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Grant, R.A., Mitchinson, B., Fox, C.W. et al. (1 more author) (2009) Active Touch Sensing in the Rat: Anticipatory and Regulatory Control of Whisker Movements During Surface Exploration. Journal of Neurophysiology, 101 (2). pp. 862-874. ISSN 0022-3077

https://doi.org/10.1152/jn.90783.2008

Active touch sensing in the rat: Anticipatory and regulatory control of whisker movements during surface exploration

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Abstract

Animals actively regulate the position and movement of their sensory systems in order to boost the quality and quantity of the sensory information they obtain. The rat vibrissal system is recognized to be an important model system in which to investigate such “active sensing” capabilities. The current study used high-speed video analysis to investigate whisker movements in untrained, freely-moving rats encountering unexpected, vertical surfaces. A prominent feature of rat vibrissal movement is the repeated posterior-anterior sweep of the whiskers in which the macrovibrissae are seen to move largely in synchrony. Here we show that a second significant component of whisking behavior is the size of the arc, or ‘spread’, between the whiskers. Observed spread is shown to vary over the whisk cycle, and to substantially decrease during exploration of an unexpected surface. We further show that the timing of whisker movements is affected by surface contact such that (i) the whiskers rapidly cease forward protraction following an initial, unexpected contact, and may do so even more rapidly following contact with the same surface in the subsequent whisk cycle, and (ii) retraction velocity is reduced following this latter contact leading to longer second contact durations. This evidence is taken to support two hypotheses. First, that the relative velocities of different whiskers may be actively controlled by the rat, and second, that control of whisker velocity and timing may serve to increase the number and duration of whisker-surface contacts whilst ensuring that such contacts are made with a light touch.

Keywords: vibrissa, tactile sensing, active touch, whisking control

1. Introduction

Adult rats sweep their large facial whiskers (macrovibrissae) back and forth in a rhythmic behavior known as whisking that is observed under most conditions of natural locomotion and exploration (Carvell and Simons 1990; Gustafson and Felbain-Keramidas 1977; Hartmann 2001; Vincent 1912). Recent research (Mitchinson et al. 2007; Towal and Hartmann 2006; 2008) has demonstrated that exploratory whisking, in freely-moving animals, often diverges from the regular, bilaterally-symmetric and synchronous motor pattern that has been recorded when immobilized rats are trained to whisk in air (e.g. Bermejo et al. 2002; Gao et al. 2001). Specifically, asymmetries, asynchronies, and changes in whisk amplitude and timing have been documented that may be the consequence of "active sensing" control strategies. Active sensing systems use sensor information, or task knowledge, to control the position and movement of the sensory apparatus in a manner likely to boost the amount of useful sensory information obtained (Aloimonos et al. 1988; Ballard 1991; Gibson 1962; Lungarella et al. 2005). In a previous article (Mitchinson et al. 2007) we provided evidence of active modulation of bilateral whisk amplitude and timing following an initial unilateral contact with a nearby surface. Other researchers have shown evidence that the frequency of whisking or the starting position of the whiskers (the minimum protraction angle) may be controlled in a task- or behavior-specific way (e.g. Berg and Kleinfeld 2003; Carvell and Simons 1990; Sachdev et al. 2003; Sellien et al. 2005; Towal and Hartmann 2006). In the current study we set out to discover whether other parameters of whisker movement might also be subject to this kind of active regulation, and to identify some of the likely sensory consequences of these forms of anticipatory control.

Our research methodology is to observe untrained adult rats exploring simple enclosed environments and record their whisking behavior, using a high-speed digital video camera, before and during contact with smooth vertical surfaces such as walls. We focus on episodes during which rats performed three consecutive whisks with the following characteristics: the first is required to be a "pre-contact" whisk in which the whiskers make no contacts with an identified arena wall (although they may, and typically do, make contact with the floor or with a different arena wall); in the next "1st contact" whisk, at least two whiskers must make contact with the identified wall; and in the subsequent "2nd contact" whisk, at least two whiskers should make further contacts with the same wall. The animals in this study are functionally blind having a genetically-induced retinal dystrophy. Hence, although we record under bright illumination, we can assume that each rat is largely unable to anticipate contact with the target surface prior to the moment that their first whiskers touches. However, from the moment of this first contact, the rat's whisking behavior, in both the post-contact phase of the 1st contact whisk and throughout the 2nd contact whisk may change as a result of this encounter. In particular, the rat may alter the way it controls its whiskers, and its head and body, both in direct response to this initial contact and in anticipation of further contacts with the same surface. For instance, we previously demonstrated immediate, contact-induced changes in the timing of whisker control (see below) and longer-term, anticipatory modulations of whisk amplitude (Mitchinson et al., 2007). Here we will present evidence of contact-induced changes in a further whisking parameter that has been given little attention in previous studies of the whisker system: the relative spacing, or "spread", between adjacent whiskers. We began to investigate whisker spread after noting, in earlier high-speed video recordings, that the whiskers often appear to be less widely spaced when the animal is investigating a vertical surface than in the whisks immediately prior to the initial contact. Here we will provide data suggesting that this measure not only captures a significant, and previously unquantified, fraction of variance in whisking behavior, but that it also appears to be modified by active control mechanisms in anticipation of further contacts, and could function to increase the number of surface-environment contacts made in the subsequent whisk.

In the current study we also extend our earlier finding (Mitchinson et al., 2007) that, during exploratory whisking, the initial contact with a vertical surface triggers a rapid cessation of whisker protraction (and commencement of retraction) such that the whiskers palpate the surface with a relatively light touch. We have termed this active control strategy “minimal impingement” since whisker movements appear to be modulated so as to reduce whisker bending (impingement) against the contacted surface. Whereas we previously demonstrated this result for the 1st contact whisk with a surface that was encountered on just one side of the animal (a unilateral stimulus), here we investigate the extent to which minimal impingement also occurs in the 2nd contact whisk, and in situations where there are bilateral contacts during the first contact whisk.

The investigation of whisking control strategies is key to understanding the nature of the tactile stimuli that are processed in upstream neural centers, such as the somatosensory cortex, during unconstrained exploratory behavior. For instance, evidence for minimal impingement strategies suggests that the whisker stimuli that are transmitted to these structures may be less intense than might otherwise be expected; whilst “maximal contact” strategies, that involve regulating whisk amplitude or spread, could lead us to expect greater numbers of whisker-surface contacts than if control is not subject to such modulation. A further important parameter for understanding upstream sensory processing is the duration of whisker-surface contacts—whilst the whiskers are in contact with the surface the animal may be able to extract useful information about, say, surface shape or texture. Our investigation will therefore also consider how differential control of whisker movements over the first two contact whisk cycles could impact on these important determinants of the tactile signals processed by the rat brain.

2. Methods

2.1 Experimental Procedures

Animals. Ten male Royal College of Surgeons (RCS) dystrophic rats, aged 6–18 months and weighing 250–350g were used. All animals had genetic retinal degeneration (dystrophy) and hence minimal vision, they were therefore strongly reliant on tactile information from their whiskers during locomotion and exploration behavior. Observations in our laboratory of non-dystrophic RCS animals and of sighted Hooded Lister rats suggest that whisking control in dystrophic animals does not deviate in any marked way from that of normally-sighted rats. All animals were kept in a 12-h dark/light cycle at 22°C, with water and food *ad libitum*, tested during the dark (active) part of their daily cycle, and handled prior to being placed in the experimental arena. All procedures were approved by the local Ethics Committee and UK Home Office, under the terms of the UK Animals (Scientific Procedures) Act, 1986.

Apparatus. Digital video recordings were made using a Photron Fastcam PCI camera, recording at 500 frames per second, shutter-speed of 0.5ms, and resolution of

1024x1024. The camera was suspended from the ceiling above a custom-built rectangular (40cm x 40cm) viewing arena with a glass floor, ceiling, and end-wall (see Figure S1 in the Supplementary Material). The arena contained a front-silvered mirror, positioned behind the end-wall, in order to afford two viewpoints to the camera. The camera was also positioned so that it looked directly down the end and side walls in the overhead view, and the front-silvered mirror angled at approximately 45° so that the camera looked along the surface of the floor in the reflected, end-on view. The arena was illuminated from below by a custom-built, high-power light-box, and from the far end of the arena facing the end-wall by a second, suitably-angled mirror. The design and geometry of the arena thus provided uniform back-lighting in two dimensions with the field of view of the camera covering approximately 20cm x 20cm in the overhead view, and 8cm x20cm in the end-on view. In order to obtain an accurate measure of camera/arena geometry a recording was also made of a 3-dimensional calibration tool, with known shape and location, following initial positioning of the camera.

Recording. Opportunistic recordings, each 3-4 seconds in length, were taken of awake, unrestrained animals engaged in active, exploratory behavior. Each animal was filmed on between 2 and 11 occasions with up to 12 clips recorded, per rat, in each filming session. Each recording was initiated by an experimenter viewing the camera scene on a monitor window and pressing a trigger when the animal entered the field of view. A total of 334 recordings were obtained in this way with between 15 and 82 per animal.

Data selection. Video clips were selected for whisker tracking and detailed analysis as follows. To qualify for analysis each video was required to contain three consecutive whisks during which the rat approached and contacted an identified arena wall, with whiskers on the side of the snout ipsilateral to the initial contact clearly visible in the overhead view throughout. Further these three whisks were required to be of the following types, as noted previously: an initial pre-contact whisk in which the whiskers did not contact the identified wall; a 1st contact whisk, in which at least two whiskers made contact with this vertical surface; and a 2nd contact whisk in which at least two whiskers made a further contact with the same surface. The constraint that there should be contacts on at least two whiskers in each cycle was enforced in order to reduce the possibility of including clips in which surface contacts were so slight that they might be below the rat's detection thresholds (Stuttgen et al. 2006). To exclude some of the more atypical interactions with surfaces we also required that the same two whiskers made the initial contact with the wall in both the 1st and 2nd contact whisks. In total, 60 clips (between 1 and 15 per animal) were identified that satisfied these criteria.

Whisker tracking and head tracking. For the 60 selected clips, and for each of the three selected whisks, five whiskers, ipsilateral to the initial contact, were tracked on an LCD flat-screen monitor by a human observer using uncompressed video and a purpose-built tracking tool. Whisker tracking, in this case, used only the overhead view and involved tracking two points, one near the base of the whisker, the other 2/3s of the way out along the whisker shaft (see Figure S1 in the Supplementary Material). This is referred to as the overhead tracking set below. The tracked whiskers were assumed to correspond to whisker columns 0-4, although our results do not depend on this assumption. In order to estimate head movements, the tip of the snout and the midpoint of the head were also tracked in the overhead view, and the height of the snout above the floor in the end-on view. Note that, whilst technologies have recently been developed for automated tracking of whisker movement (Knutsen et al. 2008; Knutsen et al. 2005; Voigts et al. 2008), the difficult problem of tracking multiple whiskers in a complete, intact whisker field has yet to be automated. No smoothing was performed on the tracked whisker angular position or head-movement data, for whisker velocity a moving average filter, that computes a running average of three adjacent points, was used to reduce any effects of tracking inaccuracies.

3D whisker-tip trajectory reconstruction. In order to better evaluate the contribution of head movements to the patterns of whisker movement observed in the overhead view, four representative clips were selected for 3D reconstruction of whisker-tip trajectories. Tracking and reconstruction were performed as follows (see Supplementary Material for full details). First, the tips of all visible whiskers on the side of the animal ipsilateral to the first contact were tracked by a human observer in both the overhead and end-on views. In the Supplementary Material we present data indicating that our camera footage was of sufficient quality to allow whisker tip detection to within 1-3mm. Given this tracking data, describing the position of the set of whisker tips in each view, and knowing the geometry of the camera/arena setup (from the calibration tool), it is possible to map the set of points in each 2D plane, into lines in 3D-space and to apply a stereo correspondence algorithm to determine the best possible (least mean squared error) match between the two sets of detected whisker tips. From this data the trajectory of each matched whisker tip could then be reconstructed in 3 dimensions. Calculation of whisker trajectories using this method is time-consuming, therefore it was applied to only four example clips for the purpose of comparison with data obtained in the overhead view.

2.2 Data analysis

The overhead tracking data, for each clip, was analyzed to obtain the descriptive measures listed in Table 1. Note that for the calculation of *per-whisk* summary measures (Table 1c, d) the point of minimum protraction between two successive protraction-retraction phases was taken as the separation boundary between consecutive whisks. In a small number of whisks a brief change of direction was noted mid-whisk. Following Towal and Hartmann (2008), such "double-pump" whisks were treated as forming part of a single whisk rather than as two separate ones. To detect, and correct for, the effects of these double-pumps a plot of the mean angular position was inspected for each clip with protraction minima and maxima (computed algorithmically) overlaid. Where either the minimal or maximal positions appear to be falsely aligned with double-pump episodes the search for these boundary points was re-computed over a restricted time-range; this method resulted in 10 (out of 240) protraction minima being repositioned and zero maxima. The clips were also examined to determine whether contacts with the target surface, in the 1st contact whisk, occurred on one or both sides of the snout. Two sub-sets were identified for further analysis, the unilateral set (n= 25) in which contact, during the first contact whisk, was on one side only, and the bilateral set (n= 35) in which there were whisker-surface contacts on both sides of the snout in the first contact whisk.

3. Results

Our presentation of results is structured as follows. In 3.1 we provide a Principal Components Analysis (PCA) of our whisker movement data and show that the two main components of whisking determined algorithmically correspond with the theoretically meaningful measures of the mean angular position of the whiskers and whisker spread. We then use cross-covariance analysis to briefly examine the phase relationship between these two components. Next, in 3.2, we quantitatively characterize the whisking behavior of the rat during exploration of an unexpected surface by analyzing variation in summary measures of whisk control (table 1c), head movement (1d), and surface contact (1e) across the pre-contact, and 1st and 2nd contact whisks. Armed with a good understanding of the differences between the three whisk types, section 3.3 then considers whisker spread in more detail, evaluating several alternatives to the hypothesis that spread is controlled using differential whisker velocities and in anticipation of surface contacts. Finding that anticipatory control of whisker velocity is supported by the available data, section 3.4 then examines whether such control is consistent with a "maximizing contact" strategy. We then turn our attention to the "minimal impingement" aspect of our active touch hypothesis and consider whether this is supported by our new data concerning the timing of cessation of protraction following contact. Finally, we look at the duration of whisker-surface contacts and explore the relationship of this important variable to several elements of whisker control, particularly the angular velocity of the whiskers during the retraction phase.

Statistical considerations

The primary focus of this investigation is on contrasts within triplets of consecutive whisks, data were therefore pooled across animals with the video clip of each tracked whisking episode taken as the fundamental unit for analysis. Except where otherwise specified, therefore, the results presented were calculated for the 60 selected clips in the overhead tracking data-set. Following the procedures recommended by Tabachnick and Fidell (2007) all variables were checked for checked for outliers, normality (using the Kolmogorov Smirnov test), and sphericity (using Mauchly's test). For distributions containing outliers, relevant analyses were performed twice, with and without outliers; all such analyses were robust to this procedure and the results reported here include all of the data points. Some violations of normality were detected and a number of variables were therefore log transformed to correct for positive skew. For variables that showed significant sphericity, significance values for univariate ANOVAs were calculated using the Greenhouse-Geisser correction. Post-hoc tests (Bonferroni) were used to identify the principal differences between the pre-contact, 1st contact and 2nd contact whisks. An alpha-level of 0.05 (two-tailed) was used for statistical tests corrected for multiple comparisons when required using a Bonferroni correction. Such corrections were applied whenever several univariate analyses were used to examine a specific sub-domain of active touch sensing such as whisker control, head position and movement, and whisker-surface contact. Multivariate Analysis of Variance (MANOVA) was also used to test for overall differences between whisk types in relation to each of these classes of data. Effect sizes are reported using the partial η^2 measure. Following Cohen (1988), $0.01 < \eta^2 \leq 0.06$ can be interpreted as a small effect, $0.06 < \eta^2 \leq 0.14$ as a medium-sized effect, and $\eta^2 > 0.14$ as a large effect.

Significant results are summarized in the text, tables and figures below, with standard error bars included in graphs where appropriate. Further details of statistical analyses are provided in the Supplementary Material where indicated. To guard against the possibility of Type I errors due to data pooling (Machlis et al. 1985), the analyses reported in tables 2-4 below were all re-computed, with animal identify as a between subject factor, and using data from just the four animals who each generated more than five eligible clips (giving 47 clips in total). Results of these analyses were consistent with those for the pooled data, in that all significant results remained significant when animal identity was included. Between subject tests showed a small difference in maximum protraction ($F_{(1,43)}$ =3.245, p=0.031, partial η^2= 0.185) indicating that some animals whisked somewhat more strongly than others. There were no significant interactions between animal identity and whisk type.

3.1 The principal components of whisking behavior

To better characterize the nature of rat whisking control a PCA analysis was run on the raw whisker angular position data from all five tracked whiskers and across all three specified whisk types (pre-contact, 1st contact, 2nd contact). Three components were found to be present in this data-set as illustrated in Figure 1:

- *Component 1* explained 80.4% (pre-contact whisk), 76.8% (1st contact) and 70.1% (2nd contact) of the variance in whisker positions (Figure 1 top), and was extremely well correlated (r> 0.99) with the mean angular position across all whisk types. Hence, as might be expected, the main component of whisking, as seen from above, is the characteristic forward and backward sweep of the whiskers moving together.
- *Component 2* explained 13.4% (pre-contact whisk), 15.5% (1st contact) and 20.2% (2nd contact) of the variance in whisker positions (Figure 1 center) and was well

correlated well with whisker spread (pre-contact r= 0.90, 1st r= 0.91, 2nd r= 0.92). Interestingly, therefore, changes in the angular separation of the whiskers, over the course of the whisk cycle, constitute the second largest component of whisking behavior.

- *Component 3* explained 3.1% (pre-contact whisk), 3.8% (1st contact) and 4.6% (2nd contact) of the variance in whisker positions (Figure 1 bottom) but was not significantly correlated with any of the measured whisking parameters. Component 3 is best described as the middle whisker columns (1-3) tending to protract more than the two outer columns (0 and 4). Although the proportion of variance explained is small, this component was present in every whisk type suggesting it is unlikely to be an artifact of the measurement/analysis process (in contrast, components 4 and 5 did not have a consistent shape across whisks and so are probably not meaningful).

In summary, then, although the whiskers largely all move together (70-80% of variance captured by mean angular position), there is important variation in relative whisker positions (13–20%) that is well-characterized by the measure of whisker spread. Using these two components together can account for 90-94% of all the variance in the whisker position data seen in the overhead view.

The phase relationship of whisking's principal components

Having established mean angular position and spread as the two main components of whisking it is useful to briefly examine the phase relationship of these two measures over the course of the whisk cycle. An effective tool for this purpose is cross-covariance analysis (Chatfield 2003). The top panel of Figure 2 shows the average cross-covariance across the 60 tracked clips for each whisk type. For each clip, and each whisk-type within that clip, we then found the best-fit phase lag between mean angular position and spread calculated as the peak of the corresponding cross-covariance plot. Histograms of these peak fits are plotted in the lower panel of Figure 2. The average cross-covariance and peak histograms both indicate that, in pre-contact and 1st contact whisks, spread peaks reliably 0-6 milliseconds before angular position. However, this relationship breaks down somewhat in the 2nd contact whisk. Here we see a weaker (flatter) pattern in the average cross-covariance and a more scattered distribution in the best-fit phase-lag, with out of phase relationships (more than 10ms difference between the angular position and spread peaks) in 26 (43%) of the 60 whisks.

The temporal relationship between spread and angular position seen in the pre-contact and 1st contact whisks is consistent with observations by Sachdev (Sachdev et al. 2002), made in head-fixed animals whisking in air, who described spread as being maximal at, or close to, maximum protraction. That this relationship is much less in evidence for the 2nd contact whisk is consistent with the hypothesis, explored below, that active control mechanisms may be influencing whisker spread when the rat is able to anticipate contact with a vertical surface.

3.2 Variation across whisk types in summary measures of whisker control, head position, and whisker-surface contacts

Variation in whisker control across whisk types

To begin our investigation of changes in whisk control following unexpected surface contacts a MANOVA was conducted using whisk type as a 3-way within–subjects factor and the summary whisker movement measures (see Table 1c) maximum protraction angle, minimum protraction angle, mean spread, mean protraction velocity, mean retraction velocity, and whisk duration as dependant variables. This analysis revealed a significant multivariate difference between whisk types ($F_{(12,48)}=7.686$, $p<0.001$, Wilks' lambda = 0.342), with partial η^2 of 0.658 showing this to be a large effect size. To determine which aspects of whisking were contributing to this result, separate univariate ANOVAs were then carried out on each of these six variables, as reported in Table 2. In this table the columns pre-contact, 1st contact, and 2nd contact show the mean and standard deviations of the relevant measure for that whisk type, and the following two columns the percentage change in the mean for the two contact whisks compared to the pre-contact value. The associated analyses, shown in the remaining columns, indicate that all of the variables showed reductions between the pre-contact and 2nd contact whisk, with the 1st contact whisk being, on the whole, more similar to the pre-contact whisk than to the 2nd contact whisk (as indicated by the post-hoc analyses). Two parameters stand out as showing large changes by the 2nd contact whisk—the mean spread and the mean retraction velocity—both measures fell by over 20% over the course of the three whisks. Smaller, but still significant changes of 7-10% occurred in minimum and maximum protraction angles of the whisk and the mean protraction velocity, whilst the 10% drop in whisk duration failed to reach significance due to high variance. Figure 3 provides graphs illustrating each of the significant trends. Examples of the reduction in overall spread are also provided in Supplementary Video 1 and in the sequence of snap-shots in Figure 4. Comparison of clips with bilateral and unilateral 1st contacts using a 2x3 mixed ANOVA showed a main effect of a significant reduction in spread ($F_{(2,116)} = 24.675$, $p<0.001$, partial $\eta^2= 0.298$) between the 2nd contact whisk and the two previous whisks, no overall difference between bilateral and unilateral contacts ($F_{(1,58)} = 1.079$, $p=0.303$), and an interaction effect between whisk type and whether the initial contact was on one or both sides ($F_{(2,116)} = 9.423$, $p< 0.001$, partial $\eta^2= 0.140$). This latter effect, which is illustrated in Figure S3 in the Supplementary Material, showed that the reduction in spread was more pronounced on whisks with bilateral surface contacts.

Variation in head position and movement across whisk types

Whilst our primary focus here is on changes in whisker movements it is important to consider whether there may be consistent patterns in the positioning and movement of the rat head during exploratory whisking. This matters both because head movement can impact on the sensory consequences of whisking (movement toward a surface, for instance, will increase bending of any contacting whiskers), and because head/body movement is likely to be an important element of the overall control strategy used by the rat to position its whiskers. Ideally we would like to be able to measure the position and velocity of the head for all six of the available degrees of freedom (three translational, and three rotational). Unfortunately, whilst it was straightforward to extract measures of horizontal position and movement from our high-speed video (translation along two horizontal axes and rotation around the vertical axis), vertical translation and the two remaining rotations could not be obtained from the majority of clips. Of these missing measures, the most important for our analysis of whisking behavior is rotation around the coronal axis or ‘head tilt’, as changes in tilt can impact significantly on apparent whisker movement recorded in the overhead view. To partially address this issue, however, we were able to track the elevation of the tip of the snout in the vertical view. Snout elevation is redundantly determined by the combination of head tilt and vertical translation of the head (through, for example, crouching or rearing movements). However, since the rat's capacity for vertical translation is limited, we know that low values of snout elevation will be indicative of negative tilt (the head angled downwards to the floor), high values of positive tilt (the head angled upward towards the ceiling), and intermediate values of the head being closer to horizontal. Snout elevation can therefore serve as a partial surrogate for head tilt in evaluating the effects of head-movement on observed whisking behavior and will be used for this purpose in section 3.3.

Seven head position and movement parameters—distance to wall, velocities towards and along the wall, head orientation, head angular velocity, snout elevation and snout vertical velocity (see Table 1d)—were selected for quantitative analysis as being most relevant to understanding whisker movement and positioning with respect to a vertical surface. A preliminary MANOVA again showed a strongly significant difference between whisk types ($F_{(12,48)} = 34.828$, $p<0.001$, Wilks' Lambda = 0.086, partial $\eta^2 = 0.914$) whilst subsequent univariate ANOVAs, shown in Table 3, identified distance to the wall, velocity towards the wall and snout vertical velocity as each showing significant changes across the three whisks. The first of these results confirms that the rat moves progressively closer to the wall during the vast majority of analyzed episodes, and the second that velocity with respect to the wall drops markedly (~50%, $p<0.001$) by the 2nd contact whisk, indicating a significant impact of the initial whisker-surface contact on the rat's subsequent locomotion behavior. Absolute vertical velocity, measured at the snout, whilst rather variable, also increased by 50% in the contact whisks relative to pre-contact ($p<0.001$). Thus, on encountering the vertical surface, movement toward the surface reduced whilst movement across the surface increased. By including the measures of head rotation and movement along the wall (parallel to the floor), we can estimate that, during a typical ~100 ms whisk cycle, each rat moved 9-12 mm horizontally, raised or lowered its snout by 6–10 mm, and rotated its head through 5–6°. In other words, these animals were rarely stationary, and often moved at quite significant speeds whilst exploring nearby surfaces with their whiskers.

Variation in whisker-surface contact across whisk types

We next examine, in more detail, the relationship between whisker movement and surface contact for the two contact whisks. From the previous analysis (Table 3) we know that the rat generally moves closer to the surface of interest, we can therefore expect that the number of whiskers making contact with the surface will increase significantly on a second contact whisk, that contacts will more often involve the shorter rostral whiskers, and that they will usually occur at somewhat smaller whisk amplitudes. Two other variables that have potentially important sensory consequences, and therefore deserve attention, are the velocity of the whisker at the point of contact, and the duration of whisker-surface contact (examined here for the whisker making the initial contact in each whisk). Finally, since we previously proposed "minimal impingement" as a general characteristic of exploratory whisking (Mitchinson et al., 2007) we also expect that control of whisker movement following contact will show the rapid cessation of protraction found in our earlier study in both the 1st and 2nd contact whisks.

To test the above predictions and to quantify key unknowns we examined the six contact-related variables defined in Table 1e—number of contacts, column number of the initial contact whisker, mean angular position at contact, angular velocity prior to contact, contact duration and time from contact to maximum protraction. Two limitations of this data should be made clear. First, the measure number of contacts, records the number of tracked whiskers touching the vertical surface during the whisk cycle of interest not the total number of contacting whiskers. Second, contact duration was calculated only for the first whisker to touch the surface, although this is also generally the last whisker to leave the surface. Furthermore, in 25 (42%) of the 2nd contact whisks contact continued beyond the end of the whisk cycle. Contact duration measures for these whisks were therefore calculated as the time from the initial contact to the end of the whisk cycle.

A MANOVA for the above contact-related measures again showed a large difference between whisk types ($F_{(6,54)}$= 28.477, p<0.001, Wilks' Lambda = 0.240, partial η^2 = 0.760). Four of the six subsequent univariate analyses found significant differences between the 1st and 2nd contacts as shown in Table 4. The first three findings confirm our expectations of more contacts on tracked whiskers in the 2nd contact whisk (p=0.001), that 2nd contacts more often involved the most rostral whiskers (p<0.001), and usually occurred at smaller angular positions (by ~10%, p<0.01). The next two findings show that the instantaneous whisk velocity prior to contact was slightly faster (+9%) in the 2nd contact whisk though not significantly so (due to high variance), and that the mean duration of contacts in 2nd contact whisks was markedly longer (by more than 40%, p<0.001). Finally, we found that time from contact to maximum protraction was less than 15ms in both whisks, and briefer (-22%) in the 2nd contact whisk, although this latter finding was not significant (p= 0.038) compared against a Bonferroni-corrected alpha of 0.008. The findings of more contacts, longer contact durations, and rapid cessation of protraction will each be examined further in sections 3.4 below. To conclude the current section, however, we briefly consider the impact of head movements on whisker-surface contacts.

The effects of head movement on effective contact velocity

The nature of surface contacts, and of the sensory signals they generate, depends on the combined effects of whisker and head movement control. From Table 3, we can see that rat's head and body movements during whisking are of sufficient magnitude to impact upon whisker deflections. These impacts can arise either by changing the effective speed of the whiskers as they meet the contacted surface, by changing the duration of contact, or by causing movement of the whisker shaft as it "sticks, or slips" (Ritt et al. 2008) across a surface. In the following we consider the likely impact of head movement on the effective velocity of the initial contact; effects during contacts will be briefly considered in section 3.4.

Because the surfaces in our arena are flat, the vast majority of whisker-surface contacts in our data-set were observed to begin at or near the tip of the whisker. We therefore make the simplifying assumption that the velocity at the whisker tip is a good approximation for the velocity at the point of contact on the whisker shaft. Using measurements of the lengths of contacting whiskers estimated over three successive video frames, and the formula

$$\textit{whisker tip velocity} = (2\pi * \textit{whisker length}) * (\textit{whisker angular velocity}/360),$$

we estimate that the mean velocity at the tip, immediately prior to contact, was 0.440 mm/msec (s.d. 0.320) for the 1st contact whisk and 0.438 (s.d. 0.374) for the 2nd. To establish the effective tip velocity at contact we next consider head movements.

Mean head angular velocity of approximately 6°, in both contact whisk types, suggests that the effective tip velocity could increase or decrease by ±5% as the result of head rotation in a typical whisk. Translational velocity towards the wall was generally greater in the 1st contact whisk but was predominantly positive in both contact whisks. Comparing whisker tip and head translation velocities suggests that movement towards the wall increased the effective tip velocity at contact by around 27%, to 0.594 mm/msec (s.d. 0.338) in the 1st contact whisk, and by 13% to 0.545 mm/msec (s.d. 0.382) in the 2nd. Overall, then, head movements contributed significantly to the speed of the initial whisker-surface impact.

3.3 A closer look at whisker spread

In the previous two sections, whisker spread was first identified as the 2nd largest component of whisking behavior, and then as one of the two whisker movement parameters (the other being retraction velocity which we will consider later) that change most significantly when a rat explores an unexpected vertical surface. We propose the hypothesis that variation in observed whisker spread is at least partly the consequence of differential control of whisker velocity, and that significant changes in spread arise in response to surface contacts and in anticipation of future contacts. Evidence in support of this view will be provided by evaluating three alternative explanations of the data presented so far: (i) that variations in apparent spread occur primarily as the consequence of head movements (particularly head tilt) and thus are not due to differences in how the whiskers themselves are controlled; (ii) that variation in spread across whisks arises as the result of correlated changes in other whisker control parameters and can be reduced or eliminated by controlling for these covariates, and (iii) that changes in spread occur only after surface contacts and not prior to, and in anticipation of, such contacts. In the following we consider, and present evidence against, each of these alternative explanations.

Can apparent changes in spread be explained by head movement?

As previously noted, a change in the orientation of the whisking plane can substantially affect the apparent spacing between whiskers observed in the overhead view, hence the differences in whisker spread that we have identified could have arisen partly, or wholly, as the consequence of changes in head position. To investigate this possibility we performed three analyses as detailed below.

First, we looked at snout elevation, which we suggested above could serve as a partial surrogate for head tilt in absence of a direct measure of that variable. The analysis shown in Table 3 found high variance in this measure, and a non-significant increase in the mean value in the 2nd contact whisk. It also showed that there were changes in snout elevation during most whisks, and particularly during contact whisks. To investigate the possible effects of changes in head position on observed spread we plotted a scattergram, shown in Figure 5, of snout elevation against mean spread for all three whisk types in all 60 clips. We then fitted separate polynomial curves to this distribution for each whisk type. Two important observations arise from inspecting these figures. First, it can be seen that the curve for the 2nd contact whisk data lies beneath that for the other two types and does not overlap them at any point. This confirms that the observed reduction in spread in that whisk type, compared to the others, is relatively independent of this measure of head position. Second, it is noteworthy that all three curves in Figure 5 are mildly U-shaped with the largest spread values occurring when the snout is near the floor or the ceiling, and the smallest when the snout is at medium height. This is the opposite of what one would expect if spread, as recorded in the overhead camera, was changing solely, or primarily, as the result of changes in head tilt. In that case, spread should be maximal somewhere in the central range of elevations where whisker motion is parallel with the viewing plane of the camera, and should be smallest at the extremes where the whisking plane angles away from, or towards, the camera. That the range of spread values for different snout elevations shows the opposite trend implies that tracking in the overhead view may be causing us to underestimate, rather than over-estimate, the extent to which spread is varying within the plane of whiskers at different head tilts.

Next, we performed an analysis in which the head-movement and the whisker-movement explanations of spread essentially make opposite predictions. Specifically, we looked separately at the protraction velocities for the most rostral and caudal tracked whiskers across each of the whisk types. We know from Table 2 that the whiskers are on average moving a little slower in the 2nd contact whisk than in the previous two. However, for spread to be reduced in this whisk the most caudal whiskers may have to move faster than in earlier whisks in order to match their velocities more closely to those of the rostral ones. This is true, of course, only if the changes in spread are the consequence of differential control of whisker velocities—a shift in the angle of the whisking plane, as the result of head movement, should effect all observed whisker velocities equally. The 2x3 within-subjects ANOVA analysis illustrated in Figure 6 tests these predictions. Here we see that while there was no main effect of whisk type on whisker velocity ($F_{(2,\ 118)}$= 0.335, p= 0.716) the more rostral whiskers did protract faster than the most caudal ones overall ($F_{(1,\ 59)}$= 24.675,

$p<0.001$, partial $\eta^2= 0.298$). Furthermore, there was a significant interaction ($F_{(2, 118)}= 11.045$, $p<0.001$, partial $\eta^2= 0.158$) such that by the 2nd contact whisk, both whiskers were moving at approximately the same speed, and the most caudal whiskers were moving substantially faster than in the preceeding whisks. We therefore conclude that a significant part of the observed variance in whisker spread is due to the way in which the whiskers themselves are controlled.

Finally, on this question, we look at some illustrative data that compares whisker spread, as measured in the overhead view, with an alternative estimate of relative whisker spacing calculated within a co-ordinate frame defined by the whiskers themselves. Specifically, two representative clips were chosen for tracking in both overhead and end-on views and their 3d whisker-tip trajectories calculated as described in Methods. For both clips we then computed a per-frame, *head-invariant spread* measure as the average distance between all pairs of tracked whisker tip positions. A comparison between this new estimate of whisker spacing and the original viewpoint-dependent spread measure, for both whisking episodes, is shown in Figure 7. In considering this figure it is worth noting that the head-invariant measure is sensitive to changes in spread along the line of sight of the camera that are not detectable in the overhead view, thus the two traces should not be expected to be closely aligned. Nevertheless, the graphs do show a reasonable match (correlations of $r= 0.72$ for the upper clip and of $r= 0.535$ for the lower clip), and a similar reduction in spread over the three whisk types, suggesting that spread, as measured in the overhead view, captures a significant portion of the variance of a measure of whisker spacing that is independent of head movement.

Are apparent changes in spread the result of correlated changes in other whisk parameters?

Whisker spread was correlated with a number of other whisk control parameters in our data. Specifically, measured across all whisk types (i.e. n= 180), there were significant, though relatively small, positive correlations with mean protraction velocity (Pearson's r= 0.254, p=0.001) and maximum protraction (r= 0.181, p=0.015), and a non-significant but positive correlation with minimum protraction (r= 0.137, p=0.068). These relationships are potentially important because we know that the mean value for each of these variables is lower on the 2nd contact whisk (Table 2). To establish the extent to which variation in spread is independent of changes in these other whisk control measures we performed the following analyses. First, the relationship between mean spread and each of the three variables was examined using bivariate scatterplots, and polynomial curve fits, as shown in Figure S4 in the Supplementary Material. The plot for protraction velocity shows a mild increase in spread with increasing velocity, but no interaction with whisk type. For both minimum and maximum protraction, however, there was some convergence of spread values for different whisk types for large values of maximum protraction, and for both large and small values of minimum protraction. To control for the effects of covariation with these two variables a univariate ANOVA was therefore performed using values of mean spread calculated solely within the arc x to y degrees of the protraction phase, where x= max(minimum protraction) and y=min(maximum protraction), and where x and y where calculated separately within each clip across all three whisk types. Details of this analysis are provided in Table 5. After controlling for differences in minimum and maximum protraction in this way, mean spread was still found to decrease substantially by the second contact whisk (p<0.001) and by about 18% compared to the pre-contact whisk, which is a similar reduction to that seen overall in the protraction phase (16.5%). We therefore conclude that the variation in spread seen across whisk types is not explained by differences in the protraction start and end positions.

Do changes in spread occur prior to surface contacts?

Differences in observed spread between pre-contact and contact whisks could occur throughout the whisk cycle or, could arise, primarily or wholly, as the result of changes in whisker movement taking place after the whiskers have touched the surface. The previous analysis indicates that this is unlikely, however, to confirm that there were significant changes in whisker spread prior to any surface contact, an analysis was conducted in which mean spread was calculated solely within the arc x to z degrees of the protraction phase where x= max(minimum protraction) (as above) and z=min(mean position prior to contact). Again, as in the previous test, mean spread still showed a significant decrease (in excess of 14%) by the second contact whisk ($p<0.001$, see Table 5) confirming that there is a significant reduction in whisker spacing prior to surface contact. In this context it is also worth looking briefly at differences in spread in the retraction phase of the whisk (also analyzed in Table 5). Again, and as expected, this showed a significant reduction across the whisk types ($p<0.001$), however, notably, here the reduction in spread began in the 1st contact whisk (-14% compared to pre-contact). This result suggests that, following the initial contact, whisker control begins to adapt almost immediately to provide reduced whisker spread during further exploration of the contacted surface.

3.4 The sensory consequences of whisker control

The active touch hypothesis for rat whisking postulates that the control of whisker positioning is regulated on a moment-to-moment basis so as to provide the animal with better or more task-relevant tactile sensory signals. In this final sub-section we examine three aspects of whisker-surface interactions—the quantity of whisker-surface contacts, the amount of bending during contacts, and the duration of contacts—and attempt to pin-point some of the elements of whisker control that could be actively regulated in order to modify each of them.

Increasing the quantity of surface contacts by controlling whisker spread and head tilt

Reducing spread through differential control of whisker movement necessarily brings the whisker tips closer together. If then, the whiskers are moved towards an area of proximal space where a surface was recently encountered, then we should expect a greater number of contacts than if the whiskers are more widely spaced. Thus controlling spread should allow the rat to focus tactile attention into regions of space where objects or surfaces are expected, and increase the density of sensory signals obtained there. Given the complexity of the whisker control system, however, we would like to be able to support this assertion with some quantitative evidence that control of spread can serve as a "maximizing contact" strategy. Since we cannot currently perform a control experiment in the rat in which modulation of whisk spread is disabled, our next best option is to examine whisks with different numbers of contacts and use statistical methods to determine whether spread usefully discriminates between them. To this end we calculated correlations between the number of contacts on tracked whiskers and a range of potential predictor variables for the combined set of 120 1st and 2nd contact whisks. Full details of the parameters tested are given in the Supplementary Material. This procedure identified mean spread (Pearson's r= -0.279), mean protraction velocity (r= -0.185) and snout elevation (r= +0.332) as significant, and thus promising, candidate predictors. Further investigation revealed that lower values of mean spread were most discriminative, thus *inverse* mean spread correlated with number of contacts at r= +0.336. To assess the influence of these candidate predictors, a step-wise, multiple linear regression was performed, for all 120 contact whisks, with three head position parameters (inverse distance to wall, orientation to the wall, and snout elevation) and two whisk control parameters (inverse mean spread and mean protraction velocity). This analysis showed that the number of contacts increased both with the inverse mean spread (p= 0.019), and with increasing snout elevation (p= 0.024). Partial correlations for these two variables (i.e. after removing variance due to other selected predictors) were +0.202 for inverse mean spread and +0.195 for snout elevation. Further details of this analysis, together with residual plots confirming that the relationships were approximately linear, are provided in the Supplementary Material. We conclude that the rat can increase the number of surface contacts by reducing whisker spread. The increase in contacts due to greater snout elevation remains to be explained and is briefly considered next.

Figure 8 shows the whisker tip trajectories for a 1st contact whisk (left) and a 2nd contact whisk (right), calculated using tracking data from both camera views using our 3D trajectory reconstruction algorithm, and then rotated so that they can be observed in the side-on plane (i.e. perpendicular to both the wall and the arena). For illustrative purposes the tracked video clips used to generate these trajectories are also provided as Supplementary Videos 2 and 3, and color plots, showing the trajectories of individual tracked whiskers, in Figure S6 in the Supplementary Material. The left panel shows that during a whisk with low elevation many whiskers, and particularly the more caudal ones, make contact with the floor, and would do so even if the rat were closer to the wall. Increased floor contact, and reduced wall contact, is likely simply because the rat's head tilts down towards the floor at a significant angle. For the whisk with higher snout elevation, shown in the right panel, whisker movement is close to being perpendicular to the wall, and the head position near horizontal, so we can expect, and do observe, many more wall contacts and few floor contacts. What happens for still higher elevations? When the head tilts above the horizontal this will bring some of the longer more caudal whiskers closer to wall, increasing the likelihood that these whiskers will touch even as some of the dorsal whiskers rotate away from the wall (and may begin to touch the ceiling). We can thus conclude that tilting the head upwards is, overall, a useful "maximizing contact" strategy for exploring walls, whilst tilting downward is clearly favorable for whisking during floor traversal.

Controlling bending against surfaces through rapid cessation of protraction following contact

In our previous study (Mitchinson et al. 2007) we found that, following a unilateral surface contact, the whiskers on that side of snout cease protraction on average 13 milliseconds after the initial touch. In the current study we used a larger sample size (60 clips compared to 22), a higher frame rate (500 frames per second compared to 250), and measured the average *time from contact to maximum protraction* across all five tracked whiskers. As previously shown in Table 4, performing this analysis for data from the 1st contact whisk produced a mean time to maximum protraction of 14.30 milliseconds, i.e. a result that is well within the expected margin of error of our previous investigation (±2 milliseconds). When the same calculation was performed for the 2nd contact whisk, interestingly, the time to maximum protraction fell to 11.25 milliseconds, a latency that was marginally faster than for the first contact, although this result should be treated with some caution due to the relative high p-value ($p = 0.038$). To further test the robustness of these estimates we separately examined the time to maximum protraction for each of the tracked whisker columns. As shown in in Figure S7 in the Supplementary Material, the difference between 1st and 2nd contact whisk was found consistently across all columns, whilst there was also an interesting trend for the more rostral whiskers to reach maximum protraction earlier than the more caudal ones by up to five milliseconds. Time to maximum protraction was also compared for whisker columns that did, and did not, make contact with the wall, these were found to be very similar ($F_{(1,\ 59)} = 0.001$, $p = 0.974$) indicating that the contacts themselves were not significantly distorting this measure. An analysis by contact type (bilateral vs. unilateral) also found no significant effect on the timing of maximum protraction ($F_{(1,58)} = 1.08$, $p=0.095$). Overall then we can conclude that rapid cessation of protraction is a general and consistent feature of whisker-surface contacts during exploratory whisking, which may possibly be more pronounced in subsequent whisks that in the initial contact, and whose effect will be to reduce bending of the whiskers against the surface compared to non-modulated whisks.

Contact duration—a further candidate for active control?

On first inspection, the finding that whisker-surface contacts have much longer duration appears to be inconsistent with the rapid cessation of protraction, and reduced head velocity towards the wall in the 2nd contact whisk. However, the likely explanation for these longer contact times is easily found by reviewing Table 2—here we saw that whisk retraction velocity was at a significantly slower pace on the 2nd contact whisk than on the first. We next divided the retraction phase into two halves and found that the decrease in retraction velocity in the 2nd contact whisk was much more evident in the first half of the retraction phase (-54%, $p<0.001$) than in the second half (-9%, $p= 0.237$). This establishes that slower retraction occurs during the period of the whisk following peak protraction and thus most likely to impact on contact duration. To confirm that retraction velocity was genuinely slower following the 2nd contact, and not simply that drag on the contacting whiskers created the appearance of slower retraction, we looked at retraction velocity on the most caudal tracked whisker since this rarely contacts the vertical surface (only 3 contacts in the 60 2nd contact whisks). For this whisker too, velocity during the first half of the retraction phase was also considerably slower on the 2nd contact whisk (-49% compared to -47% for the most rostral whisker, both $p<0.001$). Details of these additional analyses are provided in the Supplementary Material.

To further establish which control factors most influence contact duration we again performed a sequential multiple linear regression, this time including four head position and movement parameters (velocity towards the wall, the angle at which the whisker contacted the wall, snout elevation, and snout vertical velocity) and three whisker control parameters (mean protraction and retraction velocities, time from contact to maximum protraction) that were likely predictors of duration. The dependent variable was contact duration measured for the 95 1st and 2nd contact whisks in which contact with the surface ceased before the end of the whisk cycle (60 1st contact and 35 2nd contact whisks). This analysis showed that contact duration was most strongly predicted by time from contact to maximum protraction (part correlation of r=+0.487), retraction velocity (r=-0.293), snout vertical velocity (r=-0.246) and snout elevation (r=+0.183). Further details of this analysis, including residual plots confirming that the relationships were approximately linear, are provided in the Supplementary Material. The high positive correlation with the time from contact to maximum protraction confirms the importance of controlling protraction cessation, using sensory feedback, to the tactile experience of the rat. The negative correlation with retraction velocity shows that this parameter is the next most important element of whisking strategy in determining the duration of whisker-surface contact signals. We leave to the discussion consideration of why retraction velocity is reduced in the 2nd contact whisk, and whether increasing contact duration through this mechanism should be considered as an additional active touch strategy.

4. Discussion

Sensory signals are generally ambiguous, sometimes entirely meaningless, in the absence of knowledge of how the sensor that generated those signals was controlled. This is particularly true of touch where signals are only obtained through physical contact, and where the trajectory of the sensor with respect to the surface co-determines, with the surface properties of the object, the nature of the signals that are obtained. Increasing evidence, in this article and others, indicates that the sensor (whisker) trajectories of the rat vibrissal system are carefully controlled, modified on the basis of recent sensory experience and in anticipation of future experience, and directed at obtaining high-quality, task-relevant information. This type of active sensing control is also apparent in human fingertip touch (Chapman 1994; Lederman and Klatzky 1993; Smith et al. 2002) suggesting that the rat whisker system can be a useful model in which to investigate "sensorimotor contingencies" (O'Regan and Noe 2001) similar to those underlying our own tactile experience of the world. In the following, our new findings in relation to active touch sensing in the rat are summarised and evaluated, beginning with the evidence that whisker spread is actively controlled, then turning to the active touch sensing strategies that appear to utilised by the rat.

Control of whisker spread

Whisker spread explain a significant portion of whisking variance

Although changes in the horizontal spacing of whiskers have been previously noted (Sachdev, 2002), this is the first study to have quantified the contribution of these changes to the overall observed whisking pattern. We found that 13-19% of the variance in whisker movement of freely moving animals, tracked from overhead, can be accounted for in terms of one summary parameter—the 'spread', or angle of arc between the rostral-most and caudal-most tracked whisker. Further, together with the mean angular rotation of the whisker field these two parameters can account up to 93% of the variance seen in the overhead view.

Whisker spread varies across different whisk types

It is important to be clear that we regard the spread parameter as simply a descriptive measure that usefully summarizes some of the observed changes in whisking behavior. We have no direct evidence that the rat brain encodes spread as a specific control parameter (any more than it encodes amplitude, frequency, or set-point as control parameters—all of which are also descriptive concepts). That the spacing between whiskers changes with time, is consistent with, but does not necessarily require, active control of underlying mechanisms. Passive, rather than active, control (such as might be provided by purely mechanical properties of the vibrissal system) would imply that whisker spread should vary across the whisk cycle in a predictable and consistent manner across all types of whisk. To obtain evidence that observed changes in spread are not simply passive we needed to demonstrate variability across different whisking contexts, therefore we investigated whether anticipation of a proximal vertical surface could change the pattern of spread changes over the course of a whisk cycle. Our data demonstrates such variability. Specifically, we have shown that in the 2nd contact whisk, whisker spread and angular position can become decoupled and that spread is typically reduced compared to preceding whisk cycles.

Candidate explanations for the observed variance in spread across whisk types

Observed spread thus appears to vary across whisking contexts, but what is the source of this variation? Our analysis has tested several alternative explanations. First we considered whether the observed changes in spread might be more apparent than real and simply the consequence of the principal plane of whisker movement tilting with respect to the overhead camera. Three pieces of data from our analysis speak against this possibility: (i) that the reduction in spread in the 2nd contact whisk occurred right across the range of head elevations; (ii) that there was evidence of increased velocity of the more caudal whiskers in the 2nd contact whisk whilst the more rostral whiskers were slowed (a finding that is consistent with reduced spread and that cannot be explained by changes in head tilt); and (iii) that we saw similar variation over time, for two exemplar clips, when whisker spacing was analyzed in 3d as when spread was measured in the overhead camera view alone. We conclude, therefore, that there are significant changes in whisker spread between the 2nd contact whisk and earlier whisks that are not explained by head movement. (However, see below, for a hypothesis as to how both head control and whisker control may be used synergetically to control how the whiskers sample the environment). The next hypothesis tested, and shown to be false, was that apparent changes in spread were due to changes in covarying whisker control parameters, such as maximum protraction. Finally we examined whether changes in spread were the consequence of surface contact, and did not foreshadow it. To counter this we showed evidence of significantly reduced spread in that portion of the whisk cycle that occurs prior to contact with the target surface. Together these results support the conclusion that the observed changes in spread were not simply the consequence of head movements, changes in other aspects of whisker control, or the result of the whiskers bending against the contacted surface.

Could changes in whisker spread involve control of the whisking musculature?

Whilst we have ruled out the most plausible alternatives, based on the current data we cannot test directly the hypothesis that the apparent changes in whisker spread involved control of the whisking musculature. Results from other laboratories (Berg and Kleinfeld 2003; Dorfl 1982; Hill et al. 2008; Klein and Rhoades 1985; Wineski 1985) show, however, that the rat does have sufficient degrees of freedom of whisker control to effect some differential movement of either individual whiskers or whisker columns. Moreover, some divergent movement of the whiskers has been observed in animals trained to make texture discriminations (Carvell and Simons, 1990), and in head-fixed animals trained to whisk for reward (Sachdev et al. 2002). That the rat has the capacity to focus its whisker field towards a target has also been suggested before in the context of the 'foveal whisking' behavior described by Berg and Kleinfeld (2003). In the following we briefly compare some of the observations made in that study with our current results.

Whisking modulation and whisking modes

Berg and Kleinfeld (2003) used high-speed videography and electromyographic recording of the whisking musculature to investigate whisking behavior in rats that were trained to explore a maze to obtain food rewards. They described two general modes of whisking behavior that were distinguished both by their spectral properties (whisk amplitude and frequency) and by differential patterns of activation in the whisking musculature. The first mode, termed 'exploratory whisking' consisted of bouts of relatively large amplitude whisks occurring at a frequency 5-15hz. In the second, less frequent, ‘foveal whisking’ mode, rats exhibited bouts of relatively small amplitude but high frequency (15-25hz) whisking. During general maze traversal, while the animals searched for a food resource, they exhibited exploratory whisking, however, the animals shifted to the foveal mode when required to ‘crane their necks’ across a gap to reach a food tube.

The changes in whisking control during exploration of surfaces described in the current article are more subtle than the marked switch from one whisking mode to another described by Berg and Kleinfeld. Indeed, in the current data, the frequency and velocity of the whisker movement changed relatively little on surface contact, and, instead, we saw differences in some less well-studied whisking parameters such as the whisker spread and the mean retraction velocity. We consider, then, that the whisking patterns we have observed here fall within the general class of ‘exploratory whisking’ described by Berg and Kleinfeld, and we suggest that, within this mode, the rat has the capacity to modulate whisking control on a per-whisk basis, and, to some degree, per-whisker (or whisker column) basis. It is worth noting that Berg and Kleinfeld describe foveal whisking as involving the vibrissae being “clustered in front of the head in a relatively dense pattern” (p. 109). Although this clustering is not precisely quantified it does seem consistent with what we are calling a change in whisker spread. If differential use of the whisking musculature can bring about the substantial changes in whisker movement seen following the transition to foveal whisking, it seems reasonable to suppose that similar, but subtler changes in muscular control could also underpin the reduction in whisker spread we have observed when rats explore a proximal surface.

Active touch sensing in the rat

We have previously proposed (Mitchinson et al., 2007) that rat whisking employs active control strategies that serve to increase the number of whiskers contacting surfaces of interest (“maximizing contact”) whilst controlling the amount of bending against those surfaces (“minimizing impingement”). In the current study, the reduction in whisker spread, and associated changes in head tilt, found in the 2nd contact whisk, are consistent with both strategies as they allow an increased number of whiskers to make contact with the vertical wall without requiring that the whiskers necessarily press harder against that surface. Several other aspects of whisking and head control that might also be considered to be part of the rat’s active sensing strategy are considered below.

Minimizing impingement by controlling cessation of protraction

Consistent with our earlier findings (Mitchinson et al., 2007), the current study found that whisker protraction ceased rapidly following an initial contact with a surface (mean of 14.30 ms from contact to maximum protraction in the 1st contact whisk). In the case of unilateral contacts, we previously found a difference between the ipsilateral (to the contact) whisker field where protraction stopped soon after contact, and the contralateral field (where there was no contact) where it did not. From this we inferred the existence of a fast sensory feedback loop controlling the timing of whisker protraction to implement a minimal impingement strategy and ensure that contacts were made with a relatively ‘light touch’. Our new data suggests that rapid cessation of protraction occurs for both unilateral and bilateral contacts, and may even be quicker on the 2nd contact whisk (mean latency 11.25 ms). The latter finding, if supported by future studies, would imply some additional element of anticipatory control. The literature on classical conditioning shows that the latency of a reflex response, such as the rabbit eye-blink, is significantly reduced when the animal can anticipate the timing of the unconditioned stimulus (Gormezano et al. 1983). Thus, similarly, the rat's ability to anticipate a forthcoming surface contact could influence the control circuitry underlying the proposed whisking sensory feedback loop enabling it to respond more rapidly when an expected whisker deflection takes place.

Controlling the duration of whisker surface contacts

An unanticipated finding of the current study was that the duration of contacts with surfaces was generally much longer in the 2nd contact whisk. Duration of contact was found to be best predicted by two whisking control parameters—the time from contact to maximum protraction (discussed above), and the retraction velocity (especially in the first half of the retraction phase). These two parameters oppose each other, but, by their interplay, it would appear that the rat could control the duration of contact, the speed at which the whisker is drawn across the surface, and the amount of bending in the whisker shaft. We think it is possible that the slower retraction during the 2nd contact whisk can be understood as an active touch strategy aimed at prolonging contact and thereby aiding the extraction of information about surface characteristics such as texture. Thus, perhaps, the 1st contact whisk could be thought as locating the surface in space, and the 2nd as discerning more details concerning the nature of that surface. However, it is important to consider that there may be alternative explanations of reduced retraction velocity on the 2nd contact whisk that are not directly concerned with contact duration or with the sensory consequences of this contact. For instance, one possibility is that there might be compensatory mechanisms within the whisker pattern generator that act to reduce whisk retraction velocity following early cessation of protraction due to surface contact. Such a mechanism might conceivably operate so as to prevent a strong mismatch in phase between the left and right whisker fields, since it can be generally observed that the two fields have a strong tendency to return to synchronized movement following perturbation. Evaluation of this alternative will require a better understanding of the coupled motor pattern generators that generate whisker movements in the two fields, and of their modulation by sensory signals. Future research on this topic should also benefit from the investigation of generative computational and robotic models of whisker geometry, musculature, and neural control systems (e.g. Hill et al. 2008; Mitchinson et al. 2006; Pearson et al. 2007).

Combining head and whisker movement to optimize surface exploration

Whilst going somewhat beyond the current data, we now propose the following hypothesis, consistent with the above active sensing strategies, that could serve as a further simplifying principle for understanding whisking control in exploring animals.

The rat appears to control its whiskers so that the spacing between the whiskers is reduced relative to the surface of interest. Thus if this is a vertical surface we see reduced spread in the overhead view (as demonstrated by our data), if a horizontal surface (e.g. the floor) we see reduced spread in the end-on view (consistent with our informal observations of video recordings but remaining to be demonstrated quantitatively). A strong version of this hypothesis would suggest that the rat also seeks to increase spacing parallel to the surface of interest, in order to simultaneously explore as much of that surface as possible. Thus when proceeding across the floor the whiskers appear relatively spread out when viewed from above, and directed at the area of the floor around and immediately in front of the animal in its direction of motion (see, e.g. Figure 9 left). In contrast, when investigating a vertical wall, the whiskers appear close together in the overhead view and much more widely separated in the end-on view (see, e.g. Figure 9 right). These changes in whisker spacing are likely brought about partly through differential control of the whiskers and partly through controlled positioning of the head with respect to the surface of interest. Thus obtaining a better understanding of the interaction between head movements and whisking movements will be important in order to be able to fully characterize the active touch sensing strategies of the rat.

5. Acknowledgements

The authors are grateful to Peter Redgrave for scientific advice and to Marion Simkins, Andy Ham, and Malcolm Benn for technical support.

6. Grants

This research was supported financially by the European Union ICEA (IST- 027819) and BIOTACT (ICT-215910) projects. Robyn Grant was funded by a doctoral training grant from the UK Engineering and Physical Sciences Research Council (EPSRC).

Figure Legends

Figure 1. The principal components of rat whisking. The first three principal components of whisking account for 70-80% (component 1, top), 13-19% (component 2, center), and 4-5% (component 3, bottom) of the variance in whisker angles seen in the overhead view. Here the histograms on the left indicate the weighting on each tracked whisker (0 most caudal, 4 most rostral) for each component. The images on the right illustrate the components graphically and cumulatively (top component 1, center 1+2, bottom 1+2+3). Each image shows the whiskers at minimum protraction on the left-hand side of the rat snout and at maximum retraction, as determined by the effects of the principal components (white arrows), on the right-hand side. Dotted white lines indicate the mean angular position. Note that the first two components are highly correlated with mean angular position and whisker spread respectively and together account for 89-93% of the variance in observed whisker positions.

Figure 2. Differences in the temporal coupling between whisk spread and angular position. *Top:* Cross-covariance of spread and mean amplitude averaged across all 60 clips. *Bottom:* Histograms of the best-fit phase lag (peak cross-covariance) between spread and mean angular position. Plots are calculated for each of the three whisks types: pre-contact (top), 1st contact (middle), and 2nd contact (bottom). The coupling between spread and angular position is weaker in the 2nd contact whisk. For instance in the upper half of the figure we see that the average cross-covariance has a smaller and earlier peak in the 2nd contact whisk than in either the pre-contact or 1st contact whisks, whilst in the lower half we see that the changes

in spread and angular position are significantly out of phase in nearly half (43%) of 2nd contact whisks.

Figure 3. Changes in whisk spread, minimum and maximum protraction, and whisker velocity on encountering an unexpected vertical surface. From top to bottom: Maximum, minimum, and mean spread (degrees); minimum and maximum protraction (degrees); and mean protraction and retraction velocities for pre-contact, 1st contact, and 2nd contact whisks. All of the whisk parameters illustrated here show significant reductions by the 2nd contact whisk as detailed in Table 2.

Figure 4. Snapshots of whiskers at maximum protraction for 4 consecutive whisks. From bottom to top: pre-contact, 1st contact, 2nd contact, and 3rd contact. Whisker spread is significantly reduced by the 2nd contact whisk and remains low in the subsequent whisk. These snapshots are taken from the clip provided as Supplementary Video 1.

Figure 5. Scattergram of whisker spread against snout elevation with polynomial best-fit curves for different whisk types. The plot shows that whisker spread (y-axis) is reduced in the 2nd contact whisk across the full range of snout elevation (x-axis values). That the best-fit curves are mildly U-shaped suggests that tracking in the overhead view may lead to under-estimation, rather than over-estimation, of the extent to which spread varies within the plane of the whiskers.

Figure 6. Changes in the protraction velocities of the most rostral and most caudal tracked whiskers on encountering an unexpected surface. In the pre-

contact whisk the most rostral whisker moves significantly faster than the most caudal one, however, the protraction velocities converge by 2nd contact whisk consistent with a substantial reduction in whisker spread in that whisk. Note that this result cannot be accounted for by head movement. Means (s.d.s) for pre-, 1st and 2nd contact whisks were rostral 0.52 (0.31), 0.53 (0.28), 0.42 (0.21); caudal 0.34 (0.23), 0.35 (0.19), 0.42 (0.20).

Figure 7. Comparing changes in spread as measured in two- and three-dimensions. The plots show a comparison of spread as measured in the overhead view (solid line) with the head-movement invariant measure of spread (dotted line) computed from 3D reconstruction of whisker tip trajectories for two clips.

Figure 8. **Whisker tip trajectories for a 1st contact (top) and a 2nd contact whisk (bottom) plotted in a reconstructed side-on view.** In the 1st contact whisk the head tilts downwards hence many contacts are made with the floor and relatively few with the wall. In the 2nd contact whisk the snout is raised and the angle of the head is near horizontal, consequently nearly all tracked whisker-surfaces contacts are made with the end-wall. Thin lines show trajectories of individual whiskers matched across views using a least mean square error minimization algorithm. The tip of the snout and of the right ear were tracked in the 1st contact whisk (top) allowing the position of the head to be approximated (thick outline). In the 2nd contact whisk (bottom) points on the head could not be tracked in both views, hence only the approximate position of the snout is shown. The glass floor and end-wall are also depicted (thick gray lines). Axes show distance to wall and height above the floor in millimeters. The clips

from which the tracks were reconstructed are provided as Supplementary Videos 2 and 3.

Figure 9. Control of whisker spread and head position in active touch. Snapshots consistent with the hypothesis that the rat uses it body, neck and whisker musculature so as to reduce whisker spread perpendicular to a surface of interest, while increasing spread parallel to that surface. Thus when the rat is moving across the floor spread is reduced in the end-on view (left top) and increased in the overhead view (left bottom), whilst when exploring a wall, two whisks later, spread is increased in the end-on view (right top) and reduced in the overhead view (right bottom).

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Tables

Table 1. Definitions of whisking, head movement, and contact-related measures.

Name	Units	Description
A. Whisker movement measures per video frame (overhead view)		
Angular position	degrees	Angle from the whisker shaft to the head midline such that forward movement (protraction) causes an increase in angle
Mean angular position	degrees	Mean angular position across all five tracked whiskers
Velocity	deg/msec	Rate of change of the mean angular position
Spread	degrees	Difference between the largest and smallest instantaneous angular positions of the five tracked whiskers
B. Head position measures per video frame		
Snout elevation and vertical velocity	mm	Distance from the snout tip to the floor (vertical view) and the rate of change in this measure
Head orientation and angular velocity	degrees, deg/msec	Absolute angle of the head relative to the wall (overhead view), with zero being perpendicular, and the rate of change in this measure
Distance and velocity towards wall	mm, mm/msec	Length of the perpendicular from the snout tip to the wall (overhead view) and distance moved in current frame
Velocity along wall	mm/msec	Distance moved parallel to the wall and floor in current frame (overhead view)
C. Summary whisker movement measures per whisk (or per specified portion of a whisk)		
Minimum and maximum protraction	degrees	Minimum and maximum values of the mean angular position. Minimum protraction is also sometimes referred to as peak retraction or the whisking "set-point"
Mean, minimum, and maximum spread	degrees	Summary measures of spread
Mean protraction and retraction velocities	deg/msec	Summary measures of velocity calculated separately for the protraction and retraction phases of the whisk
Whisk duration	msec	Time from the previous minimum protraction to the next
D. Summary head position measures per whisk		
Mean distance and mean velocities towards and along wall	mm mm/sec	Mean distance to the wall and mean velocities towards and along the wall over the duration of the whisk
Mean head orientation and angular velocity	degrees, deg/msec	Mean head orientation over the duration of the whisk, and the absolute value of the mean head angular velocity
Mean snout elevation and vertical velocity	mm, mm/msec	Mean snout elevation over the duration of the whisk, and the absolute value of the mean snout velocity
E. Measures relating to the initial contact with the wall within a whisk		
Number of contacts on tracked whiskers	2–5	Total number of tracked whiskers making contact with the wall over the course of the whisk
Column number of initial contact whisker	0–4	Column number as estimated from overhead view where 0 is the most caudal tracked column and 4 most rostral
Mean angular position at contact	degrees	Mean angular position in the frame immediately prior to the first surface contact
Velocity prior to contact	deg/msec	Instantaneous angular velocity of the whisker making first contact calculated from the two frames preceding the contact

Contact duration	msec	Time from initial contact to the first contacting whisker becoming detached from the surface (measured for the most rostral whisker if two whiskers make simultaneous first contact)
Time from contact to max. protraction	msec	Time from the initial contact to maximum protraction averaged across all five tracked whiskers
F. Measures calculated from 3D whisker tip trajectory data		
Head-invariant mean spread		Mean Euclidian distance (in 3d space) between pairs of whiskers, averaged over all possible whisker pairs

Table 2. Analyses of summary whisker movement measures

Measure	Mean, standard dev.			% change		ANOVA			
	Pre-contact	1st Contact	2nd Contact	1st	2nd	$F_{(2,118)}$	p	Partial η^2	Post-hoc
Max. protraction (deg)	113.5, 12.0	111.1, 12.3	101.9, 13.0	-2%	-10%	41.23	<0.001[a,b]	0.411[d]	p,1>2
Min. protraction (deg)	75.5, 13.6	72.7, 10.9	70.1, 11.6	-4%	-7%	13.50	<0.001[a,b]	0.186[d]	p,1>2
Mean spread (deg)	72.2, 18.4	67.4, 19.8	57.2, 21.0	-7%	-21%	44.76	<0.001[a,b]	0.431[d]	p>1>2
Mean protraction velocity (deg/msec)	1.080, 0.45	1.180, 0.47	1.00, 0.36	+9%	-8%	5.50	0.005[a]	0.085[c]	1>2
Mean retraction Velocity (deg/msec)	0.89, 0.32	0.92, 0.32	0.70, 0.35	+2%	-22%	11.33	<0.001[a]	0.161[d]	p,1>2
Whisk duration (msec)	107.3, 27.1	106.8, 25.5	98.9, 28.9	-1%	-8%	2.35	0.099	0.038	n.a.

a. significant using Bonferroni corrected alpha of 0.008
b. incorporates Greenhouse-Geiser correction for non-sphericity
c. medium-size effect ($0.06 < \text{partial } \eta^2 \leq 0.14$)
d. strong effect ($\text{partial } \eta^2 > 0.14$)

For post-hoc tests p= pre-contact, 1= 1st contact, 2= 2nd contact, n.a.= not applicable

Table 3. Analyses of summary head position and movement measures

Measure	Mean, standard dev.			% change		ANOVA			
	Pre-contact	1^{st} Contact	2^{nd} Contact	1^{st}	2^{nd}	$F_{(2,118)}$	p	Partial η^2	Post-hoc
Distance to wall (mm)	39.2, 11.0	26.2, 9.9	17.5, 10.7	-33%	-55%	263.0	<0.001[a,b]	0.817[d]	p>1>2
Velocity towards wall (mm/msec)	0.124, 0.067	0.118, 0.067	0.057, 0.068	-4.8%	-54%	26.859	<0.001[a]	0.313 [d]	p,1>2
Velocity along wall (mm/msec)	0.066, 0.045	0.079, 0.053	0.074, 0.072	+20%	+12%	0.854	0.428 [b]	0.063	n.a.
Head orientation (degrees)	72.3, 22.4	74.1, 21.9	74.3, 23.4	+2.5%	+2.8%	1.64	0.199[b]	0.027	n.a
Head ang. velocity (deg/msec)	0.056, 0.062	0.059, 0.051	0.060, 0.051	+5.3%	+12.5%	0.114	0.893	0.002	n.a
Snout elevation (mm)	32.9, 29.0	31.9, 29.0	36.2, 25.7	-3%	+10%	2.23	0.112[b]	0.036	n.a.
Snout vert. velocity (mm/msec)	0.066, 0.065	0.099, 0.083	0.103, 0.109	+50%	+56%	3.992	0.021	0.063 [c]	n.sig.

a. significant using Bonferroni corrected alpha of 0.007

b. incorporates Greenhouse-Geiser correction for non-sphericity

c. medium-size effect ($0.06 < \text{partial } \eta^2 \leq 0.14$)

d. strong effect (partial $\eta^2 > 0.14$)

p= pre-contact, 1= 1st contact, 2= 2nd contact, n.a.= not applicable, n.sig= non significant

Table 4. Comparisons between 1st and 2nd contact whisks

Measure	1st Contact	2nd Contact	Direction or % change	ANOVA		
				$F_{(1,59)}$	p	Partial η2
Number of contacts (2-5)	2.47, 0.75	2.82, 0.77	2>1	13.149	0.001[a,b]	0.182[d]
Column no. of initial contact whisker (0-4)	2.98, 0.75	3.48, 0.75	2>1	17.067	<0.001[a,b]	0.224[d]
Mean angular position at contact (degrees)	125.1, 20.41	113.1, 19.75	-9.6%	50.272	<0.001[a]	0.460[d]
Velocity prior to contact (degrees/msec)	0.75, 0.48	0.81, 0.66	+9.0%	0.393	0.533	0.007
Contact duration (msec)	31.17, 14.08	43.80[e], 19.40[e]	+40.5%	13.365	0.001[a,b]	0.185[d]
Time from contact to max. protraction (msec)	14.30, 9.95	11.25, 6.96	-21.3%	4.482	0.038[b]	0.071[c]

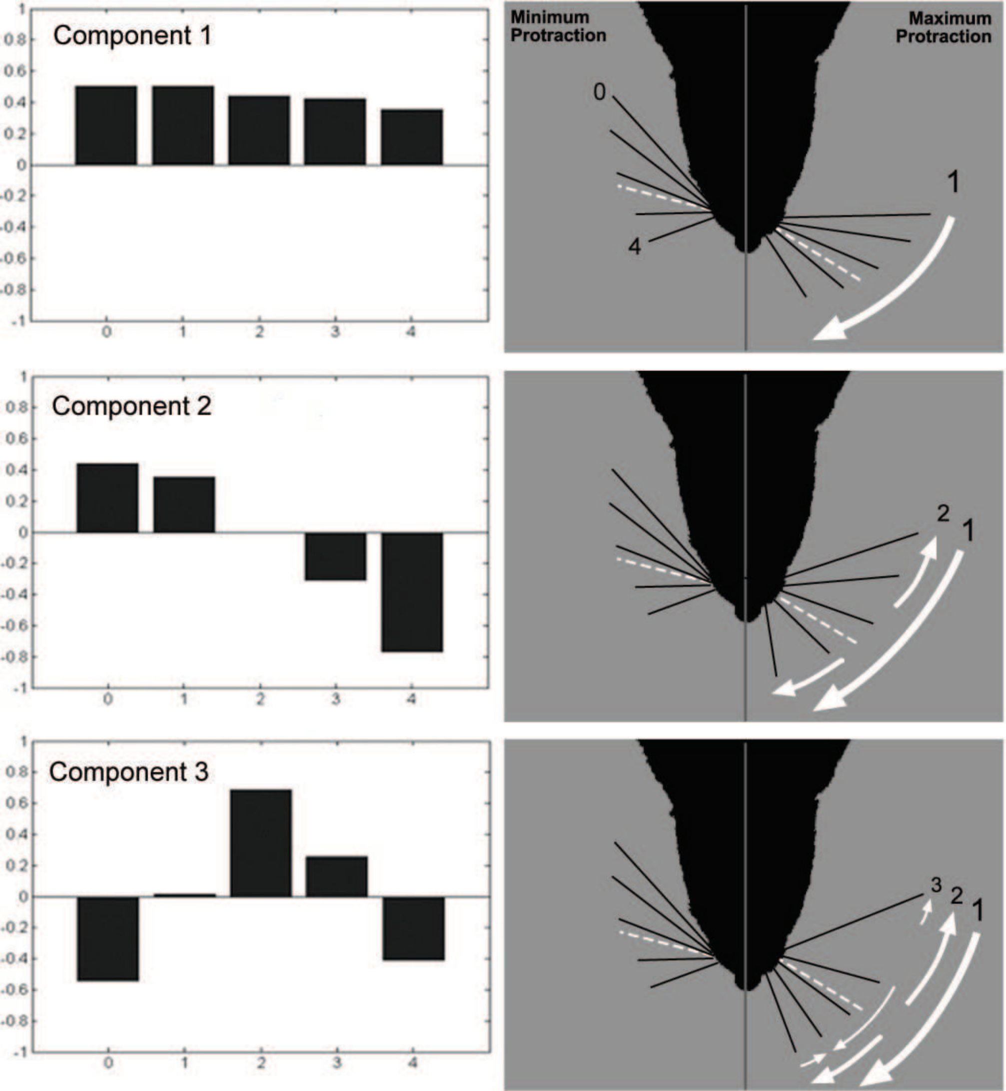
a. significant using Bonferroni corrected alpha of 0.008
b. log transformed prior to testing to correct for positive skew (Kolmogorov Smirnov test)
c. medium-size effect ($0.06 <$ partial $\eta^2 \leq 0.14$)
d. strong effect (partial $\eta^2 > 0.14$)
e. Includes clipped durations for 25 contacts that lasted beyond the end of the whisk

Table 5. Changes in spread after controlling for differences in protraction or contact

Measure	Mean, standard dev.			% change		ANOVA			
	Pre-contact	1st Contact	2nd Contact	1st	2nd	$F_{(2,118)}$	p	Partial η^2	Post-hoc
Mn. spread (protraction control)	74.35, 17.35	71.08, 19.29	61.07, 20.20	-4.4%	-17.9%	35.91	<0.001[a]	0.378[d]	p,1>2
Mn. spread (contact control)	69.36, 16.36	67.22, 18.26	59.47, 19.01	-3.1%	-14.3%	15.66	<0.001[a]	0.210[d]	p,1>2
Protraction spread	72.55, 17.31	69.11, 18.44	60.68, 19.52	-4.8%	-16.4%	24.51	<0.001[a]	0.294[d]	p,1>2
Retraction spread	70.28, 20.67	60.38, 20.88	53.82 21.50	-14.1%	-23.5%	43.56	<.0001[a]	0.425 [d]	p>1>2

a. significant using Bonferroni corrected alpha of 0.0125

d. strong effect (partial $\eta^2 > 0.14$)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Component 2
Component 3
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0.6
0.4
0.2
0
-0.2
-0.4
-0.6
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-1
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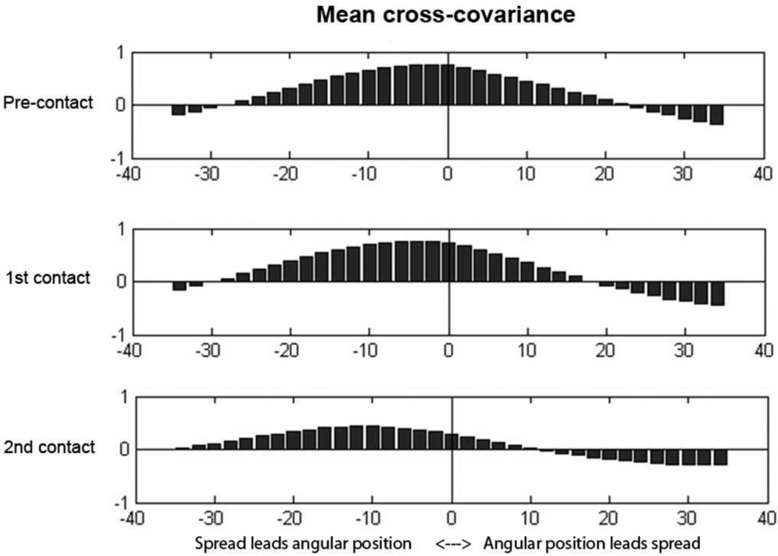
3
4
Minimum Protraction
Maximum Protraction
0
4
1
2
1
3
2
1


Mean cross-covariance
Pre-contact
1st contact
2nd contact
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-1
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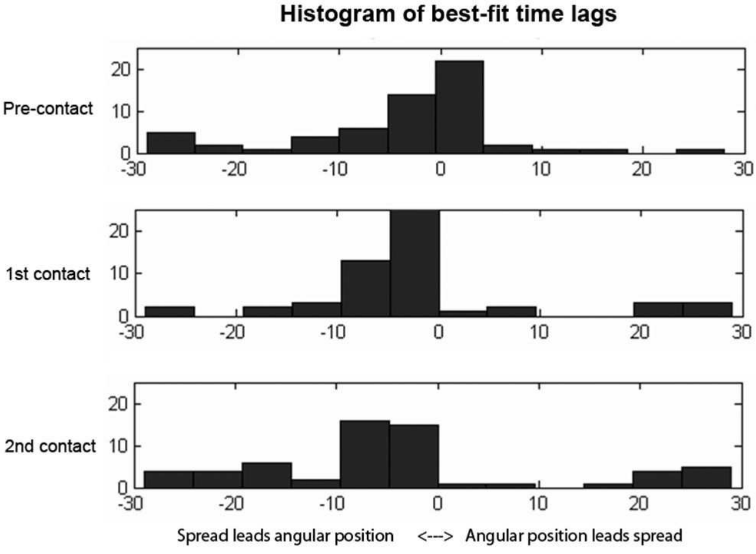
-20
-10
0
10
20
30
40
Spread leads angular position <---> Angular position leads spread


Histogram of best-fit time lags
Pre-contact
1st contact
2nd contact
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10
0
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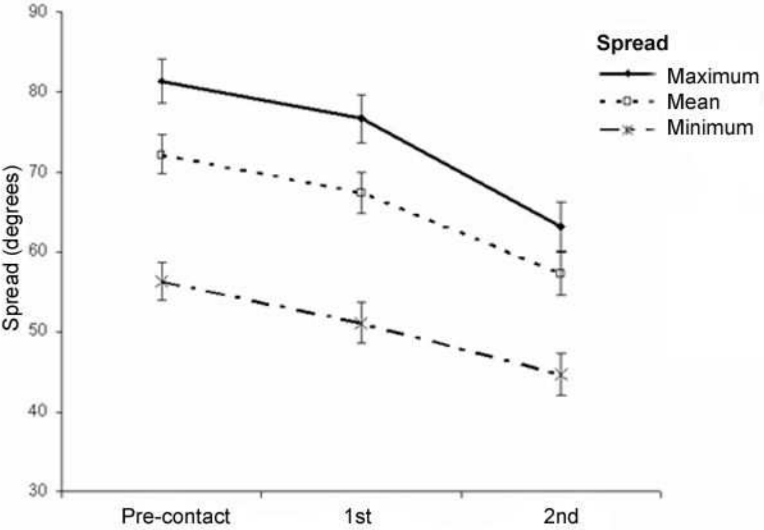
0
10
20
30
Spread leads angular position <---> Angular position leads spread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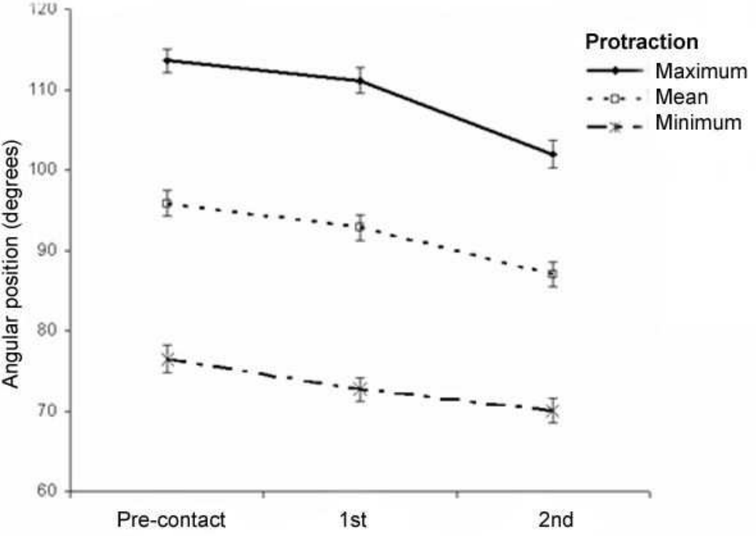
Maximum
Mean
Minimum
Spread (degrees)
90
80
70
60
50
40
30
Pre-contact
1st
2nd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Maximum
Mean
Minimum
Angular position (degrees)
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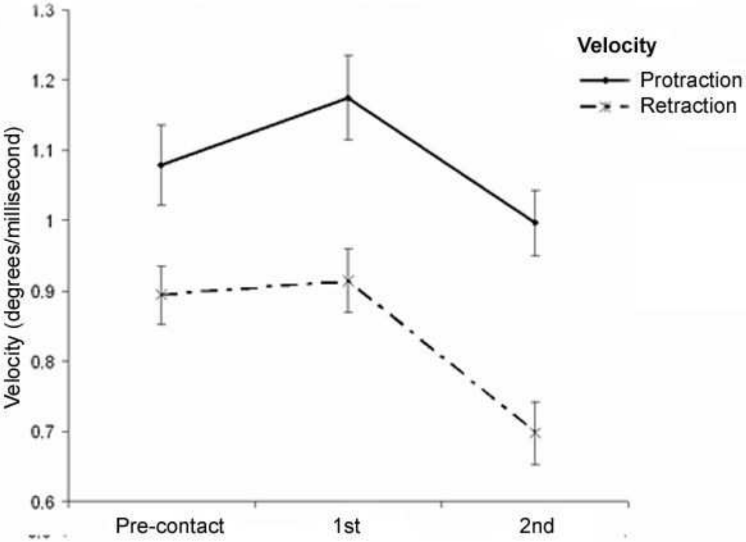
100
90
80
70
60
Pre-contact
1st
2nd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Protraction
Retraction
Velocity (degrees/millisecond)
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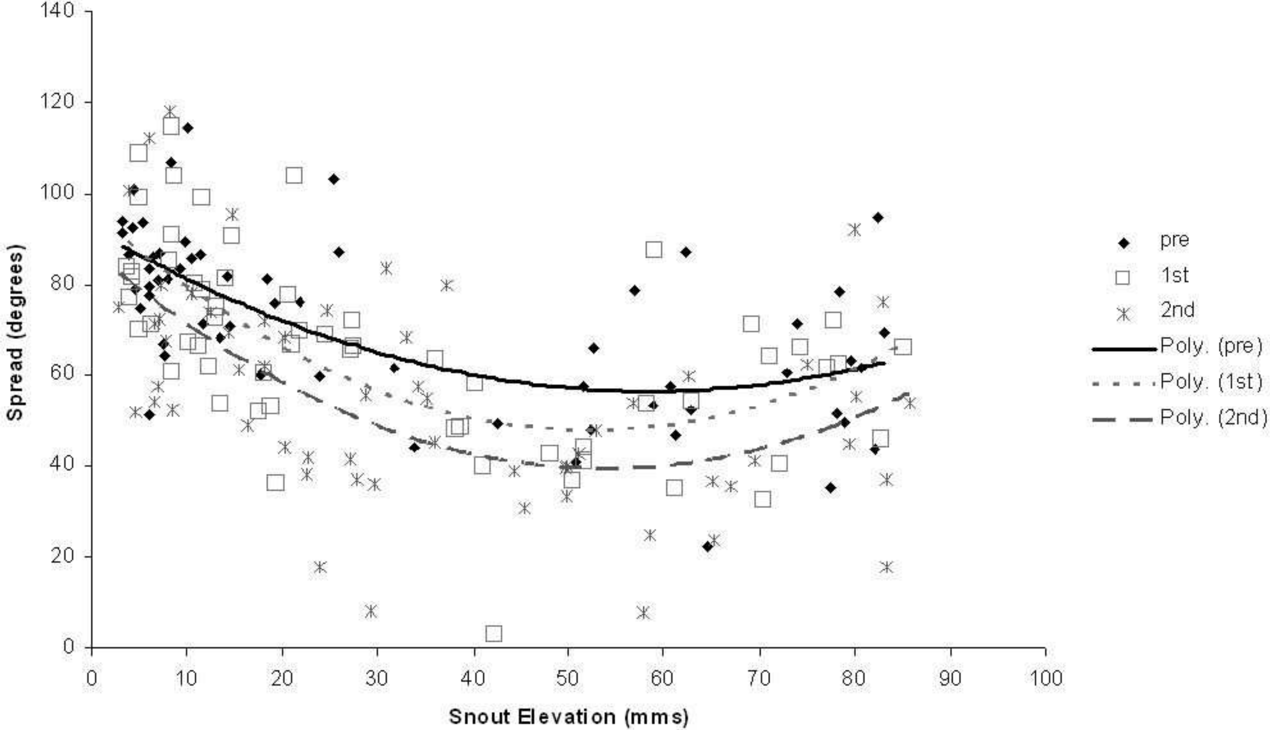
0.7
0.6
Pre-contact
1st
2nd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60
80
100
120
140
Snout Elevation (mms)
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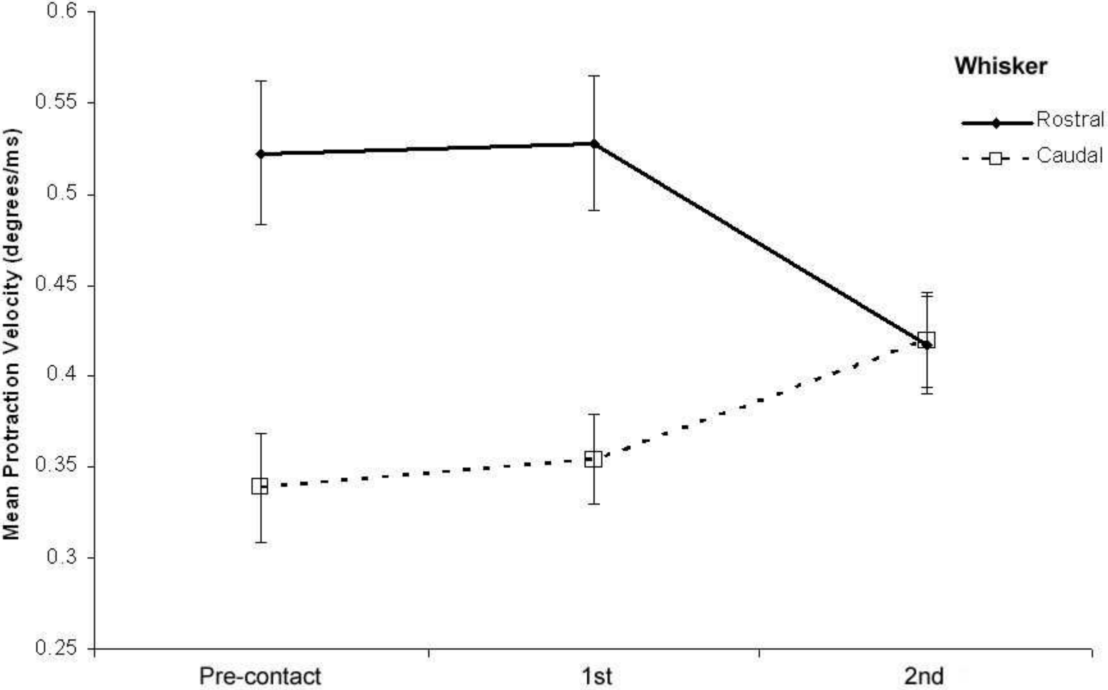
10
20
30
40
50
60
70
80
90
100
◆ pre
☐ 1st
✳ 2nd
Poly. (pre)
Poly. (1st)
Poly. (2nd)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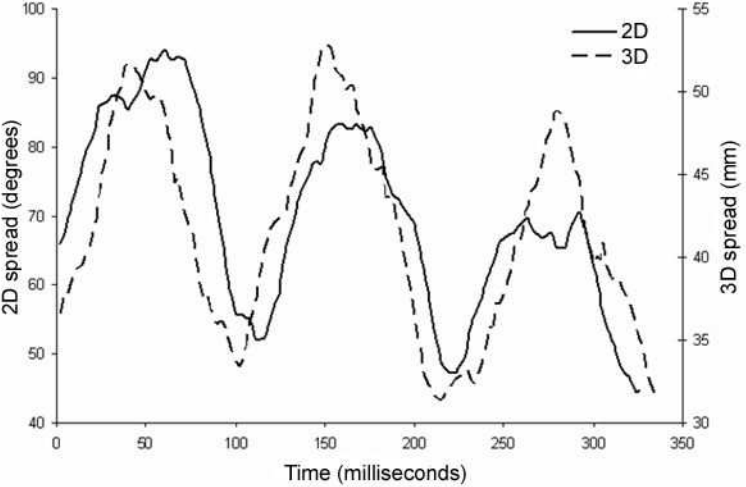
Rostral
Caudal
Pre-contact
1st
2nd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3D
2D spread (degrees)
100
90
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70
60
50
40
3D spread (mm)
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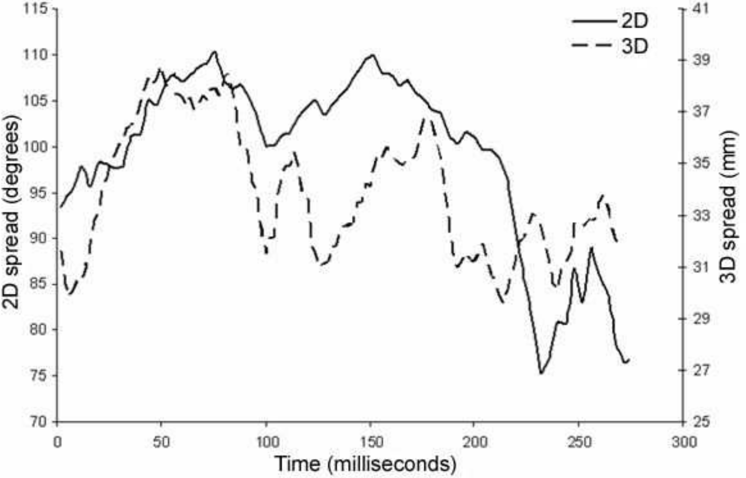
0
50
100
150
200
250
300
350
Time (milliseconds)


2D
3D
2D spread (degrees)
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110
105
100
95
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85
80
75
70
3D spread (mm)
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37
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33
31
29
27
25
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50
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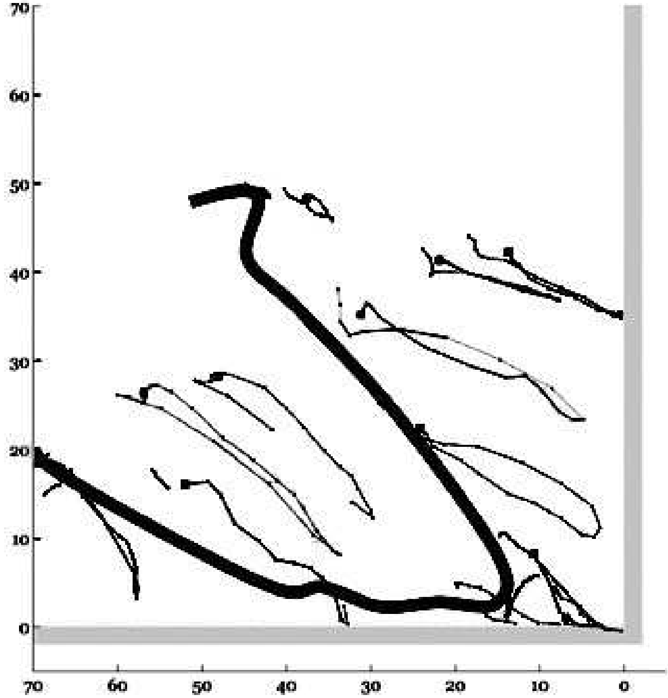
250
300
Time (milliseconds)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10
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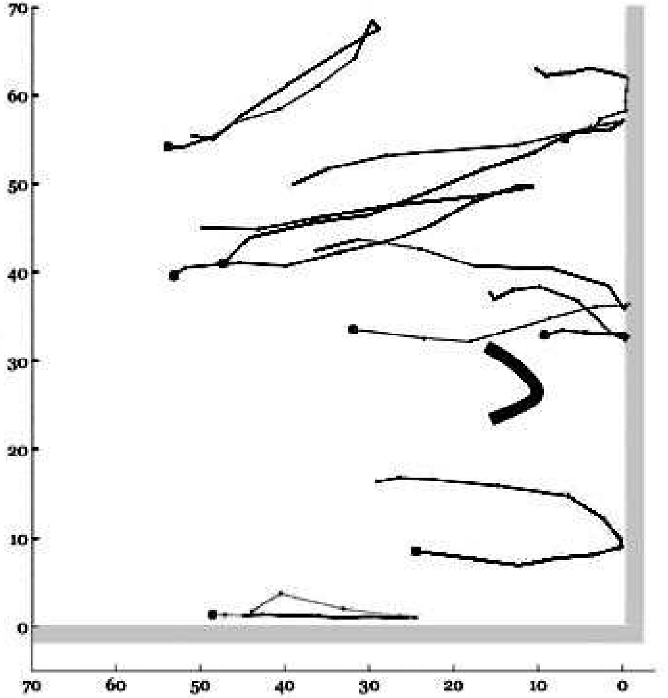
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