) Typical example of a histogram of pre-contact velocities in one rat (no. 5). The distribution clearly shows a bimodal distribution of pre-contact velocities. The first peak spans velocities within the interval of -0.03 to 0.03 m/s and could be well fit by a Gaussian, suggesting that pre-contact velocities within this range are a good indicator of passive contacts. The second peak is centered on velocities of -0.25 m/s in this case and represents active contacts. Note that some 'active' contacts occurred during whisker retraction (negative velocities exceeding -0.03 m/s). (b) Waveforms of kinematic parameters in a short interval around active and passive contacts (same rat). The vertical broken line indicates time of contact $t_0$, defined as the time when output voltage from the contact detector surpassed a threshold. Due to the whisker’s mass inertia and flexibility, the peak negative acceleration during contacts appeared 3-4 ms post-contact (lowermost panel). Thin gray box around $t_0$ represents the window in which pre-contact kinematic parameters (position, velocity, and acceleration) were determined. The wider gray box in the lower panel is the time window in which the above-mentioned peaks of negative peri-contact acceleration were determined.

Traces from one rat of whisker position, velocity, and acceleration around active and passive contacts that were classified according to this criterion are shown in Figure 2b. By definition, active and passive contacts differed in their pre-contact velocities and had differing, but partly overlapping, ranges of pre-contact positions and accelerations (because of the spurious whisker movements mentioned above, passive contacts displayed accelerations different from zero in many cases). Nonetheless, the kinetic impact of contacts on the whisker was comparable in both cases: the whisker was accelerated back-wards, as visible in the sharp negative deflections of peri-contact accelerations (Fig. 2b, bottom).

The general nature of the modulation of tactile processing is demonstrated in Figure 3. Contact with the rod elicited a strong negative deflection of the LFP which was then followed by a positive wave lasting for ~100 ms. The amplitude of the negative deflection served as the measure of response magnitude. The mean evoked LFP amplitude recorded in barrel column C1 of the session shown in Figure 3a was clearly smaller after active touch compared to passive touch. In order to standardize the difference between A and P contact responses across animals, we computed a simple $A/P$ ratio: the mean response amplitude due to active contacts divided by the mean response amplitude due to passive contacts. It is shown for the total sample in Figure 3b ($n = 5$ with mechanical stimulation, rats 1, 2, 3, 5 and 7; $n = 2$ with contact-triggered electrical stimulation via a cuff electrode, rats 4 and 6, all recordings from C1 barrel column). The differences between active and passive contacts were found to be significant in all cases [all data in the format (rat no., $A/P$, number of passive contacts, number of active contacts): (1, 0.26, 14, 180), (2, 0.45, 59, 170), (3, 0.50, 30, 331), (4, 0.67, 33, 236), (5, 0.68, 122, 865), (6, 0.70, 25, 232), (7, 0.71, 73, 351), Bonferroni corrected $t$-tests, $P < 0.01$; Bonferroni correction included all 9 sessions evaluated in this study; see also Fig. 8b]. As numbers of active and passive contacts varied between sessions and were high in some sessions, we also derived the statistical effect size, a measure that is independent of sample size. This parameter ranged between 0.6 and 2.5, which is commonly considered to indicate medium to large effects (Cohen, 1988). Mean evoked LFP waveforms of the two cases which yielded the highest and lowest $A/P$ ratio are depicted in Figures 3a and 7a respectively (rats 1 and 7).

This result was also reflected by spike data recorded from the same electrodes. The example in Figure 3c shows peristimulus time histograms (PSTH) constructed from multi-unit spikes recorded from three neighboring electrodes including the one located in the main barrel column (C1). The excitatory response near 5 ms post-contact was clearly smaller after active contacts than for passive contacts. Moreover, it was evident that the pre-contact firing rate was higher before active contacts compared to passive ones. Triggering the PSTHs to M events (defined as maximum velocity during a whisking stroke not followed by a contact; see Materials and Methods) revealed a tonic elevation of firing rate during a whisking bout. Figure 3d is subdivided into PSTHs that show firing rates aligned on the first whisker stroke in a bout, strokes within a bout and the last stroke in a bout. The relatively low firing rate before a bout of whisker movement, for all three units shown, increased tonically during the bout and relaxed back to resting levels at the end of the bout. Data from the total sample of seven rats/sessions are shown in Figure 3e,f. Excess spikes (for definition, see Materials and Methods) generated by active contacts are plotted against those obtained with passive contacts in Figure 3e. Similarly, the movement-related firing rate before active contacts is plotted against the one measured before passive contacts (Fig. 3f). The $A/P$ ratios of these measures were determined by fitting straight lines to the results obtained from 50 multi-unit spike recordings in seven animals [out of a total of 84; only those that passed the 0.01 confidence limit for an excitatory response were selected (Abeles, 1982)]. Firing rate responses were on average 0.3 times less for active than for passive responses. Movement-related firing rate, on the other hand, was 1.4 times higher before active contacts than...
before passive contacts. Other response parameters like latency and response duration (not shown) did not differ between the two groups.

Next, we aimed at elucidating in more detail how kinematic parameters of whisking modulated tactile processing. To this end, neuronal activity around active and passive contacts was plotted against whisker position, velocity and acceleration immediately before and during the contact. Three of the kinematic variables describe self-initiated whisker movement by the animal before the contact and are therefore labeled ‘movement-related’ (pre-contact position, velocity and acceleration, Fig. 4a–d). The fourth variable depended additionally on the impact of the rod on the whisker during contact (labeled ‘contact-related’; peri-contact acceleration, Fig. 4e–g). Figure 4a exemplifies the relationship of LFP amplitudes to movement-related parameters. First and foremost, the scatter plot of response versus pre-contact whisker velocity reflects our finding that passive contacts yielded higher responses than active contacts (Fig. 4a, middle panel). Notably, all of the highest responses were confined to a very small abscissa range close to zero, demonstrating a steep, switch-like dependence of responses on whisker movement. By design, the overwhelming majority of active contacts occurred during the protracting phase of the whisker. The small number of active contacts in the retracting phase of the whisker, recognizable by negative abscissa values, yielded virtually the same response amplitudes as the ones during protraction. The differences of A/P ratios for protracting versus retracting whiskers before contact were very small (~0.04, ~0.04, 0.08 in three animals that showed >5 active contacts during retraction). Other than the step-wise difference in response amplitudes between active and passive touch, the graphs shown in Figure 4a did not reveal obvious relationships...
of kinematic parameters to response amplitudes within each group of contacts (note that pre-contact acceleration values were nonzero for the majority of passive contacts due to the spurious whisker movements mentioned above). Population data confirm the impression gained from this example. Figure 4 shows correlations of kinematic parameters with LFP responses, spike responses and pre-contact spike rates, respectively, for all sessions. Velocity was, by definition, close to zero before passive touch and, therefore, was not analyzed for this type of contact. The general result was that neither responses to contacts (LFP amplitudes and excess spikes) nor the pre-contact spike rates were consistently correlated with pre-contact position, velocity and acceleration (Fig. 4b–d). Correlation coefficients were generally small and mostly non-significant.

In line with previous studies (Temereanca and Simons, 2003; Wilent and Contreras, 2004; Lee and Simons, 2004), stronger contacts tended to evoke stronger responses (Fig. 4e). However, the correlation of contact strength with response amplitude was not statistically significant ($P > 0.05$) for either LFPs or spikes (Fig. 4f,g). It is important to point out that active touch resulted on average in stronger contacts than passive touch (Fig. 2b), because active contacts were most often the result of a collision of rod and whisker moving in opposite directions. This was the case in four of five animals receiving mechanical sensory stimulation; in one rat active and passive contact strengths were on average equal [values are given in format (rat #, average of peak negative acceleration $P$ in mm/s$^2$, average of peak negative acceleration $A$ in mm/s$^2$), (1, -80.0, -76.3), (2, -24.8, -52.6), (3, -57.2, -118.8), (5, -79.8, -150.0),]
[7, -50.6, -96.4]). Thus, the main effect of active touch — lower neuronal responses — cannot be explained by confounding active contacts with lower contact strengths. Moreover, the difference in active and passive response amplitudes persisted under the conditions of electrical stimulation of the infraorbital nerve after its transection (reported below). In summary, for both immobile and moving whiskers, the kinematics of movement before and/or after contact appear not to be strong determinants of response strength. Rather, the processing of active and passive touch can be described as a quasi-binary process, determined by the absence or presence of whisker movement immediately before the contact.

**Temporal Characteristics of the Switch**

An obvious question to ask is how fast the observed switch operates. Inspection of raw data suggested that the ‘average’ whisker movement in an immediate pre-contact interval of 100 ms duration or less was a determinant of response strength, very much like the instantaneous measure of pre-contact velocity that was used as the basic criterion differentiating between active and passive contacts. Figure 5 confirms this for one experimental session. Average whisker movement was assessed by the root mean square of whisker velocity, RMS$_{vel}$, in [-75 0] ms pre-contact. Clearly, low-response contacts were elicited by a wide range of RMS$_{vel}$ values distant from zero, whereas high-amplitude responses followed contacts with a whisker which was largely immobile in this interval (Fig. 5a).

We extended this simple approach by comparing RMS$_{vel}$ in two pre-contact time intervals, [-250] and [-250 -150] ms. Our aim was to detect transitions in whisking intensity within the 250 ms pre-contact, either from rest to whisking or the reverse. Relating these different modes of transition to response amplitudes should thus reveal to what degree whisker movement more distant in time from the contact influenced response amplitudes, and hence the rapidity of the switch. To this end, we divided the total of all responses (of the same experiment) into a low response group and a high response group. The high response group was further subdivided into two groups, those with a ‘waning’ transition (high movement in [-250-150]) ms) → (low movement in [-25 0] ms) and those without (Fig. 5b, upper row). The low response group was subdivided similarly,

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**Figure 5.** The insensitivity of response amplitude to transitions of whisking activity within 100 ms before a contact indicates fast switching. (a) LFP response amplitude was predicted by the RMS of whisker velocity immediately before the contact (rat 2). RMS computed in the interval [-75 0] ms pre-contact is plotted for each contact (gray dots). The thick line represents the same data smoothed by a triangular running window (width 21 bins). The contacts are ordered according to evoked LFP amplitude (broken line). The asterisk code on top of the graph represents contacts classified as active (A, gray) and passive (P, black). (b) Traces of absolute whisker velocity around contacts were aligned as columns. Trial number (ordinate on the right). The plots in the upper and lower rows represent high- and low-response trials, respectively. Within rows, the first plot depicts trials at high or low movement intensities without velocity transitions and the second plot shows trials with waning or waxing whisker movements, as defined by RMS$_{vel}$ in two intervals, [-250-150] and [-25 0] ms. No-transition trials were those with low/low or high/high combinations of RMS$_{vel}$ in these intervals, the thresholds corresponding to the medians of the RMS$_{vel}$ in the respective time interval. Transitions of the waning and waxing type were defined by high/low and low/high combinations, respectively. Within each gray map, trials were sorted in ascending order according to response amplitude (white broken line, ordinate on the left). The range of the grayscale was clipped to reveal movement at low RMS$_{vel}$ (top, right: [0, 0.17] m/s; top, left: [0, 0.16] m/s; bottom right: [0, 0.29] m/s; bottom, left: [0, 0.40] m/s). Boxed line graphs to the right of the gray-coded plots indicate average absolute velocity computed from each group (broken line depicts the criterion of 0.03 m/s to classify trials as active and passive, note log scale on abscissa). (c) Average dynamics of whisker movement changes shortly before contact (same session as in a and b). Trials below the 33rd percentile of RMS$_{vel}$ values in [-250-150] were selected for this graph. The plot shows RMS$_{vel}$ in small pre-contact intervals of 25 ms duration divided by RMS$_{vel}$ in [-250 -150] ms for trials with high (triangles) and low (circles) responses. The criteria dividing high and low response amplitudes were the 33rd percentile and the 66th percentile of the total sample, respectively. Abscissa values indicate interval centers. The asterisks mark significant deviation of the two curves (Wilcoxon rank sum test, $P < 0.01$, low response, $n = 10$; high response, $n = 9$). The histogram in the inset denotes the frequency distribution of the first intervals in which the curves first deviated significantly from each other for the total sample of nine sessions.
the transition being of a 'waxing' type (low movement in [-250–150] ms) → (high movement in [-25 0] ms) (Fig. 5b, lower row). Figure 5b shows grayscale-coded contour plots of absolute whisker velocity in single trials of the four groups. The curves next to these plots depict the mean absolute velocity in absolute whisker velocity in single trials of the four groups. The distant pre-contact interval (taming this analysis had a relatively weakly moving whisker in the present session the analysis dealing with waxing movement not immediately preceding contacts (> ~100 ms distant) hardly affected response amplitudes, as judged from the similarity of response amplitude distributions in trials that did and did not contain such transitions, respectively (compare white broken curves in left and right panes, Fig. 5b). For transitions from rest to whisking (waxing type), this analysis yielded a similar picture for all experimental sessions included in our sample. The reverse case, the waning type, was difficult to assess in some sessions, because some animals, while generating abrupt changes from rest to whisking, changed in a more sluggish and ill-defined way from whisking to rest. Therefore, we present population data only for the transition from rest to whisking. For the present session the analysis dealing with waxing movement is shown in Figure 5c. By definition, all sweeps/contacts entering this analysis had a relatively weakly moving whisker in the distant pre-contact interval ([-250–150] ms). The contacts were then divided into low and high response groups. Next, we computed the RMSvel in adjacent, non-overlapping time intervals of 25 ms length, covering ~150 to 0 ms pre-contact, and normalized the values by the RMSvel in [-150–250] ms. This was done on a sweep-by-sweep basis. The expectation was that in the high response group, on average, movement intensity would remain low while the low response group would show a significant increment of movement intensity at one point. This point in time, at which the low and high response groups significantly deviated from each other, was located very close to the contacts (~60 ms) in this session. Finally, the population data including all nine sessions of the present sample (including the sessions/rats with transected infraorbital nerve; see Fig. 8) are shown in the inset. This plots the frequency distribution of the deviation times and shows that, in all but one session, significant deviation set in within a 100 ms interval prior to contact. In the remaining session the first significant deviation occurred between 125 and 100 ms pre-contact.

In the preceding analysis, switching was found to occur over the course of rapid transitions of whisking activity prior to contact. An additional, direct demonstration of fast switching would be based on the responses of contacts of different type occurring in quick succession. Because of the nature of rhythmic whisking and methodological constraints, small inter-contact intervals were rare in the present sample, none falling below 75 ms. Still, comparing responses of contact pairs confirmed the findings of the previous analysis (Fig. 6). We selected all contact pairs across animals that were at least 1 s after any previous contact. They were then classified into four groups, comprising passive-passive, passive-active, passive-active and active-active combinations. In order to be able to detect adaptation within pairs of neuronal signals which were already known to differ according to the class of contact, we applied a normalizing procedure to the LFP responses. The LFP response amplitude to the second contact in a pair was normalized to that of the first contact. It was then corrected for the A/P quotient found in the respective animal and plotted versus the inter-stimulus interval (ISI, Fig. 6). Cortical sensory LFP responses display a well known inter-trial variability (Arieli et al., 1996; Petersen et al., 2003; Sachdev et al., 2004). Therefore, the data show a large variation around zero. On average, however, the second response in a pair was unaffected by the preceding response; no significant functional relationship could be established between response amplitude and ISI. While for the cases of passive-active and active-active combinations we base this observation on ISIs with a lower bound of 75 ms, passive contacts usually followed any kind of preceding contact with a latency of at least 200 ms (corresponding to the minimal interval the hardware propelling the rod could achieve). In conclusion, these results — together with those of the preceding analysis — indicate that switching can occur within intervals close to and shorter than 100 ms.

The analysis of contact pairs suggests that repetitive contacts have no effect on response amplitudes — at least with inter-contact intervals that could be obtained with the present experimental conditions. To further test this notion, we determined whether the contact rate before any given contact influenced the evoked LFP amplitude in a systematic way. Indeed, the average contact rate (including both types of contacts) in the period of 1 s before contact did not predict LFP amplitudes. This finding holds separately for both classes of contacts. Regression analysis of pre-contact rate and LFP amplitudes yielded r² values of <0.01 for all seven cases (including the two sessions with transected infraorbital nerves as reported below).
Effects of the Switch on Spatial Representation and Waveform

The combination of temporally well defined stimuli and multielectrode recordings permitted us to examine both temporal and spatial aspects of the responses. As predicted from the somatotopic representation of whiskers in barrel cortex, the LFP response was strongest within the main barrel column and tapered off at adjacent sites (Fig. 7a). At recording sites remote from the main barrel column, active responses tended to be disproportionately smaller than passive contacts (Fig. 7c,d,e). The correlation coefficients expressing this relation ranged between 0.61 and 0.96, and were significant at $P < 0.05$ for 4 out of 6 rats; the other two reached significance levels of $P = 0.10$ (coefficient $= 0.61$; asterisks in Fig. 7c) and $P = 0.19$ (coefficient $= 0.95$; crosses in Fig. 7c). (One animal was excluded from this analysis as only two electrodes gave evoked LFP responses.) Despite the confinement of active responses to a smaller cortical area, the waveforms of active responses were very similar to those of passive responses. The differences between the waveforms could be well described by a simple multiplication. Baseline-corrected and peak-normalized evoked LFPs resulting from active contacts were nearly identical to correspondingly normalized, passively evoked LFPs up to 100 ms after stimulation (Fig. 7b). In order to verify this observation for all animals, we quantified the difference between the averaged and normalized active and passive evoked LFPs by computing their mean squared differences (MSD). At sites with a substantial tactile response (average peak amplitude at recording site divided by average peak amplitude found in the main barrel $> 0.3$) MSD values were close to zero (Fig. 7d,e). This indicates that within the main responsive area, LFP waveforms evoked by active and passive contacts were quite similar.

Figure 7. Horizontal spread of responses to active contacts is smaller than that evoked by passive contacts. (a) Mean whisker trajectories (upper plot) and evoked LFPs from all recording sites (lower plots) of one animal (no. 7) resulting from active (gray) and passive (black) contacts. Peak responses differed between the contact classes (A/P ratio 0.71 at γC1). (b) Same data as in (a) but peak-normalized to demonstrate that the waveforms were very similar. (c) A/P ratios from all recording sites in six animals (coded by symbols) that showed responses $>10\%$ of that obtained in the barrel column C1. Abscissa is each site’s mean passive response amplitude normalized to the one found in barrel C1 (for scale of abscissa see e). Ordinate values are the sites’ A/P ratios normalized to those in C1. The lines are the best linear fit for each rat (identified by the symbol to the left of the ordinate). Segments with a negative slope indicate disproportionate attenuation of active responses in the periphery of the C1 barrel column. The numbers on the right side are correlation coefficients obtained for each rat (four coefficients were significant at $P < 0.05$; data from rats symbolized by asterisks ($P = 0.10$) and crosses ($P = 0.19$) failed to reach significance). (d) MSD (ordinate) between active and passive evoked LFP waveforms which had been peak-normalized in a post-contact interval of 100 ms. MSD values are small if the waveforms have a similar shape. MSD values are close to zero for response amplitudes $>0.3$ times the maximum amplitude in barrel column C1, indicating that active evoked LFPs in the main responsive region are downsampled, almost identical versions of passive evoked LFPs. (e) Means and standard deviations of the data shown in (c) and (d) in bins of width 0.2. Scale on absciassas in (c, d) are the same as in (e).

Origin of the Modulatory Signal: Central versus Peripheral

In order to differentiate between a peripheral and a central origin of the modulatory signal, we performed a deafferentation procedure with two animals: all sensory afferents originating from the whisker pad were blocked permanently by transecting the infraorbital nerves (IONs) bilaterally. We reintroduced (artificial) tactile inputs by single pulse electrical stimulation via a cuff electrode at the caudal end of the transected nerve contralateral to the cortical recording sites. This manipulation deprived the central sensory pathway of information about whisker kinematics stemming from the whisker follicles, e.g. positional signals (Szwed et al., 2003). Therefore, it should abolish switching if it depended on those signals. Technically, the experiments were carried out exactly as the ones described above (Figs 1 and 2), with the exception that mechanical contact of the whisker with the rod triggered electrical stimulation at the IONs. For each animal, we first performed experiments with an intact ION in order to ascertain whether electrically evoked LFPs showed the same switching between active and passive contacts as sensory evoked LFPs (rats 4 and 6, Fig. 8a, top). Cutting the nerve led to a decrement of LFP amplitudes due to the mechanical manipulation close to the cuff electrode during surgery. Nevertheless, the waveforms evoked by active and passive contacts under intact and transected nerve conditions were remarkably similar, and the A/P ratio remained virtually the same (Fig. 8a, bottom). Figure 8b plots the mean LFP amplitudes in the two rats before and after transection of the nerves. The difference between active and passive contact responses was highly significant in all cases [all data in the format (rat no., A/P, number of passive contacts, number of active contacts): (4, 0.67, 33, 236), (4 (IONs cut), 0.75, 223, 683), (6, 0.70, 25, 232), (6 (IONs cut), 0.68, 96, 389), Bonferroni corrected t-tests, $P < 0.01$, Bonferroni correction included all nine sessions evaluated in this study; see also Fig. 3b]. Qualitatively the same result was obtained with spike data. Figure 8c demonstrates PSTHs from six multi-unit recordings obtained in a session after bilateral transection of the IONs. The response pattern deviated somewhat from the ones typically seen with mechanical stimulation. In some cases, the short latency peak was followed by an overt inhibition which could in turn be followed by a second (rebound) excitation (Fig. 8c, see e.g. first, fourth and sixth row of PSTHs). Despite these differences, the response pattern was attenuated in the case of
active contacts and background activity was higher. Twelve units out of 34 that responded to electrical stimulation of the transected ION revealed similar ratios of excess spikes and background rate (Fig. 8d, e). In conclusion, these experiments indicated that the switch between low and high response amplitudes due to active and passive contacts, respectively, was independent of peripheral sensory inputs, a fact which indicates that central sources must be the basis of the modulatory influences seen here.

Association of Switching: Movement versus State of Alertness

The results obtained so far are compatible with the idea that the switch between active and passive sensory processing is accomplished by signals that are related to the generation or control of movements. However, the state of alertness has been shown to modulate amplitudes of electrically evoked responses in barrel cortex (Castro-Alamancos, 2004b). An actively whisking animal is undoubtedly alert rather than drowsy. Therefore, in our experimental setting, passive contacts were likely processed in a state of alertness not drastically different from that during whisking: most passive contacts were preceded by active whisker movement (with or without contact) by at least a few seconds (see also Supplementary Fig. 1). In order to have a crude verification of this assumption, we performed a spectral analysis on LFP sweeps for the 800 ms before contact. Since responses to contacts in the sweeps would have spoiled the analysis, the results are derived from a subset of contacts with an inter-contact interval of >800 ms. Figure 9a exemplifies power spectra found for active and passive contacts in one session. They were similar in the two conditions. Since the power in the delta frequency band (1–4 Hz) appeared to be the best marker of the state of alertness in our experimental situation (see Discussion), we correlated response amplitudes with the power in this frequency band in a trial-by-trial fashion (Fig. 9b). In all nine sessions of the present sample, non-significant \( r^2 \) values (\( P > 0.05 \)) were found for the relationship of delta band power with response amplitudes amongst passive or active contacts alone or combined. Figure 9c shows, for all sessions and in the same format as Figure 3b, values of the average delta band power before and after contact. No significant relationship could be found using multiple Student’s t-tests (before and after Bonferroni correction). In summary, these results argue against the possibility that delta power, and therefore, alertness, played a role in determining response amplitudes in our experiments.

Discussion

From previous work it was known that tactile responses in barrel cortex can be modulated according to the behavioral state (Fanselow and Nicolelis, 1999; Castro-Alamancos, 2004a; Krupa et al., 2004). In these studies, the animals were generally moderate or high alertness levels were maintained throughout the experiments. It is unlikely that this experimental setting could not have provided adequate alertness levels because there were no significant differences in the results obtained in the present study and those reported in previous studies. Furthermore, the results obtained in the present study are consistent with the idea that there is a switch between active and passive sensory processing that is controlled by signals related to the generation or control of movements. However, the state of alertness has been shown to modulate amplitudes of electrically evoked responses in barrel cortex (Castro-Alamancos, 2004b). In our experimental setting, passive contacts were likely processed in a state of alertness not drastically different from that during whisking. Therefore, in our experimental setting, passive contacts were likely processed in a state of alertness not drastically different from that during whisking: most passive contacts were preceded by active whisker movement (with or without contact) by at least a few seconds (see also Supplementary Fig. 1). In order to have a crude verification of this assumption, we performed a spectral analysis on LFP sweeps for the 800 ms before contact. Since responses to contacts in the sweeps would have spoiled the analysis, the results are derived from a subset of contacts with an inter-contact interval of >800 ms. Figure 9a exemplifies power spectra found for active and passive contacts in one session. They were similar in the two conditions. Since the power in the delta frequency band (1–4 Hz) appeared to be the best marker of the state of alertness in our experimental situation (see Discussion), we correlated response amplitudes with the power in this frequency band in a trial-by-trial fashion (Fig. 9b). In all nine sessions of the present sample, non-significant \( r^2 \) values (\( P > 0.05 \)) were found for the relationship of delta band power with response amplitudes amongst passive or active contacts alone or combined. Figure 9c shows, for all sessions and in the same format as Figure 3b, values of the average delta band power before and after contact. No significant relationship could be found using multiple Student’s t-tests (before and after Bonferroni correction). In summary, these results argue against the possibility that delta power, and therefore, alertness, played a role in determining response amplitudes in our experiments.
freely moving and/or trained to discriminate the width of an aperture with their whiskers (Krupa et al., 2004). Responses in barrel cortex were found to be reduced in states of motor activity as compared to light anesthesia, quiet wakefulness and sleep. However, the exact relationship of modulatory signals to movement kinematics remained unknown. Such knowledge is critical because it will help to decide from which source the modulatory signal is derived. Toward this goal, the present study advanced the level of experimental control by the combination of three techniques (each of them available before) that had not been applied in conjuction so far. We used highly precise measurement of whisker trajectories and contacts in awake, behaviorally trained rats (Bermejo et al., 1998). Furthermore, multielectrode electrophysiological assessment of tactile signals in the deep layers of barrel cortex (e.g. Nicolelis et al., 1995) was applied, and finally, signal flow at the primary somatosensory cortex was manipulated by transection and electrical stimulation (e.g. Gao et al., 2001). These advances allowed us to obtain the following novel findings: first, modulatory effects on tactile processing — elevation of background firing rate and reduction of tactile response amplitudes — were linked to whisking kinematics in a switch-like manner. The dynamics of change between the two states was faster than ~100 ms and was not caused by adaptation due to repetitive contacts. Second, active touch was accompanied by a refinement of spatial representation of tactile signals. Third, transecting the ION and substituting contact information by electrical stimulation at the nerve’s proximal trunk did not affect tactile modulation, indicating a central origin of the modulatory signal. Fourth, power in the delta band (1–4 Hz) of field potentials prior to active and passive touch does not support the possibility that the state of alertness was an influencing factor in the present experimental conditions.

Together, these results point to motor commands as modulators of tactile signals in deeper layers of barrel cortex. In the following, in order to elaborate this conclusion, we define the expected characteristics of each hypothesized source of modulatory signals and discuss the new constraints which our results impose on these hypotheses.

**Peripheral Sensory Signals**

The first candidate source of modulatory signals to be considered consists of the hair receptors in the whisker follicle. Some of these are activated during self-initiated whisker movement without contact (Fye et al., 1997; Szwed et al., 2003). In order to exclude their input from the afferent pathway, we transected the ION and mimicked contact-elicited sensory inputs by single pulse electrical stimulation in a subset of our animals. If movement-related signals from these receptors played a role in shaping contact-elicited responses, their modulatory impact should have been revealed in this condition. This expectation was not met. The switch between active and passive LFP responses and concomitant characteristic firing patterns persisted. Furthermore, LFP response waveforms were similar before and after nerve transection, indicating that the cortical representation of electrically evoked signals under active and passive touch did not fundamentally change after transection of the nerve. Therefore, these results strongly suggest that movement-related activation of hair follicle receptors did not play a substantial role in modulating the strength of contact-evoked responses. Furthermore, a possible role for dynamic encoding on the level of receptors (i.e. response adaptation to repetitive stimulation, Gibson and Welker, 1983) is excluded as well by these experiments.

**Central Bottom-up Mechanisms**

Further up in the chain of somatosensory processing, dynamic responses to repetitive whisker deflections are characterized by suppression (in thalamus and cortex, Chung et al., 2002; Garabedian et al., 2003; Khatri et al., 2004). For the present discussion, it is important to note that the transection of the peripheral nerve did not impair these mechanisms and that, indeed, thalamocortical response suppression has been observed with repetitive electrical stimulation at the ION (Fanselow and Nicolelis, 1999; Castro-Alamancos, 2004a). Therefore, we tested whether a systematic influence of prior contact rate on response amplitudes existed in our data. This was not the case — neither for mechanical contacts while the nerve was intact nor for electrical stimulation after nerve transection. Our failure to observe dynamic responses does not exclude their existence; rather, it must be attributed to the present experimental variables which seemingly did not favor their occurrence: first, inter-contact intervals achieved in the present study were rarely below 100 ms, the range in which response suppression becomes predominant (Kryzi et al., 1994; Webber and Stanley, 2004). Second, wakefulness may shift the impact of stimulus frequency on suppression strength to higher frequencies (i.e. shorter inter-contact intervals), as suggested by the comparison of recordings obtained under light anesthesia using fentanyl (Khatri et al., 2004) and deeper states with pentobarbital (Garabedian et al., 2005). Thus, we conclude that the switch of tactile processing observed here does not correspond to adaptation or other suppressive phenomena originating in the afferent (bottom-up) stream of sensory signals. Notwithstanding this conclusion, the cellular mechanisms underlying bottom-up
response suppression may very well be part of the presumed central (top-down) response-suppressing machinery: the location of these mechanisms (thalamocortical circuits) and their universality and ubiquity (e.g. dynamic synaptic transmission or interaction of intracortical excitation and inhibition) clearly point to this possibility. For example, it is a well established idea that internal, non-sensory afferents to thalamic nuclei may switch thalamocortical units to tonic firing mode and depress thalamocortical synapses (Castro-Alamancos and Oldford, 2002; for review, see Guillery and Sherman, 2002). In particular, the widely interconnected infragranular layers of barrel cortex, the presumed recording sites in the present study, are likely targets of such interferences. One of these layers’ many inputs, the posterior-medial thalamic nucleus, is known to be controlled by a variety of non-sensory, central instances — amongst them motor cortex (Deschénes et al., 1998).

In summary, the present results allow the strong conclusion that a central modulatory signal exists. We next want to differentiate further amongst central signals that are movement-related and thus appear as possible candidates for the observed modulation. We consider two possibilities: (i) signals controlling the state of consciousness and arousal, and (ii) motor commands.

Central Signals Controlling States of Alertness
The state of consciousness and arousal, in principle, could be a determinant of sensory response amplitudes in our experiments, as it is well known that subcortical brain regions associated with arousal alter cortical activity (Buzsaki et al., 1988; Moruzzi and Magoun, 1959; Detari et al., 1997; Manns et al., 2000) and cholinergic ‘activation’ of the thalamocortical system via the brainstem reticular formation reduces responses to simulated tactile stimuli (Castro-Alamancos, 2004b). Two arguments can be put forward which render a contribution of changes in states of alertness highly unlikely. First, our experiments were specifically designed as to minimize the influence of general behavioral states. Rod movement was tuned to discourage inactivity as a behavioral strategy (see Materials and Methods) and sessions containing prolonged sequences of passive touches were not included in the data set. As a result, active and passive contacts are well intermingled in our data sets and the time series of active contacts does not suggest a general gradient of whisking activity (and concomitant gradient of alertness) during the session (Supplementary Fig. 1). Second, there is evidence that alertness may fluctuate more dynamically — for instance, alertness in primates and rats changes on a characteristic time scale of 15–20 s (Oakson and Steriade, 1983; Novak et al., 1992; Rajkowska et al., 1994; Makeig and Jung, 1996). To address this possibility, we performed a spectral analysis of single trial, pre-contact LFPs in time windows (800 ms) wide enough to measure delta power but small enough to yield a snapshot of the ongoing dynamics of alertness. The rationale of this analysis is based on a wealth of studies reporting that the power in different frequency bands of EEG or LFP correlates to (and thus indicates) the state of alertness. Gamma activity correlates to some degree with alertness, but the usefulness of this rhythm as an indicator of alertness is hampered by the fact that it seems to be associated with an anticipation of tactile signals (Hamada et al., 1999). High power in the delta band (1–4 Hz) is a prominent marker of low levels of alertness and sleep and has been attributed to the withdrawal of cholinergic activity in neocortex (e.g. Buzsaki et al., 1988; Makeig and Jung, 1996; Makeig et al., 2000). Our analysis indicated that response amplitudes were independent of delta power before the contact. Before taking this result as an indication that alertness did not play a role for the present response modulation one possible caveat must be regarded: Alert rats have a propensity to whisk while drowsy ones do not (Bushnell, 1998). Could systematic differences in whisking intensities before active and passive contacts have contributed to pre-contact delta power and thus contaminated its usefulness as a marker for alertness? Two arguments speak against this possibility. First, the same result as for the total sample was found if delta power was related to response amplitude within each class of contacts separately. Second, absolute delta power was not consistently different between active and passive contacts. Therefore, if we accept that delta power reflects states of alertness, we can exclude that alertness played a role for signal modulation in our experiments. An important qualification of this conclusion is that the spectral analysis as employed here acts as a control for our specific experimental environment. The results neither justify the general conclusion that whisking has no LFP correlate [e.g. the theta band is known to partly synchronize with whisking rhythms (Komisaruk, 1970; Gray, 1971; Hamada et al., 1999; O’Connor et al., 2002; Ahrens and Kleinfeld, 2004)], nor are they in contradiction to the notion that alertness does modulate tactile processing in circumstances not studied here (Castro-Alamancos, 2004a).

Central Signals Derived from Motor Commands
Our demonstration that the modulation of response amplitudes shows a temporal coupling with whisker trajectories in the range of ~100 ms accords best with the possibility that signals derived from the motor system are at its base. Structurally, the existence of such interactions is well established. Anatomical and electrophysiological evidence suggests that stations on all levels of the motor hierarchy from brainstem to motor cortex send connections to structures in the somatosensory system at several hierarchical levels (Shin and Chapin, 1989, 1990a,b; Seki et al., 2003; Nguyen and Kleinfeld, 2005). In particular, infragranular layers of barrel cortex, the presumptive site of recording in the present study, are known to obtain a variety of non-sensory input, notably from motor cortex both with and without intercalation of the posterior-medial thalamic nucleus (Miyashita et al., 1994; Deschénes et al., 1998). Varying levels of origin in the motor system imply that the signal characteristics and the information content of motor signals sent to somatotot sensory structures may be very different from one level of interaction to the next. This characterization embraces the present finding that the modulatory signal did not reflect the whisking rhythm and points to a higher motor center as the presumptive origin. The rhythm of whisking is very likely generated by a sub-cortical pattern generator (Welker, 1964; Gao et al., 2001; Hattox et al., 2003), leaving the possibility that upstream of the oscillator non-rhythmic motor commands exist, for instance in motor cortex and related structures. One candidate site has been recently described, a sub-area in the whisker representation of motor cortex called RW (rhythmic whisking) that does not need to be rhythmically activated at frequencies of 5–10 Hz in order to generate whisking (Haiss and Schwarz, 2005). A neighboring sub-area called RF (’retraction and face’) may be involved to adjust the set point of rhythmic
whisking (Haiss and Schwarz, 2005). If one recalls that our definition of 'passiveness' entails whisker immobility but not necessarily the absence of (isometric) muscle activity, it becomes feasible that signals generated by these two areas may reciprocally set the tactile system for processing of active and passive touch. In conclusion, the characteristics of the central modulatory signal found here — (i) temporally tight coupling to whisker trajectories, (ii) non-rhythmical, (iii) no graded coding for kinematic parameters and (iv) central origin — leave its derivation from motor signals a highly likely contender. Furthermore, as we want to elaborate in the final paragraphs, it helps to constrain arguments in the debate about its presumptive functional use.

Functional Considerations
Could the suppression of afferent signals be interpreted in the framework of the re-afference principle or corollary discharge (von Holst and Mittelstaedt, 1950; Sperry, 1950)? This theory predicts that an internal signal derived from a motor signal (the efference copy or corollary discharge) is used to subtract the self-initiated, predictable part of afferent information (re-afference) and, therefore, make the novel, unpredictable part of afferent information (ex-afference) stand out. The present findings do not match these expectations because, first, the internal signal is non-rhythmic and thus cannot be a negative image of the presumably rhythmic re-afferent signal. Second, the suppression affects the ex-afference, i.e. the contact-related responses, which according to the predictions of the hypothesis should be spared. Third, the ION transection should decouple the internal command from the re-afference and in effect isolate the internal signal (see e.g. Bell, 2001), a prediction that is incompatible with our finding that movement-related signals showed similar characteristics before and after nerve transection. The third argument also speaks against a more general version of the re-afference principle in which the internal signal would exert an unspecific gating function, i.e. a suppression of all afferent signals — ex-afference and re-afference. This scenario would still predict a decoupling of re-afference and internal signal by nerve transection for which we did not obtain evidence (compare e.g. Seki et al., 2003).

The characteristics of interaction of central movement-related and external contact-related signals in our data, thus, do not favor the notion that this kind of central signaling is used exclusively for canceling self-initiated activity or gating sensory signals. Rather, it appears to add movement-related information to the contact-related signals by reducing the gain of the response and reducing its spatial spread on the cortical surface. In line with this consideration are earlier studies that found effects of central movement-related signaling beyond the cancellation of self-initiated effects; for example, enhancement of tactile signals during reaching movements in monkeys (Nelson et al., 1991), pre-saccadic shifts of receptive fields (Dahamel et al., 1992) or storing movement-related information in short term memory (Sommer and Wurtz, 2002). Which central movement-related information could be added to contact-related information? It has been postulated that active scanning movement of tactile sensors provides richer information about spatial patterns of textures, because — different from passive touch — they are additionally encoded in temporal patterns of afferent signals (Ahissar et al., 1997; Gamzu and Ahissar, 2001). The prerequisite for the usefulness of such a code, however, is that information about movement-related kinematic parameters is available for its decoding. Unit firing rates did not seem to carry information about pre-contact kinematic parameters (Fig. 4). However, the present experiment tested the effect on punctual contacts and, thus, did not require that the animal made use of kinematic information. Therefore, before ruling out the possibility that kinematic information is contained in modulatory signals they have to be reassessed under conditions of texture discrimination. Other possible information carried by the modulatory signals may be related to the animal’s selective attention. Active touch may require a shift of the focus of attention either toward the tactile modality in general or to certain spatial features of the expected sensory input (Posner, 1980; Juan et al., 2004). There is evidence from the visual system in humans that a close link exists between endogenously generated attention and movement trajectories for explorative eye and hand movements (Deubel and Schneider, 1996; Deubel et al., 1998). Furthermore, the neuronal basis of visual attention has been suggested to involve motor signals for overt shifts of attention (accompanied by explorative movements) as well covert ones (not accompanied by movement) (Rizzolatti et al., 1987, 1994). Clearly, these possibilities are compatible with our present conclusion that the origin of the modulatory signal is best searched in the motor system and have to be studied in a focused way by future experiments.

Supplementary Material
Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

Notes
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