Whisking and whisker kinematics during a texture classification task

Yanfang Zuo, Igor Perkon and Mathew E. Diamond*  

International School for Advanced Studies (SISSA), Cognitive Neuroscience Sector, 
Italian Institute of Technology—SISSA Unit, Via Bonomea 265, 34136 Trieste, Italy

Rats explore objects by rhythmically whisking with their vibrissae. The goal of the present study is to learn more about the motor output used by rats to acquire texture information as well as the whisker motion evoked by texture contact. We trained four rats to discriminate between different grooved textures and used high-speed video to characterize whisker motion during the task. The variance in whisking parameters among subjects was notable. After whisker trimming, the animals changed their behaviour in ways that appear consistent with an optimization of whisker movement to compensate for lost information. These results lead to the intriguing notion that the rats use an information-seeking ‘cognitive’ motor strategy, instead of a rigid motor programme. Distinct stick/slip events occurred during texture palpation and their frequency increased in relation to the spatial frequency of the grooves. The results allow a preliminary assessment of three candidate texture-coding mechanisms—the number of grooves encountered during each touch, the temporal difference between groove contacts and the spatial pattern of groove contacts across the whiskers.

Keywords: whisking; vibrissae; texture classification task; touch; stick/slip

1. INTRODUCTION

Whisker-mediated touch is an important channel through which rodents collect information from the nearby environment [1,2]. The animals actively sweep their vibrissae in a rhythmic forward and backward motion, called whisking, to encounter and palpate objects [3,4]. Whisking has been observed during texture discrimination [5–10], distance estimation [11,12], shape judgement [13,14] and object localization in the horizontal dimension [3,15]. It has been suggested that whisking kinematics is tuned to task requirements [3,8,14–16]. For instance, in a previous study, rats were trained either to detect the presence versus absence of a cube, or else to discriminate between the same cube versus a sphere [14]. The rats trained in object discrimination showed shorter whisk duration, smaller protraction amplitude and higher frequency compared with those trained in object detection.

Carvell & Simons [8] first quantified whisking frequency and speed during the discrimination of textures in a study that emphasized the animals’ fine capacities in detecting shallow grooves. In a subsequent study, they focused on individual differences, finding that whisking frequency varied with and among subjects; successful performance in texture discrimination was positively correlated with the amount of time spent whisking and with a shift towards higher whisking frequencies of 8–15 Hz [17]. Conversely, rats whose whiskers were trimmed shortly after birth failed to perform a difficult discrimination, and these animals whisked at frequencies below the normal range [18].

Later studies used higher temporal and spatial resolution to focus on the kinematics of single vibrissae during contact with textures. Contact with coarse, irregular surfaces was found to generate large amplitude, high-velocity ‘stick/slip’ events, while smooth surfaces generated smaller amplitude stick/slip events [6,10,19–21]. Additional work addressed how whisker motion is encoded by neurons at the level of the trigeminal ganglion (primary sensory neurons) and the primary somatosensory cortex: coarse textures, because of the larger amplitude of the stick/slip events, were translated into higher firing rates and smooth ones were translated to lower firing rates [6,7,20–22].

While knowledge was accumulating about the micromotion of whiskers, new methods in high-speed video and image processing were developed to address once again the earlier question: what is the motor output adopted by rats in order to collect information about texture? In this study, we present a preliminary characterization of whisking and whisker kinematics during a texture identification task. One issue of particular interest was the effect of trimming whiskers in trained rats. We wished to evaluate two alternative hypotheses: (i) motor patterns involved with texture discrimination, once stabilized, remain fixed independently of changes in the sensory apparatus, or (ii) motor patterns adapt to changes in the sensory apparatus.
apparatus. The first case would suggest that the rat performs actions by selecting hard-wired motor programmes from an available repertoire, while the second would suggest that the sensory and motor systems act in a coordinated manner driven by the goal of acquiring the information needed to solve the task.

2. MATERIAL AND METHODS

(a) Subjects

Four Wistar rats (Harlan Italy, S. Pietro al Natisone) weighing about 350 g were individually housed on an inverted 13/11 light/dark cycle, and experiments were performed during the dark phase. After the rats arrived at the laboratory, they were given one week to acclimatize to the housing conditions with free access to food and water. Twenty-four hours prior to the onset of training, and throughout the training, rats were water-restricted but had free access to food in the home cage. Water was given during training as a reward and was also available ad libitum for half an hour after training.

(b) Apparatus

The arena was situated in a Faraday room. Dim visible light was used in the early phases of training so that the rat would be oriented in its environment. In the later test phase, during which the present data were collected, the visible light was extinguished. To permit video recording, invisible infrared light was used.

The apparatus was custom-made in aluminium and consisted of one rectangular platform (36 × 11 cm, elevated 30 cm above the table), whose shorter edge faced an octagonal platform (side length, 10 cm) across a gap of adjustable width (see electronic supplementary material, figure S1 and fig. 1 in Itskov et al. [23]). A Panasonic overhead dome camera recorded the session at 25 frames per second.

Five discriminanda were used in different combinations in different rats. Each textured plate was Plexiglas. One plate was smooth, while the other four contained regularly spaced grooves of 1 mm width and 1 mm depth. The grooved plates were distinguished from each other by the spacing between grooves: 1, 2, 4 or 8 mm (figure 1). Each plate contained regularly spaced grooves of 1 mm width and 1 mm depth. The grooved plates were distinguished from each other by the spacing between grooves: 1, 2, 4 or 8 mm (figure 1). Discriminanda were mounted with the surface facing upwards, 45° with respect to vertical and to horizontal. All plates were water-restricted but had free access to food in the home cage. Water was given during training as a reward and was also available ad libitum for half an hour after training.

(c) Texture classification task

Rats were handled and habituated to the training arena under dim visible light for one week. Training sessions were held once a day for about 1 h. On each trial, one of the textured plates was presented to the rat. The rat perched on the front edge of the rectangular platform and extended itself forward to contact the discriminandum with its whiskers. The gap distance was titrated so that the rat could not make contact with its nose or with the microvibrissae around the snout and lips. After palpating the texture, the rat withdrew and turned to either left or right to lick the drinking spout. Only if it approached the correct drinking spout was it given a water reward (0.1 ml); for an incorrect choice, it received no water. The correct drinking spout for a given texture was determined by a relationship that was fixed over time for each rat (table 1). The next trial started as soon as the high-speed video was saved on the computer, a delay of about 25 s. Between trials, the discriminandum mount was turned about its vertical axis by a computer-controlled stepping motor. This allowed for randomized and automated switching between discriminanda. The session lasted until the rat failed to return to the discriminandum, signifying it was saturated, usually after 100–200 trials.

Associations between texture and reward location were fixed for each animal but were varied across rats. Experimental conditions are shown in table 1. Because we did not wish to impose our preconceptions about which discriminations might be difficult or easy for the rats, the grouping in different rats was random.

(d) Whisker trimming

The whiskers were trimmed in rats 2–4 by the following procedure. After administration of the short-acting sedative medetomidine (0.1 mg kg⁻¹) by the intraperitoneal route, all the long snout whiskers on both sides, except those of the C and D rows, were clipped as close as possible to the skin. Across the following weeks, whiskers were re-clipped as necessary to prevent their contact with the discriminanda.

(e) Video recording and analysis

Vibrissal motion and contact was recorded by a high-speed (1000 fps, 256 × 512 pixels) digital video camera (Motionpro 2000; Redlake) triggered by a light sensor positioned near the discriminandum. Backlight illumination for the high-speed video came from a light emitting diode emitting infrared light at wavelength 880 nm. Video clips were 1 s long (1000 frames).

Video clips were analysed off-line. For touch analysis, we extracted touch times (onset–offset) of all the whiskers by visual examination. For a touch to be counted, the whisker had to be in contact with the texture plate and show a bending owing to contact. Trials in which whisker touches could not be discerned with confidence were excluded from the analysis.

An example of whisking in a typical trial is shown in figure 1b. Table 2 gives the definitions of whisking variables and the values of these variables for the trial of figure 1b.

Turn direction affected contact time in the following manner. When the rat turned right, the right whiskers retracted and the left protracted as the head began to rotate to the side, consistent with the report of Grant et al. [1]. The protracted whiskers remained in contact with the texture for several tens of

Phil. Trans. R. Soc. B (2011)
milliseconds longer than the retracted whiskers. Thus, left whisker contact time was extended in right turns and right whisker contact was extended in left turns. Since one of our purposes was to determine whether touch time varied according to the contacted texture, and since texture was bound to turn direction, it was necessary to control for the influence of turn direction on contact time. We did so by normalizing the values of left-turn trials to the mean value of all correct left-turn trials (normalized value of each left-turn trial = the value of that trial/mean value of all the correct left-turn trials), and similarly, by normalizing the values of right-turn trials to the mean value of the correct right-turn trials (normalized value of each right-turn trial = the value of that trial/mean value of all the correct right-turn trials). These normalizations allowed us to determine whether whisking values differed between the two textures associated with a given turn direction. As the total number of trials varied between textures, mean values were calculated for each texture, respectively, then the mean of the mean values was appropriately weighted by the distribution of stimuli.

The kinematics of whisking was documented by a software suite that automatically computes the mean angle of all the whiskers on one side of the snout [24].
Table 2. Definition of whisking variables.

<table>
<thead>
<tr>
<th>variable</th>
<th>definition</th>
<th>values in sample trial (figure 1b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>contact count</td>
<td>number of touches per trial for any whisker combination</td>
<td>3</td>
</tr>
<tr>
<td>contact duration</td>
<td>mean duration of contact for any whisker combination</td>
<td>35 ms</td>
</tr>
<tr>
<td>whisker count per contact</td>
<td>mean number of whiskers in contact with the texture during touch</td>
<td>3</td>
</tr>
<tr>
<td>exploration duration</td>
<td>time from onset of first contact by any whisker to the offset of last</td>
<td>245 ms</td>
</tr>
<tr>
<td>contact by any whisker</td>
<td>contact count × contact duration</td>
<td>106 ms</td>
</tr>
<tr>
<td>total contact duration</td>
<td>whisker count per contact × total contact duration</td>
<td>318 ms</td>
</tr>
<tr>
<td>total touch time of all the</td>
<td></td>
<td></td>
</tr>
<tr>
<td>whiskers</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3. RESULTS

(a) Performance in the texture classification task and the effect of whisker trimming

Performance (per cent correct) was computed for every session of each rat. Rat 1 performed the task at 66.7 ± 2.1% correct, averaged across 19 sessions and all textures. Performance was above chance (t-test versus 50%, p < 0.001). The performance upon encountering individual textures was calculated and exceeded chance level in all cases (2 mm, 72.6 ± 2.1%, p < 0.001; 4 mm, 60.3 ± 2.2%, p < 0.001; 8 mm, 61.9 ± 1.9%, p < 0.0001; smooth, 72.3 ± 2.7%, p < 0.001). One-way ANOVA was used to compare the rat’s performance upon encountering different textures. A significant difference was found (figure 2a, p < 0.0001). Tukey’s post hoc test showed higher performance for the 2 mm texture and the smooth texture than for the 4 and 8 mm textures. One can speculate that the rat frequently mistook the latter two textures for each other but could more readily assign the extreme textures—lowest and highest spatial frequencies—to the correct category.

Rats 2–4 (but not rat 1) were used in a neuro-physiological study (neuronal data not reported here). In these rats, all whiskers except those of the C and D rows were trimmed bilaterally after electrode implantation to force them to use the whiskers projecting to the recorded neurons. After trimming, no overt behavioural changes were noted (exploration, grooming, appetite). However, as described below, the grooming led to changes in performance as well as alterations in the way the rats palpatated the textured surfaces.

The rats were reintroduced to the texture discrimination apparatus beginning 2 days after trimming. The time course of average performance across the three rats is shown in figure 2b. It is clear that the animals’ behaviour passed through three phases: (i) a period of consistent performance across sessions prior to whisker trimming, which we refer to as ‘steady state’, (ii) a period of ‘transition’ after trimming, where performance varied across sessions, and (iii) a second period of steady state after trimming. Whisker trimming caused a drop in performance by about 15 per cent, from about 80 to 65 per cent correct. However, after 3–4 days of re-training, the performance increased to a stable level.

Two-way ANOVA tests (texture × trimming) were used to examine the effects of trimming and texture on performance for each rat. For each rat, performance in three to four steady-state sessions before trimming and 7–10 steady-state sessions after trimming was analysed.

Merging the before- and after-trimming sessions, significant main effects reveal that the three rats showed different performance for different textures: rat 2 (figure 2c; main effect of texture, p < 0.001) and rat 3 (figure 2d; main effect of texture, p < 0.01) showed higher performance for the smooth and most densely grooved plates (1 mm for rat 2, 2 mm for rat 3), and lower performance for the intermediate grooved plate (4 mm); rat 4 demonstrated the opposite trend, with a higher performance for the less densely grooved plate (figure 2e; main effect of texture, p < 0.05). These results suggest that the degree of difficulty was based on the interaction between the textures’ physical properties and the categorization rules (which textures had to be discriminated from each other, and which grouped); there was no texture property that caused the identical challenge across rats.

A significant main effect of trimming was also found for the three rats, indicating that whisker removal disrupted texture discrimination (figure 2c, rat 2, main effect of trimming, p < 0.05; figure 2d, rat 3, p < 0.05; figure 2e, rat 4, p < 0.05).

(b) Characteristics of whisking

Analysis of video clips was carried out for one to four sessions per rat. We first asked whether at steady state—the period across which performance was stable—a given rat maintained consistent whisking parameters. Pre-trimming and post-trimming conditions were examined separately. Extracting the basic characteristics of motor output (those defined in figure 1b), we detected no significant changes across sessions within an individual rat, indicating a stable motor strategy within individuals. In contrast, during the ‘transition’ shortly after trimming, motor strategies were non-stationary. Characterizing these periods will require further analysis and a larger dataset. Here, we present results derived only from steady-state sessions. Since different texture–response direction rules were used for different rats, and because rats had distinctive whisking strategies, data for each rat are presented separately.

As the rats leaned forward, they seemed to search for the discriminanda by repetitively protracting and retracting their vibrissae. Upon contacting the discriminandum, they continued to rhythmically palpate the surface. In some trials, left–right phase symmetry was maintained after contact (electronic supplementary material, video S1; pre-trimming) while in other trials, left–right phase symmetry appeared to be
disrupted upon contact (electronic supplementary material, video S2; post-trimming). The determinants of left–right coherence will be an interesting topic for future work.

Modal frequency was computed on each trial by dividing the number of whisker protractions (local maxima; figure 1b) by time. The average frequency was 10.2 Hz; the range extended from 6 to 14 Hz. Frequencies in different rats were similar.

An earlier study detected a relation between whisking frequency and discrimination accuracy [17]. We tested whether whisking frequency was related to either performance or the texture encountered. Unlike the previous study, in our data, there was no difference in whisking frequency between correct and incorrect trials (two-way ANOVA, performance × texture, main effect of performance, \( p > 0.05 \)). There was also no difference in whisking frequency across different textures (main effect of texture, \( p > 0.05 \)). The first result indicates that, under our experimental conditions, better sensation was not achieved by higher frequency or by correlated parameters. The second result suggests that at least some aspects of the motor programme were fixed at the outset of each trial and were not adjusted online according to the surface contacted.

(c) Overall characteristics of texture exploration and the effects of trimming

In our experiments, confirming earlier work [7,8,17], whisker-mediated object identification was highly efficient. Measures of whisking and touch, before and
after trimming, are given in table 3. Prior to trimming, on a typical trial, an individual whisker made one to three contacts of approximately 20–50 ms duration each (except rat 3 whose whiskers usually made four to five contacts), summing to a total touch time of approximately 50–200 ms. More than one whisker contacted the discriminandum during each protraction. The total contact time of all whiskers together was approximately 100–750 ms. The exploration time from first whisker contact to the onset of the rats’ movement towards the reward location was approximately 100–300 ms. The variance among subjects for all these measures is notable.

Whisker trimming did not change whisking frequency. The grand average across sessions and rats was 10.2 ± 0.1 Hz (compared with 10.3 ± 0.2 Hz before trimming; results not illustrated). In contrast, other features of whisking were affected. From table 3, it can be discerned that, after trimming, fewer whiskers made simultaneous contact with the texture, as could be expected (main effect of trimming, \( p < 0.0001 \)). Rat 3 increased the duration of each contact, and few whiskers contacting the texture, the total contact time of all the whiskers was dramatically decreased.

It is interesting to go beyond the data of table 3 to ask whether whisking and touch parameters were reflected in the accuracy of the animals’ judgement. Because the analysis across all rats is lengthy, only rat 3 is illustrated as an example (electronic supplementary material, figure S2). Two-way ANOVA (performance × trimming) was used to examine the effects of performance (correct or incorrect) and trimming (pre- or post-trimming). Surprisingly, there were no differences for most whisking parameters between correct and incorrect trials. An exception is the whisker counts per contact. After whisker trimming, rat 3 tended to contact the textures with more whiskers on correct trials than on incorrect trials (electronic supplementary material, figures S2a; t-test, \( p < 0.05 \)).

### (d) Dependence of exploration characteristics on the contacted texture

Next, we asked whether variations in whisking characteristics were associated with errors on specific textures—such findings might provide insight into how the rats acquired and integrated vibrissal signals. Two-way ANOVA (performance × texture) was used to compare exploration parameters across textures on correct versus incorrect trials. In rat 1, no differences were found on whisker count per touch (figure 3a; performance × texture, \( p > 0.05 \)) or duration of each contact (figure 3b; performance × texture, \( p > 0.05 \)). However, there were significant interactions between the two variables on contact count (figure 3c; \( p < 0.01 \)), exploration duration (figure 3d; \( p < 0.01 \)), contact duration (figure 3e; \( p < 0.001 \)) and total touch time of all the whiskers (figure 3f; \( p < 0.01 \)). A Bonferroni post-test revealed significant differences across textures on incorrect trials (figure 3c, contact count, \( p < 0.01 \); figure 3d, exploration duration, \( p < 0.01 \);
Supplementary material, figure S3

Differences were found for contact count (electronic supplementary material, video S3). By contrast, no significant differences were found on any of the measures. The results of Bonferroni post-tests between correct and incorrect trials are shown between the curves. n.s., no significant difference, *p < 0.05, ***p < 0.0001. The shading refers to the textures associated with the right turn; no shading denotes left. Dashed line, incorrect; solid line, correct.

Figure 3. Exploration characteristics separated by textures in rat 1. Data are shown after normalization by turn direction. (a) Whisker count per contact. (b) Contact duration. (c) Contact count. (d) Exploration duration. (e) Total contact duration. (f) Total touch time of all the whiskers. Results of two-way ANOVAs are shown in the left lower corner of each panel. The results of Bonferroni post-tests between correct and incorrect trials are shown between the curves. n.s., no significant difference, *p < 0.05, ***p < 0.0001. The shading refers to the textures associated with the right turn; no shading denotes left. Dashed line, incorrect; solid line, correct.

Figure 4, contact duration, p < 0.001; figure 3f, total contact time of all the whiskers, p < 0.01), but not on correct trials (figure 3c, contact count, p > 0.05; figure 3d, exploration duration, p > 0.05; figure 3e, total contact duration, p > 0.05; figure 3f, total contact time of all the whiskers, p > 0.05). The results revealed that these measures were higher for the smoother textures (8 mm and smooth) and lower for the texture with the highest groove density (2 mm) on incorrect trials compared with correct trials.

The exploration strategy varied among subjects. Electronic supplementary material, figure S3 shows the normalized results of rat 2 after trimming. More whiskers contacted the plate during correct trials than during incorrect trials (electronic supplementary material, figure S3a; main effect of performance, p < 0.05). A significant interaction was found for duration of each contact (electronic supplementary material, figure S3b; performance × texture, p < 0.01), revealing a significantly greater sampling for the smooth texture on the correct trials. By contrast, no significant differences were found for contact count (electronic supplementary material, figure S3c; performance × texture, p > 0.05). The changes of these three independent parameters contributed to a higher value in the total contact time of all the whiskers on correct trials than on incorrect trials for the smooth texture (performance × texture; p < 0.05).

For the other two rats (rats 3 and 4), no significant differences were found on any of the measures.

(f) Whisker kinematics: stick/slip events

It has been proposed that the critical kinematic events that underlie texture discrimination are the stick/slip events, originally described as ‘the irregularities—jumps, stops and starts—induced by whisking on sandpaper’ [19]. Grooved surfaces caused a similar phenomenon to that seen on irregular, grainy surfaces [19]: whiskers became briefly stuck in the grooves during contact. The sticks usually occurred when the whiskers started to retract after reaching the most protracted position. We registered a stick by visual inspection when there was an evident bending of the whisker such that its form became concave in the direction of retraction. An example is shown in figure 4b, which shows the tracking of whisker C3 in rat 3, extracted from electronic supplementary material, video S4 (frames 530–580). To quantify the magnitude of the detected stick/slip, local angle relative to the snout was calculated for 10 equally-spaced points along the whisker. The difference of the local angle between two adjacent points was calculated. The highest local angle difference was taken as a measure of whisker curvature (figure 4c). In frame 550, the retracting whisker became lodged inside the

(e) Whisker kinematics: translation across grooves

We observed two features of whisker motion that could be informative about texture: translation across grooves and stick/slip events. Whiskers shafts or tips moved laterally along the textured surface on many trials (figure 4a and electronic supplementary material, video S3). It is logical to suppose that the number of grooves encountered during such sweeps was proportional to the spatial frequency of grooves; however, to date, we have not quantified kinematics during translation. It is clear that the lateral motion across these textures was much greater than that seen during discrimination between a smooth surface and an irregular, sandpaper-like surface [7, 25]. Further work is needed.
groove (the stick event), and angle difference was minimal until frame 550. In frame 557, the whisker sprung loose (the slip event) and reached peak angle difference. During stick/slip events, the angle difference was considerably greater than the angle difference during whisking in air (figure 4d, t-test, p < 0.0001). This signifies that sensory receptors sensitive to whisker motion could fire selectively for slip events if their angle-difference threshold lies at about 5° ms⁻¹.

How tight is the connection between a whisker stick and a slip? In rat 3, in 91.2 per cent of the cases in which we could detect a whisker stick, a release from the groove (slip) followed, and this occurred on average 12.3 ± 0.9 ms after the stick was first detected. In the remaining cases (8.8%), the whisker started to protract without releasing; the start of protraction, with no slip event, occurred on average 28.5 ± 1.9 ms after the stick was first detected. Here, we
pooled together all stick events (which were in fact stick/slip events in over 90 per cent of cases). Figure 4e shows the percentage of trials with sticks in rat 3; a trial was counted as containing a stick if any individual whisker exhibited such an event. Before whisker trimming (figure 4e), sticks occurred on average in 8.9 per cent of correct trials, and the probability was higher on the 2 mm plate (33.3%) than on the 4 mm (25%) and smooth (10.2%) ones. A χ²-test for trend showed that the probability of sticks increased with groove frequency (p < 0.05).

After whisker removal, the probability of sticks was dramatically increased (figure 4f). This observation suggests that the rat adapted its whisking trajectories after trimming, another sign that whisking is a finely controlled information-seeking action. The adaptation might consist of applying more pressure against the plate, which would presumably lead to a greater probability of sticking. Thus, in rat 3, we found sticks on 51.4 per cent of the correct trials, which was obviously greater compared with pre-trimming (χ²-test, 18.9 versus 51.4%, p < 0.0001). Similar to pre-trimming, the probability of sticks also decreased from the 2 mm (79.5%), to the 4 mm (66.7%) and smooth (15.1%) plates (χ²-test for trend, p < 0.0001).

Since the probability of sticks decreased monotonically with the decreasing spatial frequency of grooves on the plate, it is logical to propose that the stick events are the peripheral input signal that leads to the judgement of texture. If so, we should observe a significant difference in the occurrence of sticks between correct and incorrect trials. For instance, in rat 3, which was required to distinguish the smooth texture from the grooved ones (2 and 4 mm), the percentage of sticks on the smooth texture would be expected to be higher on incorrect trials or on correct trials, leading the rat to sense the smooth texture as a grooved one. By the same argument, we would expect the percentage of sticks on the 0 mm plate to be lower on error trials. However, a lower percentage of sticks on the 2 mm plate may not necessarily be connected with an incorrect decision, because the rat may perceive the texture as being the other texture in the same category (4 mm), thus leading to the correct response. Tests of these predictions showed that there was no difference in the probability of sticks between the incorrect and correct trials for all the textures, either before whisker trimming (figure 4e; χ² with Yates’ correction; 0 versus 33.3%, p > 0.05 for 2 mm; 14.3 versus 25%, p > 0.05 for 4 mm; 0 versus 10.2%, p > 0.05 for smooth) or after whisker trimming (figure 4f; χ²; 75 versus 79.5%, p > 0.05 for 2 mm; 76.5 versus 66.7%, p > 0.05 for 4 mm; 21.4 versus 15.1%, p > 0.05 for smooth). This result indicates that, contrary to our intuition, the rat did not make decisions by using stick/slip events alone to sense whether a given plate contained or did not contain a groove.

Another possibility was that the rat made its decision based not on the presence or absence of a stick event but on the number of stick events (also correlated with groove frequency) sensed on each plate. We compared the number of sticks per trial among the textures (figure 4g,h). On the 2 mm plate, more than one stick event occurred on 47.62 per cent of correct trials, and on the 4 mm plate, more than one stick event occurred on 42.9 per cent of correct trials. These numbers were significantly more than the smooth plate (5.8%) (figure 4g). But the distribution of stick counts per trial on the incorrect trials did not significantly differ from that of the correct trials (figure 4h; χ²-test; 2 mm, p > 0.05; 4 mm, p > 0.05; smooth, p > 0.05).

In addition to rat 3, the other rats also showed texture-related variation in the frequency of stick/slip events (after whisker trimming, rat 2, 45.8% for 2 mm, 12.4% for 4 mm, 1.4% for smooth; rat 4, 65.1% for 2 mm, 54.8% for 4 mm, 0% for smooth). As in rat 3, no difference was found between incorrect and correct trials. Thus, our analyses to date are consistent with the idea that stick/slip events were evoked in a graded manner by this set of textures and the events could thus contribute to texture sensing. However, the observations do not at this point provide an explanation for errors according to the presence or the frequency of stick/slip events. Two possibilities remain to explain errors. First, kinematic features other than retraction stick/slip events may contribute to sensing and to sensory errors. A strong candidate is the lateral translation during protration (figure 4a). Second, errors may originate within the central nervous system rather than in the whiskers.

4. DISCUSSION
(a) General characteristics of whisking
This is the first detailed characterization from high-speed video of whisking—the active motor output aimed at generating sensory signals—during an object identification task. We observed, consistent with previous reports [8], marked individual differences in some parameters of texture exploration (e.g. number of contacts per trial), while other parameters were conserved among subjects (e.g. mean whisking frequency of about 10 Hz). Unlike one earlier report, we did not find evidence consistent with a shift to a higher whisking frequency (15–25 Hz) during palpation of the object, so-called ‘foveal’ whisking [3]. In a previous study, a higher whisking frequency was correlated with better performance [17]; in our dataset, this correlation did not emerge. Instead, performance appeared to be more closely related to the details of the whisker–surface interaction. In rat 1, for instance, a lower contact count and the resulting lower contact time was associated with incorrect choices (figure 3c–f).

The use of high-speed video and automated image analysis allowed us to uncover details of whisker motion during texture acquisition that were unavailable to earlier studies. These details include the compensatory motor pattern generated after whisker trimming, and the motion of single whiskers in contact with the textures.

(b) Graded stimulus set
Earlier work focused on the sensation of irregular, sandpaper-like textures, while in the present study we employed a stimulus set consisting of grooved surfaces (plus a smooth one). There are two main
reasons. First, irregular surfaces are hard to characterize in a quantitative manner. By contrast, grooved textures can be defined along a graded continuum, namely the distance between grooves (‘spatial frequency’). The graded stimulus set led, as we hoped, to graded quantities of whisker kinematic events, allowing us to make preliminary conclusions about a sensory code. Second, we wished to use a stimulus set that would require the rats to discriminate surface features in space. Whereas grainy surfaces can be defined by highly local (less than 1 mm) features, textures with sparsely spaced grooves may be more dependent on integration across longer sweeps or across multiple whiskers to provide signals about the distance between grooves [17].

(c) Candidate coding mechanisms: insights from whisker trimming

Rats were found to accomplish the task whether they were required to classify the textures into higher versus lower spatial frequency of grooves, or else distinguish the intermediate exemplar from the smooth one and from the most densely grooved one. This indicates that they did not sense the plates only by the presence or absence of grooves; instead, they seemed to sense the grooves’ spatial frequency as a graded quantity. Three ways this could be accomplished are outlined here. First, the rats may make a decision based on the number of grooves detected (count coding). This count could be summed across whiskers. Second, they may gauge the distance between adjacent grooves by the time delay between encountering two grooves along the trajectory of individual whiskers (temporal coding) [15,19,26–28]. Knutsen et al. [15] reported that rats could discriminate positional offsets smaller than the inter-vibrissal distance. This vibrissal hyperacuity was hypothesized to be achieved by the temporal encoding of a moving whisker in which the horizontal location is encoded by signalling the elapsed interval between whisking onset and contact [29]. Third, they may use a spatial code, as follows. The long macrovibrissae are ordered in a regular, geometric grid with about 2–3 mm spacing in the middle and posterior part of the snout. Rats may measure the distance between grooves according to the distance between the whiskers that encountered the grooves. In Carvell and Simons’ experiment [8], three of four animals tested required the presence of two or more whiskers to perform the task in which surface features were spaced at least 1 mm apart, suggesting the importance of combining whiskers to collect spatial information. The spatial resolution of a static whisker array is limited by the inter-vibrissal spacing.

Analysis of the parameters in exploratory behaviour can help select among the three potential mechanisms. Six parameters were taken in our study. Three of these—(i) contact count per trial, (ii) contact duration of each touch, and (iii) whisker count per touch—are ‘elementary’ parameters inasmuch as they could be set by the motor system independently of each other. Three additional parameters depend on the elementary parameters: (iv) total contact duration per trial depends on number of contacts and duration of each contact; (v) exploration duration also depends on number of contacts and duration of each contact but includes another factor, the time between contacts when the whiskers are retracted; (vi) total contact time of all the whiskers is the product of all the three elementary parameters. For a given textured plate, the probability of encountering grooves would be expected to increase with the total contact time of all the whiskers, so that the total contact time parameter can be assumed to be a linear correlate of the count of contacted grooves. We observed (electronic supplementary material, video S3) that on many trials whisker shafts or tips moved laterally along the surface, encountering a number of grooves N given roughly as

\[ N = \frac{LS}{D}, \]

where LS is the lateral sweep travelled by the whisker and D is the distance between grooves on that texture. The value N could be used to generate a count code. On the other hand, the value \( N/l \), where l is the duration of the sweep, could be used to generate a temporal code (grooves per unit of time). How would whisker trimming affect the candidate codes? The reduction in the number of whiskers would reduce the spatial density of whiskers and thus directly diminish the accuracy of the spatial code. For the count code and the temporal code, the total input signal would be weakened after trimming inasmuch as fewer whiskers would generate the signals, even if each remaining whisker transmitted the same signal as pre-trimming. Thus, all three candidate codes would be negatively affected. What outcome might the compensatory whisking changes have on the candidate codes? The increase in contact duration found in rats 2, 3 and 4 after trimming (figure 2) would cause an increase in both N (number of grooves contacted) and t (time of sweep), and would thus lead to a more reliable measure of the ratio N/t. The same increase in contact duration would increase the probability of encountering grooves, leading to a more reliable measure of the count difference across textures. The increased duration would seemingly have little effect on a spatial code. In summary, the compensatory changes are more consistent with count coding and temporal coding than with spatial coding.

(d) Candidate coding mechanisms: insights from error trials

With all vibrissae intact, none of the whisking characteristics varied according to the contacted texture on correct trials, indicating that the rats initiated a motor programme on each trial that was largely unaltered by the texture-specific sensory information arriving in the course of the trial. In contrast, the motor programme did vary across textures on incorrect trials. From the uniformity on correct trials, we can surmise that the whisking deviations on incorrect trials probably resulted from the rat initiating the trial with an atypical motor set, which, in turn, affected its integration of incoming sensory signals. The data from rat 1 (figure 3) illustrate the main findings. On incorrect trials, compared with correct trials, both the contact count and the dependent total contact time were reduced on the 2 mm texture but were increased.
on the 8 mm and smooth textures (figure 3c,f). Which candidate coding mechanisms can account for this observation? If the rat used a temporal code (computing the number of grooves contacted divided by the time of sweep), increased or decreased contact time might reduce the reliability of the signal but would not cause any systematic misestimate of the texture like those observed. Nor can we posit any way in which the increased or decreased contact time would lead to texture-specific errors according to the spatial mechanism. By contrast, the count code does provide an explanation. When the rat contacted the 2 mm plate for less time, it was less likely to encounter grooves and the reduced count would cause it to (incorrectly) judge the texture as being in the category of low spatial frequency. By the same token, when the rat contacted the 8 mm and smooth plates for longer, it was more likely to encounter grooves and the increased count would cause it to (incorrectly) judge the texture as being in the category of high spatial frequency. These considerations lead to the following scenario. Trial-to-trial whisking differences lead to corresponding differences in the number of grooves encountered. Since the rat does not appear to fully normalize the incoming sensory signal according to its motor output [27], the altered sensory signal causes the rat to make mistakes. While the previous discussion of whisker-trimming effects suggested use of either a count code or a temporal code, the whisking parameters on error trials favour the count code in this rat.

Unlike in rat 1, mistakes in rat 2 were associated with the changed duration of each contact (electronic supplementary material, figure S3b) and the number of whiskers contacting at the same time (electronic supplementary material, figure S3a). This rat tended to make mistakes when it contacted the smooth plate for a shorter time (electronic supplementary material, figure S3f), which was opposite to rat 1. We cannot easily explain the errors according to a count code—shorter time on the smooth plate would decrease the likelihood of encountering grooves, so the error rate would be expected to decrease rather than increase. Temporal coding is also unlikely to explain the errors inasmuch as the ratio $N/t$ would remain constant for a given texture provided both $N$ and $t$ were altered. In contrast, spatial coding could be the origin of errors—when the rat used more whiskers to touch, the correct rate increased (electronic supplementary material, figure S3a).

Like rat 2, rat 3 also seemed to depend on spatial coding. In rat 3, the only difference found between incorrect and correct trials was that it used more whiskers to touch per contact epoch during correct trials than during incorrect trials (figure 3a). For rat 4, the existing data do not point clearly to any single mechanism. In summary, differences between rats suggest individual strategies are used in texture discrimination.

(e) Stick/slip events and other kinematic features

The probability of stick/slip occurring was higher on textures with a greater spatial frequency, on many trials, the rat could correctly assess the texture even though no distinct stick/slip event occurred, at least according to our inspection. For example, for rat 3, 66.7 per cent of 2 mm trials and 75 per cent of 4 mm trials did not present clearly detectable stick/slip events during whisker retraction, though the rat correctly classified them.

Furthermore, if the rats made decisions based exclusively on stick/slip events, then we should have found differences (in the probability or the number of stick/slip events) between correct and incorrect trials. For example, a greater number of stick/slips on the smooth texture might cause the rat to judge the texture as a grooved one. Yet, no difference between correct and incorrect trials was found either in per cent of trials with stick/slips (figure 4e,f) or number of sticks per trial (figure 4g,h). Additional, more subtle features of whisker kinematics must be at play. The next candidate mechanism to be examined will be the smaller scale vibrations that occur when the whisker moves laterally across the surface in the protraction phase (figure 4a). We have detected small movements of the whisker as it slides across grooves, and these could be translated to either a count code (number of grooves crossed) or a temporal code (time between grooves). To date, we have not quantified such events. In summary, the analysis of stick/slip events shows that these are a clear correlate of groove density and would thus be expected to be critical in sensation, especially because the high-speed release is very likely to evoke neuronal firing [22]. But further examination highlights the need to find other kinematic signatures of texture, and points to a potential role for vibrations generated by translation across the texture during the protraction phase.

Another interesting phenomenon was that the probability of stick/slips per trial increased enormously after trimming (figure 4e,f). However, the total contact time did not increase, so the increased sticks did not occur simply because the whiskers stayed on the texture longer. It appears instead that the rats adapted the whisking trajectories after trimming in a way that caused increased sticking and slipping, perhaps by applying more force. This too is a sign that whisking is a finely controlled information-seeking action.

All experiments were conducted in accordance with the National Institute of Health, international and institutional standards for the care and use of animals in research and were supervised by a consulting veterinarian.

This work was supported by grants from the Human Frontier Science Programme (contract RG0041/2009-C), the European Community (contract BIOTACT-21590), the Compagnia San Paolo, the Italian Institute of Technology through the BMI Project and the Ministry of Economic Development. We are grateful to the members of the laboratory and to various outside collaborators for valuable discussions. Fabrizio Manzino and Marco Gigante provided outstanding technical support. Video analysis was performed using the Vibrissae and Snout Analyzer (ViSA), which was developed as an instrument within the BIOTACT Whisker Tracking Tool (BWTI), jointly created by the International School of Advanced Studies in Trieste, the University of Sheffield and the Weizmann Phil. Trans. R. Soc. B (2011)
Institute under the auspices of the BIOTACT project (contract 215910). We are particularly grateful for the contributions of Vladan Rankov and Goren Gordon to programming parts of the BWTT.

REFERENCES


