Tactile object localization by anticipatory whisker motion

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Submitted 27 March 2014; accepted in final form 20 October 2014

Voigts, J. Herman, D.H. and Celikel, T. Tactile object localization by anticipatory whisker motion. J Neurophysiol 113: 620–632, 2015. First published October 22, 2014; doi:10.1152/jn.00241.2014.—Rodents use rhythmic protractions of their whiskers to locate objects in space. The amplitude of these protractions is reduced when whiskers contact objects, leading to a tendency of whiskers to only lightly touch the environment. While the impact of this process on the sensory input has been studied, little is known about how sensory input causes this change in the motor pattern. Here, using high-speed imaging of whisking in mice, we simultaneously measured whisker contacts and the resulting whisking motion. We found that mice precisely target their whisker protractions to the distance at which they expect objects. This modulation does not depend on the current sensory input and remains stable for at least one whisking cycle when there is no object contact or when the object position is changed. As a result, the timing and other information carried by whisker contacts encodes how well each protraction was matched to the object, functioning as an error signal. Whisker contacts can thus encode a mismatch between expected object locations and the actual environment.

Tactile navigation is an active sensorimotor task. Whisking animals, such as rats and mice, use their whiskers (macrovibrissae) to explore their tactile environment through rhythmic whisker protractions (Ahissar and Knutsen 2008; Brecht 2007; Carvell and Simons 1990; Deschenes et al. 2003; Diamond et al. 2008; Hill et al. 2008; Jadhav and Feldman 2010; Kleinfeld et al. 2006; Knutsen and Ahissar 2009; Mehta et al. 2007; O’Connor et al. 2010; Vincent 1912; Welker 1964). This whisking motion does not follow a fixed pattern (Voigts et al. 2008) and is modulated by whisker contact with the environment.

Multiple types of sensorimotor modulation have been observed in whisking rodents. In rats, sensory input in the form of whisker contact with the environment typically leads to a reduction in the whisker protraction amplitude (Carvell and Simons 1990; Mitchinson et al. 2007). This reduction can be as rapid as within the same protraction cycle, manifesting in fast touch-induced retraction, so-called “pump” motions (Deutsch et al. 2012; Sherman et al. 2013). This reduction in whisking amplitude leads to an overall tendency of whiskers to only lightly touch the environment, minimizing the angle of whisker deflection and with it the force that acts on whiskers during contacts as well as whisker vibrations, deflection angle, etc.

In addition, rats quickly modulate whisking amplitude as well as the spread between their whiskers after contact with an unexpected object, in order to maximize the number of whiskers touching the object while maintaining only light contacts (Grant et al. 2009), suggesting that the whisking pattern is modulated with the aim of maximizing information content of whisker contacts or to stabilize the order of contacts across whiskers (Desilets-Roy et al. 2002). Protractions are also modulated asymmetrically to compensate for lateral object contacts, so that whisker deflection strength is stabilized across both sides (Sachdev et al. 2003; Towal and Hartmann 2008). This lateral adaptation of the whisking pattern to the environment anticipates exploratory head motion (Towal and Hartmann 2006), indicating that it is actively driven by the exploratory behavior rather than a reaction to sensory inputs.

These observations demonstrate that rodents use modulation of the whisking in response to sensory input to reduce overall whisker deflection amplitude and to optimize conditions for tactile sensing.

However, even though this modulation of the whisking pattern has a profound effect on the information carried by each contact a whisker makes with an object, the interaction between the changing motor pattern and the resulting change in the information carried by whisker contacts over the course of an unrestrained bout of tactile exploration has not been quantified. If whiskers only ever lightly touch objects, then the amplitude of the deflection will not carry much information about the distance to the object, as it will remain relatively constant regardless of object distance. Instead, the modulated motor pattern leading to the light touches must be integrated with the sensory information to form a correct percept of the object. Even though the neural substrate for this integration has been studied (Curtis and Kleinfeld 2009; Hill et al. 2011; Masri et al. 2008), the kind of information that is carried by either whisker contacts or the motor pattern in freely exploring animals has not yet been examined.

To quantitatively examine the interaction between the whisking pattern and sensory input, and the impact of this interaction on the amplitude and timing of whisker contacts and hence on the sensory information carried by whisker contacts, we observed freely behaving mice locating a target with their whiskers under infrared light in the gap-crossing task (Celikel and Sakmann 2007; Harris et al. 1999; Hutson and Masterton 1986). We analyzed whisker kinematics using whisker tracking (Voigts et al. 2008) and find that whisking amplitude is reduced to match the object distance with enough precision that the motor pattern alone is sufficient to recover the animal’s distance to the object. We further find that this modulation of whisking amplitude is anticipatory in the sense that it does not depend on the sensory input in the same whisk cycle but rather remains stable even when the target object is...
moved or the whiskers miss the object altogether. Our finding extends the prior observation that whisker protractions can stop immediately after strong or unexpected whisker deflections (Grant et al. 2009; Mitchinson et al. 2007; Sachdev et al. 2003; Towal and Hartmann 2008) by showing that the overall reduction of the whisker protraction angle during tactile exploration of static objects does not depend on a fast, reflexive cessation of whisker protractions after each object contact.

We next examined the impact of this precise and stable whisking pattern modulation on the sensory encoding of object distance. Whisking modulation affects not only the amplitude of whisker deformation by leading to mostly light touches but also the timing of contacts relative to the whisking pattern. By examining the information content of parameters of whisker contacts such as the timing of contacts relative to the whisking pattern and the velocity and strength of deformation, we could infer whether these contacts could be used to directly estimate object distance.

We found that phase, deflection amplitude, and velocity of contacts encode how well each whisker protration was matched to the object distance rather than directly encoding object distance. On the basis of this analysis, we propose a sensorimotor model for object localization in which the history of sensory input (and prior expectation) determines the motor pattern while the sensory information collected in any whisk cycle encodes how well the whisking amplitude in this cycle was matched to the target, thereby serving as an error signal.

**Glossary**

<table>
<thead>
<tr>
<th>Term</th>
<th>Description</th>
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<tbody>
<tr>
<td>Whisker base angle</td>
<td>Vibrissa angle measured at the whisker base (follicle) in the horizontal plane</td>
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<tr>
<td>Vibrissa tip protraction</td>
<td>Horizontal distance of the whisker tip (located via whisker tracking) relative to the animal’s nose</td>
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<td>Target distance</td>
<td>Horizontal distance of the target platform from the animal’s nose</td>
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<td>Virtual whisker tip protraction</td>
<td>Estimate of the whisker tip protraction derived from the whisker base angle. This metric predicts the position of the whisker tip in the absence of contact-induced deformations and allows us to infer where the mouse tries to “aim” the whiskers (see RESULTS).</td>
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<tr>
<td>Mismatch of virtual tip and target</td>
<td>Distance between the estimated virtual whisker tip and the target platform. This metric quantifies how well the animal’s motor pattern predicts the position of the target.</td>
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**MATERIALS AND METHODS**

Six adult (4 mo old) C57BL/6 mice (Taconic Farms) of either sex were used according to the animal welfare guidelines of the National Institutes of Health, and experiments were approved by the Animal Care and Use Committee at the University of Southern California. Mice were housed individually and kept on a reversed 12:12-h light-dark cycle with ad libitum access to food and water. All experiments were performed during the dark phase, and each animal was acclimatized to the experimental room for >1 h before experiments started. Whisker plucking (Allen et al. 2003; Celikel et al. 2004; Foeller et al. 2005) was performed under isoflurane (Baxter) anesthesia a day before imaging experiments. Whiskers were plucked to bilateral C rows (n = 35 sequences), unilateral C row (n = 35), or C1/2 only (n = 80) on one side for the static platform experiments and C1 only for the retracting platform experiments (n = 29; see below).

**Spontaneous gap crossing.** The gap-crossing task is based on tactile exploration of an elevated target platform while the animal is perched on the edge of a second (i.e., home) platform (Celikel and Sakmann 2007; Harris et al. 1999; Hutson and Masterton 1986; Voigt et al. 2008). Mice shuttle between the two platforms for appetitive reward or, as in this study, spontaneously. At larger distances greater than ~30 mm, mice solely use their whiskers to locate the target platform of interest when training is performed under infrared light. We trained mice on the spontaneous gap-crossing task as described previously (Voigt et al. 2008) under infrared light. Animals were not food deprived, and successful gap crossings were not rewarded. The target platform was placed at distances of 3, 4, 5, 5.5, and 6 cm (N = 8, 24, 29, 37 and 52 trials, respectively) randomly. In the static platform experiments, four animals were allowed to cross the gap back and forth 16–20 times per session, and crossings from home to target platform were recorded with a high-speed camera (Redlake MotionScope M1) at 1,000 frames/s (fps) with a resolution of ~0.20 mm/pixel. Two additional mice (N = 29 gap-crossing sequences) were studied in a separate setup that allowed sudden retraction of the target platform by ~5 mm at a speed of ~13 cm/s with a pulsed magnetic field (Clem et al. 2008, see Fig. 1 for details). Whisker motion in this second setup was recorded with a different camera at 315 fps and a resolution of ~0.13 mm/pixel (Pike 032B, Allied Vision Technologies), and data were subsequently interpolated to 1,000 fps. This procedure provides sufficient resolution since the relevant variables in whisking have timescales of >3 ms and the whisker tip velocity during protractions is <1 mm/ms (see Fig. 12 in Voigt et al. 2008).

Because of the small initial gap width and the requirement for absence of target intersection before the target platform is retracted, the majority of trials in this part of the study contained only one whisker contact before target retraction (preretraction contacts: trial count: 0/4, 1/13, 2/7, 3/1). Data analysis. Data analysis was carried out with custom software in MATLAB (MathWorks). Whiskers and their contacts with the target platform were tracked as described previously (Voigt et al. 2008), and all results were checked and, if necessary, corrected by trained human observers.

The whisker tracking method produces an initially unsupervised tracking of all whiskers. Human experts then manually correct the tracking where necessary and identify whiskers (C-row whiskers 1–4). The whisker tracking results in a continuous curve of the entire whisker length from the tip to the base. Frames where tracking of entire whiskers was not possible were excluded from further analysis. Contacts between whiskers and the target platform were identified manually and assigned to identified whiskers.

The animal’s nose was tracked as previously described (Voigt et al. 2008), and the distance between the nose and the target platform edge was used to quantify the animal’s distance to the target. Data were analyzed up to the point where the animal intersected the target platform with its nose (target distance of 0 mm). The whisker angle in the a day before imaging experiments (Fig. 2B; see Fig. 3 for more example raw data for Fig. 2) was computed from the proximal ~3 mm of the whisker of the traced whisker by fitting a spline. We found that whisker tip deflections induced by whisker contact onto the target do not measurably affect the whisker at this position along its shaft (see RESULTS and Fig. 5).

The duration of protractions and retractions was computed by tracking the angular displacement of the whisker at the base after correcting head motion artifacts by detrending with a smoothed copy
we modeled the relationship between whisker base angle and true regardless of whether the actual whisker tip was deformed by contact obtain an estimate of where the animal tries to “aim” the whisker tips, by estimating the whisker tip protraction from the base angle we could Whisking motor pattern can be inferred from whisker base angle follicle serves as a good proxy for the whisking motor pattern (see Position of the whisker tip. We found that the whisker angle at the sensory input, we estimated how the base angle of each whisker predicts quantify the effect of the modulation of whisking motion on the whisk cycles with an amplitude denote this variable. The fit was computed once per whisker, using only least-squares fit. We use the term “virtual whisker tip protraction” to point) were defined as the local maxima of the smoothed (Gaussian filter, \( \sigma = 25 \text{ ms} \)) as previously described (Voigts et al. 2008). The points of maximum protraction and retraction (most protracted point = rostral set point/most retracted point = caudal set point) were defined as the local maxima of the smoothed (Gaussian filter, \( \sigma = 8 \text{ ms} \)) mean whisk angle and aligned to the nearest rostral/caudal set points in the raw unsmoothed trace.

**Estimation of whisker tip position from whisker base angle.** To quantify the effect of the modulation of whisking motion on the sensory input, we estimated how the base angle of each whisker predicts the position of the whisker tip. We found that the whisker angle at the follicle serves as a good proxy for the whisking motor pattern (see Whisking motor pattern can be inferred from whisker base angle), so that by estimating the whisker tip protraction from the base angle we could obtain an estimate of where the animal tries to “aim” the whisker tips, regardless of whether the actual whisker tip was deformed by contact with the target. To obtain this mapping of whisker angle to tip protraction, we modeled the relationship between whisker base angle and true whisker tip protraction with a second-order polynomial (Fig. 2C) using a least-squares fit. We use the term “virtual whisker tip protraction” to denote this variable. The fit was computed once per whisker, using only whisk cycles with an amplitude > 10°, and using only cycles before the whiskers made contact with the target, so that the training set was not used in the main analysis. To avoid possible bias in this procedure, no analysis relies on the absolute position of the virtual tip. Instead, we analyzed its distribution or changes within individual trials.

**Quantification of histograms.** To quantify the precision of variables for which reporting the standard deviation (SD) was not sufficient [such as the information contained in the virtual whisker tip position about the target position (see Fig. 6B, B and C)], we computed the information gain as the reduction in the Shannon entropy between the distributions:

\[
\text{Information gain} = H(\text{base}) - H(\text{test}) = \sum_{i=\text{bins}} P(\text{base}) \times \log_2 P(\text{base}) + \sum_{i=\text{bins}} P(\text{test}) \times \log_2 P(\text{test})
\]

Because this comparison is between two binned distributions, and binning affects both distributions similarly, the results are largely independent of the bin size (for example, information gain in the example from Fig. 6B, animal 1, left C1 whisker is 0.99, 0.98, and 0.97 bit for bin sizes of 0.5, 0.4, and 0.25 mm).

Overlap between distributions was computed with the normalized Whitney U statistic. We report the area under the receiver operating characteristic curve (AUC) that specifies the probability of a sample from the distribution with the lower median to be larger than a sample from the distribution with the higher median. All data were tested for normality with a Lilliefors test at a significance level of 0.05, and reported \( P \) values are from either \( t \)-tests or Wilcoxon rank sum test. Throughout, reported numbers are means ± SD, or medians and interquartile range (iqr) for non-Gaussian data.

**RESULTS**

Using high-speed infrared videography (Voigts et al. 2008), we observed mice \((n = 6, 179 \text{ trials})\) search for a target platform on the gap-crossing task (Celikel and Sakmann 2007; Harris et al. 1999; Hutson and Masterton 1986; Voigts et al. 2008), using their whiskers. In each trial, the target platform was placed at a randomly selected distance (range: 30, 40,

![Fig. 1. Method for movable target platform. A: overview and measurements of the gap-crossing setup. The platform is made from sheets of transparent acrylic. The moving target platform (red) is placed on top of the target platform and moved via a thin stainless steel wire (blue) that extends through the back of the target platform assembly. The gap width is adjusted by moving the entire “home” platform; this way, the moving “target” platform assembly can remain stationary. The width of the gap is ~4 cm. Optionally, the platforms can be made wider and restricted to ~4 cm only at the gap (not shown here). If needed, infrared motion sensors (emitter/detector pairs) can be added to the platform to allow automatic tracking of the animal's position. An array of infrared LEDs and a diffuser glass is mounted at least 14 cm below the gap. Depending on the diffuser, the LEDs, and the camera, 9-12 LEDs are needed in order to achieve sufficiently uniform illumination. Uniformity can be further improved by housing the LEDs in an enclosure made from mirror-coated acrylic. Optionally, additional LEDs can be mounted above the platforms in order to allow better tracking of the animal's head. B: overview of the moving platform assembly. The moving platform is placed on top of the acrylic target platform and retracted via a stainless steel wire. The back of the wire is attached to an audio speaker driver, and application of a voltage step will retract or protract the target platform by a few millimeters. If a fast retraction is desired (as in this report), the platform can be calibrated so that it is automatically stopped by the acrylic platform at the retracted position. C: method for retracting the platform used in this report. Instead of an audio driver, a steel plate is placed ~5 mm in front of a copper coil (Clem et al. 2008), so that application of a voltage step quickly retracts the steel plate and stops as it hits the coil enclosure. D: measurements of the moving platform assembly. The moving platform overlay can be made from thin plastic sheets (plastic from large disposable weigh boats works well) and assembled with epoxy glue. The steel wire needs to be centered to ensure proper linear motion and to minimize vibration. Speaker drivers of ~15-cm diameter work well; if higher acceleration is desired, holes in the speaker membrane can be cut to adjust the damping factor. 

\[ \frac{\text{J Neurophysiol}}{\text{DOI: 10.1152/jn.00241.2014 • www.jn.org}} \]
Whisker motor pattern can be inferred from whisker base angle. The whiskers deformed when they made contact with the target platform. We investigated whether this deformation could affect the angle of whiskers at the follicle, to test whether we could use this whisker base angle to measure the mouse’s motor pattern and to infer the animal’s intended whisker position, despite any deformation in the distal part of the whisker. The amplitude of angular whisker deformation (angular tip deflection relative to whisker base angle) relative to the value before contact onset increased slightly with the number of successive whisker contacts (Fig. 5A; \( r = 0.22 \), \( P < 0.05 \) for max. angular deflection in 20 ms after contact for C1 and C2 whiskers, excluding deflections >10°, \( N = 933 \), all relative to baseline whisker curvature before contact onsets). Target distance had a smaller effect on deflection amplitude (\( r = 0.11 \), \( P < 0.05 \)).

Overall, we found that whisker deformations were small (<10°), even for contacts at small target distances (75% of contacts <8.6°, 90% <12.4° for maximum momentary deflection in C1 and C2 and 75% <5.0° and 90% <7.0° for mean deflection 8–12 ms from onset, \( N = 933 \), relative to baseline curvature). During maximal deflection of the whisker tip, the
bending was limited to the distal half of the whisker and did not
significantly propagate to the whisker base where the base
angle was measured (Fig. 5B) (see also Figs. 10 and 11 in
Voigts et al. 2008). This result is consistent with measurements
and tapered-rod models in rat whiskers (Boubenec et al. 2012;
Hires et al. 2013) and with direct measurements of exposed
follicles in rats (Bagdasarian et al. 2013).

We further tested the possibility that contact with the target
affects the measured whisker protraction angle via flexibility of
the follicle in the skin or of the whisker pad itself: If skin
compliance affects the whisker base angle, then we expect an
increase in the base angle when mechanical force on the
whisker is removed between whisk cycles. We analyzed pairs
of whisker protractions in which a whisker first hits the target
and then protracts over and past it in the next protraction, and
we found a negligibly small increase in whisker base angle
(difference: \(0.03 \pm 0.06^\circ, \ N = 30\) protractions). We found
the same results when analyzing pairs of whisker protraction in
which the target object is suddenly retracted (see Fig. 2D for raw data). The quadratic
polynomial mapping, calculated separately for each whisker in
each trial, was used to calculate a “virtual whisker tip protraction” that gives an estimate of the intended whisker tip position
(i.e., where the whisker tip would be based on its base angle if
there were no contacts with the target). This virtual tip position
thus converts the whisker base angle (protraction in \(^\circ\)) to linear
whisker protraction in millimeters and provides a useful way to
relate the motor pattern to the protraction of the whiskers into
the target platform. While this static mapping does not account
Together, these findings show that the immediate, mechanical
contribution of object contact on the whisker base angle in
the gap-crossing task is negligible, so that the whisker base
angle can be used as a valid readout of the motor pattern.

Because contact with the target does not deform the whisker
at its base, this base angle can be used to estimate the animal’s
intended position of the whisker tip while the animal is actively
exploring an object. This procedure allows for convenient
analysis of the whisker pattern because it allows us to directly
relate the motor pattern to the object distance, regardless of
whether the actual whisker is deflected by object contacts. We
estimated the whisker tip protraction relative to the nose (in
mm) from the whisker base angle (in \(^\circ\)) with a quadratic
polynomial using tracking data from free whisking in air prior
to the first contact (see Fig. 2, B and C, and MATERIALS AND
METHODS for details and Fig. 2D for raw data). The quadratic
polynomial modulation does not depend on current sensory
input and Fig. 9A). Furthermore, whisker contacts did not
reduce whisker base angle compared with whiskers that were
not in contact with the target in the same cycle (measured
relative to angle in previous protractions, difference: \(-0.04 \pm
1.93^\circ, \ N = 434\)).

Fig. 3. Example raw whisker tip and virtual
whisker tip traces. Raw whisker tracking data
from 10 whiskers. Data are plotted as in Fig. 2D.
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for inertial deformations, torsion, or movements along the dorsoventral axis, virtual whisker tip protraction agreed well with the actual location of the whisker tip [root mean square error (RMS) 0.8 mm, \( N = 120,731 \) frames for free whisking].

Whisker protraction amplitude is matched to target distance. By using the “virtual whisker tip” that estimates the animal’s intended whisker tip protraction from the motor pattern, we next examined how precisely the reduction in protraction angle matched the whisker protraction to the target distance.

In agreement with the finding that mice reduce their angular whisking amplitude when approaching the target (Fig. 4B), we found a strong reduction of the virtual tip protraction amplitude in rostral set points (point of cessation of whisking protraction) in whisk cycles in which whiskers touched the platform (\( r = -0.81 \) for C1, \( r = 0.611 \) for C2 in animal 1; Fig. 6A; see Fig. 7 for additional data). As the animal approached the target, this reduction in whisking amplitude compensated for body motion and stabilized the virtual whisker tip position relative to the target [regression slope of 0.31 mm/mm for animal 1 (whisker C1) and 0.15 mm/mm for all data from whisker C1 across animals, compared with a slope of \(-1\) that would be observed if whisking amplitude was constant]. We also observed a small but significant negative (quadratic) curvature in the modulation of the whisker protractions \( [P < 0.05 \) rank sum, \( N = 38 \) whiskers, 37% (14/38) of tracked whiskers were individually significant, 10%, 50%, 90% quartiles of 2nd-order coefficients: \(-0.16, -0.06, 0.021 \) mm/mm²]. This could indicate that the mice try to aim for a certain amount of impingements and only start significantly modulating the whisking pattern once they reach a certain distance.

Whisker impingement, quantified by the mismatch between the most protracted virtual whisker tip and the target platform, was \( \sim0.75–1\) mm (C1 quartiles: \( 0.101, 0.75, 1.54 \) mm; C2: \(-0.12, 0.77, 1.54 \) mm).

To quantify the precision of this whisking amplitude modulation, we compared the histogram of the virtual whisker tip positions (at their most protracted points per cycle; Fig. 6, B and C, blue) to the histogram of the object distances at which the whisker made contact with the platform (Fig. 6, B and C, gray). We hypothesized that the whisking amplitude modulation compensates for self-motion, in which case the distribution of virtual whisker tip positions should be more narrow than the distribution of distances at which whisker contacts occur. Comparing the histograms in this way controlled against overestimating the precision of the amplitude modulation for whiskers that contact the object only at specific distances and

![Fig. 4. Active modulation of whisking by touch. A: histograms of whisker contacts by target distance. B: whisker protraction angle is initially increased as animals approach the target platform [area under receiver operating characteristic curve (AUC) = 0.25 between less than \(-20\) mm and less than \(-10\) mm]. Whisker protraction angle is computed at rostral set points (relative to baseline per animal and whisker). Baseline was defined for each session prior to first contact with the target. Green, data from all animals; red, data from animal 1, C1 whisker. Mean slope = \(-3.73 \pm 1.94\) mm between \(-10\) and \(2\) mm, \( N = 38\). C: duration of whisker protraction decreases with target distance. Blue, data from all animals; red, data from animal 1, C1 whisker [difference between \(-15\) mm to \(-10\) mm (far) and \(-5\) mm to 0 mm (near): AUC = 0.27, * \( P < 0.05\)]. D: whisker retraction duration in respect to distance to the target (AUC = 0.41, \( P = 0.40\)). E: whisking frequency increases as animals approach the target. Frequency is computed from the time between caudal set points. (quartiles far: 14.4, 16.9, 18.8 Hz; near: 17.2, 19.2, 22.2 Hz; AUC = 0.29, * \( P < 0.05\)). In B–E, box plots depict the quartiles (25%, median, 75%).

![Fig. 5. Quantification of whisker deformation during tactile exploration in freely behaving mice. A: whisker tip deflection angle across subsequent whisker contacts is small: the angular displacement is measured at the whisker tip relative to baseline curvature and relative to the angle before contact onset for each whisker (in \(-5\) to 0 ms). Data are from C1 and C2 whiskers \( [N = 933] \). Color denotes the order of contacts. Solid lines are median, and dashed lines are 25% and 75% quartiles. Asterisk indicates source of data for B. B: whisker deformation along the shaft during maximal whisker tip deformation at the 3rd whisker contact shown in Fig. 4A. The deformation of the distal half of the whisker does not affect the inner \(-40\%\) of the whisker.](http://jn.physiology.org/doi/pdf/10.1152/jn.00241.2014)
would hence show a narrow distribution even in the absence of precise modulation of the protraction amplitude. To quantify the sharpening between the control and virtual tip histograms (Fig. 6, B and C) we compared their SDs and their Shannon entropy (see MATERIALS AND METHODS) per whisker, which quantifies the precision of the amplitude modulation without assumption about the shape of the distributions. Both measures are independent of offset terms and are therefore unaffected by biases in the method used to estimate the virtual tip position from the whisker angle. Because we computed the entropy difference of two binned distributions, the result is largely independent of changes in bin size (for quantification see MATERIALS AND METHODS). All entropy calculations were performed with a bin size of 0.4 mm/bin (40 bins covering −12 to 4 mm from target platform).

We found that the distribution of virtual whisker tip positions relative to the target was significantly narrower than the control distribution of target-to-nose distances at which there was whisker contact, confirming that whisker protractions are targeted to the object distance (SD decrease: −1.26 and −1.11 mm; information increase: 1.05 and 0.99 bit for the data from C1 and C2 whiskers in Fig. 6B). Averaged across all whiskers, animals, and whisker deprivation conditions, the information gain was 0.71 ± 0.29 bit and the decrease in SD was −0.70 ± 0.32 mm (both \( P < 0.05, N = 13 \)).

We repeated the analysis not only using whisking cycles in which whiskers made contact with the target but using all whisk cycles after the first contact. This did not result in decreased gain in Shannon information \([0.69 \pm 0.33 \text{ bit} (P < 0.05, N = 16)] \) vs. \([0.71 \pm 0.29 \text{ bit for only protractions with contacts} \), although the decrease in SD was no longer significant \([0.19 \pm 0.67 \text{ mm} (P = 0.85, N = 16)] \) vs. \(−0.70 \pm 0.32 \text{ mm for only protractions with contacts} \) because the data now included outliers originating from nontargeted whisking that led to non-Gaussian distributions. This suggests that the precision of the targeted whisking pattern is maintained even for protractions in which whiskers missed the target platform.

These results show that the modulation of whisker protraction amplitude is precise and matches the whisker protractions to the target distance, maintaining a small but stable whisker impingement, while compensating for animal motion.

**Target distance is not directly encoded in timing or phase of contacts.** Having shown that mice modulate their whisking motor pattern, we next asked how they infer object location, given that changes in the whisking pattern will affect the incoming sensory input. Specifically, the precise matching of the whisker protraction amplitude to the target distance not only reduces the amplitude of whisker deflections (Figs. 5 and 6) but also affects the encoding of object distance through the timing of contacts within the whisking cycle. If protractions cease immediately after object contact, all contacts should occur approximately at the same phase within the whisking cycle, making a direct readout of object distance through the contact phase impossible. To quantify this effect of the motor pattern on the sensory input, we calculated the timing of contacts relative to the next rostral set point (i.e., most protracted position; Fig. 8A) and computed the phase of whisker contacts onto the platform (Fig. 8B).

Contacts occurred predominantly in the protraction phase (87% of contacts), with a fraction of touch events happening within \(±0.5 \text{ rad} (±28.6°) \) of the rostral set point (12% of contacts, \( N = 3,252 \)). We observed a small but significant correlation between contact phase and target distance \((r = −0.14, P < 0.05, \text{ slope } −0.03/\text{mm, } P < 0.05) \) when excluding contacts during retraction, \( N = 2,599 \)). However, the phase of whisker contacts was highly variable, spreading across the entire protraction cycle (Fig. 8C; SD = 0.79, 0.95, and 1.32 for \( animal \ 1 \), whiskers C1–3, respectively). This variability in contact phase increased as the animal approached the target (SD across all whiskers 0.50, 0.56, 0.64 for >8-mm, 8- to 5-mm, and <5-mm distances) because small deviations in contact position and timing translate to larger phase deviations when the whisking amplitude is significantly reduced.

Even though we observed cases of significant phase-distance correlation \((r = −0.57 \text{ for right C1 of } animal \ 3 \text{ at } 5.5 \text{ cm}) \), the lack of a clear correlation between contact phase and object location and the high variability of contact phase was consistent across whiskers (Fig. 8C) and number and spatial arrangement of whiskers.

Our results show that in the gap-crossing task the timing or phase of contacts alone, without the context of the whisking pattern, is not sufficiently informative to allow object localization.

**Fig. 6.** Whisker protraction amplitudes are precisely matched to target distance. A: red: maximum virtual tip protraction amplitude per cycle (Fig. 2C) is reduced as mice approach the target platform, compensating for self-motion. Data in red indicate the maximal position of the virtual whisker tip in each whisking cycle, regardless of when a contact occurred. Gray: diagonal at which amplitude would be fully matched to target distance. Plotted data from animal 1 (across all whiskers and animals; \( r = −0.58 \pm 0.27 \), slope = −0.68 ± 0.43 for C1, \( N = 13 \); \( r = −0.67 \pm 0.27 \), slope = −0.61 ± 0.25 for C2, \( N = 8 \); \( r = −0.65 \pm 0.17 \), slope = −0.46 ± 0.10 for C3, \( N = 4 \)) show that mice maintain a stable whisker impingement of −1 mm. See Fig. 7 for more example data. B: normalized histograms of the target distance at whisker contacts (gray), mismatch between virtual tip and target during whisker contact (blue, same as vertical offset of data in A from diagonal), and in all cycles that followed contact (dotted lines). Data from animal 1 & C: same as in B but across all mice.

\[ r = -0.810 \]

\[ N = 13 \]

\[ r = -0.670 \pm 0.27 \]

\[ N = 8 \]

\[ r = -0.650 \pm 0.17 \]

\[ N = 4 \]
Fig. 7. Example raw virtual whisker tip protraction data. Each data point represents the virtual whisker tip position (relative to the animal’s nose) at the most protracted point in one whisker protraction cycle. Green, data from −20 to −10 mm distances; red: −10 to 0 mm from cycles with whisker to platform contacts. Regression and 95% confidence intervals are plotted as solid and dotted lines, respectively.
Protraction amplitude modulation does not depend on current sensory input. Given that the timing of whisker contacts alone is not sufficient to infer object location, we examined how mice integrate sensory information to update their motor patterns. To determine the contribution of sensory input to the modulation of the protraction amplitude, we studied the whisking pattern of two mice (N = 29 trials) while they explored a target platform whose position was suddenly retracted by ~5 mm (4.88 ± 0.41 mm) upon brief tactile exploration (see MATERIALS AND METHODS for details). Our hypothesis was that if the modulation of whisker protraction is based on sensory input collected during the same whisk cycle, the protraction amplitude should increase on the next cycle following target repositioning. Conversely, if the motor modulation is anticipatory and a function of past sensory input, target motion should not immediately affect the whisker protraction amplitude. The results supported the latter prediction: The mean protraction amplitude did not increase after target repositioning (Fig. 9A; median 3.59, iqr = 0.98 mm before vs. 3.26, iqr = 0.66 mm after; P = 0.95, Wilcoxon rank sum test, N = 17 before, N = 12 after, AUC = 0.490). Repeating the analysis using only trials in which mice made a contact with the target platform directly before and after the target repositioning gave the same result (median pairwise difference = −0.11, iqr = 0.87 mm, Wilcoxon rank sum test P = 0.92, N = 12, AUC = 0.416). These findings indicate that the motor (i.e., whisking) pattern modulation by sensory input does not depend on information collected in the same whisk cycle.

This absence of rapid modulation in the whisker protraction amplitude upon target motion could have caused the whisking motor pattern (quantified via the virtual whisker tip position) to significantly "underestimate" the new target distance (Fig. 9B; median 1.01, iqr = 1.79 mm before and −0.46, iqr = 1.23 mm after repositioning, P < 0.05, Wilcoxon rank sum test, AUC = 0.085). The increase in mismatch is smaller than the 5 mm by which the platform was retracted because the mouse continued to approach the target in the meantime. In whisk cycles following the repositioning, the protraction amplitude did not increase to accommodate the new target distance; instead, animals continued to advance toward the new target location and recovered to the virtual whisker tip mismatch observed before target motion by approximately the third whisk cycle (median latency: 115 ms, iqr = 164 ms; Fig. 9B).

To further test the effect of changing sensory input on the whisking pattern, we examined trials in which the target platform did not move but whiskers first contacted the target platform but then missed it in the next whisker protraction (N = 30). To avoid a selection bias that might favor cases where the second protraction is of reduced amplitude, we only included events where the whisker missed the target platform but protracted above it after initial contact. Only data from animals with a single whisker were used, to avoid cross-whisker effects. We found that the pairwise difference in virtual tip position between hit and miss protractions was not significantly larger than 0 (−0.04 ± 0.74 mm, P = 0.62, N = 30). Although this result shows that in our experiments whisker contact did not reduce the whisker protraction amplitude in the same whisk cycle, the described events were confined to close object distances (2.97 ± 3.90 mm) that do not represent the full range of whisking behavior and relied on the animal missing the platform by whisking above it.

Together these results suggest that in the sensorimotor object location behavior employed in gap crossing the modulation of whisker protraction amplitude does not reflect sensory information collected during the same whisk cycle and persists for at least one whisk cycle, even in the absence of a whisker contact with the target object.

Contact phase carries information about mismatch between whisker protraction and object position. Our observations demonstrate that mice actively modulate their whisking amplitude, precisely matching their whisker tip protraction to the target distance (Fig. 6). This modulation of whisking amplitude does not depend on the sensory input in the same whisk cycle (Fig. 9). However, sensory input in each cycle should encode how well the whisking amplitude was matched to the target (“mismatch”; Fig. 2E), and this error measurement could be used to modulate the motor pattern in future whisk cycles. For example, in whisk cycles where the protraction amplitude overshoots the object location, whisker contacts will occur early relative to the protraction cycle and
As expected, we found that the phase of contacts was correlated with the mismatch between the virtual whisker tip position and the target location ($r = 0.34 \pm 0.13$ across all whiskers, $N = 13$). This correlation was not statistically different from that between contact phase and target distance (difference of $r$ values $0.00 \pm 0.13$, $P = 0.97$, $N = 13$). Plotting the median mismatch for each contact phase (20 bins, $-\pi$ to $\pi$; Fig. 10) showed that whisker protractions “overestimated” the distance mainly for contacts that occur midway through the protraction cycle (Fig. 10B) and “underestimated” (relative to average deflection amplitude) when the contact occurred close to the most protracted whisker position (phase $\approx 0$). This relationship is a direct consequence of the anticipatory whisking pattern that results in zero-phase (most protracted) virtual whisker positions that are well matched to the target platform (Fig. 6).

The positive mismatch values that we observe in this analysis are the result of the static lookup method used to estimate the virtual whisker tip (Fig. 2): If the whisker makes contact with the platform when the whisker base has already stopped protracting but the tip is still moving forward, the resulting prediction error (at phases close to 0) can be significantly positive.

To test whether contact phase could be used to estimate the mismatch during exploratory whisking, we subtracted the resulting phase-derived mismatch prediction from the virtual whisker tip position for each whisk cycle. This correction term decreased the mismatch (median decrease = $-0.75$ mm, $\text{IQR} = 1.40$ mm, $N = 1,062$) in 73.4% of the contacts. We found the same improvement when quantifying the whisking precision via the entropy method (see *Whisker protraction amplitude is matched to target distance*), with a median information gain over the estimate derived from the motor pattern of 0.13 bit, $\text{IQR} = 0.13$, $P < 0.05$, $N = 13$.

Similarly, we tested whether other properties of whisker touch could be used to infer the mismatch between whisker protraction and object position. We repeated the analysis using not the contact phase but instead the mean velocity of whisker tips in a 10-ms window before contact onset as well as the maximal angular whisker deformation (same method as in Fig. 4, B and C). We found slightly smaller but still significant correlations to the mismatch for contact velocity (Fig. 10C; $r = 0.29 \pm 0.16$, $P < 0.05$, $N = 13$) and deformation range ($r = -0.20 \pm 0.21$, $P < 0.05$, $N = 13$). However, unlike the phase, neither could be used to significantly improve the prediction of object position (RMS error difference relative to baseline given by virtual whisker tip; $P = 0.51$ for velocity and $P = 0.97$ for deflection amplitude, rank sum test, $N = 1,062$).

These results show that the contact phase, and to a lesser degree other contact parameters such as contact velocity and deflection amplitude, contain information about the mismatch between whisker protractions and the target object distance and could be used as feedback signals to refine the matching of the whisking amplitude to the target distance. Whisker contacts may thus encode error signals, rather than directly signaling object location, enabling mice to continually update their expectation of objects in their environment.

**DISCUSSION**

Whiskers, like eyes, are mobile sensory organs. The sensory information coming from whiskers has to be interpreted in the context of motor signals, i.e., where the whisker was positioned in space at the time of contact with the target object. The sensory information carried in the whisker contact, in return, changes the motion of the whiskers. Here, using high-speed imaging of whisker motion in freely behaving mice, we simultaneously quantified the sensory input (timing and location of whisker contacts with the target) and the whisking motion (pattern of protractions and retractions of individual whiskers).
and examined their relationship and the impact of this relationship on the information carried by whisker contacts during object localization.

We found that mice precisely match the amplitude of whisker protractions to object distance (Fig. 2) and that the whisking motor pattern alone is sufficient to infer the object distance (Fig. 6). This modulation results in whisker deflections of small amplitude (less than \( \sim 10^{\circ} \); Fig. 4A), in support of previous findings on minimal whisker impingement (Carvell and Simmons 1990; Deutsch et al. 2012; Grant et al. 2009; Mitchinson et al. 2007). This finding shows that mice aim their whisker protractions so that object contacts occur approximately toward the end of the whisker protraction cycle (Figs. 6 and 8) and so that the contact induces only minute forces on the follicle (Birdwell et al. 2007; Quist and Hartmann 2008).

We found that the modulation of whisker protractions does not depend on immediate sensory input within a whisk cycle (Fig. 9) and conclude that the whisking pattern must be modulated by prior sensory input and that the whisking pattern for contacting expected objects is anticipatory rather than a reaction to whisker contacts within any whisking cycle. This result is consistent with the observation that whisker bending upon object contact is more pronounced for unexpected than for expected contacts (Mitchinson et al. 2007). However, given the latency from contact onset to cessation of whisker protraction (15 ± 8 ms, \( N = 10,042 \) contacts), it remains likely that a fast low-level (i.e., brain stem) sensorimotor feedback loop (Kleinfeld et al. 1999) could also contribute to cessation of whisker protractions, as has been shown in rats (Deutsch et al. 2012; Grant et al. 2009; Sherman et al. 2013). This difference could be due to the amplitude of whisker deformations or due to different behavior for expected vs. unexpected contacts. Specifically, our experiments involved retraction of the target object between whisks rather than introduction of an unexpected obstacle. Another likely contributor to the observed modulation is superior colliculus, which can regulate whisker retractions in rats (Hemelt and Keller 2008).

Because of the unrestricted free whisking behavior in gap crossing we also cannot exclude that early whisker contacts at large distances were sufficient for the mice to estimate the target distance and that later whisking at closer distances was at least partially driven by compensation for self-motion rather than by continuous sensory input. However, mice seem to minimize the time they spend palpating the target in the gap-crossing task (Celikel et al. 2004), suggesting that most, if not all, sensory input is needed to successfully locate the target.

The significant modulation of whisking amplitude that we observed must in turn affect the information carried by whisker contacts. To understand this effect on the encoding of object location, we analyzed the phase of object contacts relative to the whisking pattern. We found that because of the active matching of whisking amplitude to target distance (i.e., the mice try to touch the object at the end of the protraction cycle), the timing of whisker contacts relative to the phase of the whisking pattern is highly variable and thus the contact phase is unlikely to directly encode target distance (Fig. 8). However, we found that the phase, and to a lesser degree other characteristics of whisker contacts, encodes the mismatch between the position where the animal aimed its whiskers and the true object position (Fig. 10). This mismatch estimate could consequently be interpreted as a cycle-by-cycle error signal that informs further modulation of the whisking pattern.

We propose that the principal function of this adaptive whisking is to compensate for changes in body motion and stabilize the characteristics of the whisker contact across whisker protraction cycles. This view is supported by the absence of whisking modulation in head-fixed animals (Harvey et al. 2001; O’Connor et al. 2010: Figs. 8 and 10 show that whisker protraction arcs are targeted to go-position but fully intersect the target bar position, and Fig. 13 shows strong whisker deflections).

In combining these findings, we propose a sensorimotor mechanism (Fig. 11) for object localization in which mice iteratively integrate sensory information by modulating their whisker protraction amplitude to match an expected object...
and true object position. This mechanism results in two central variables: the (fast changing) cycle-by-cycle sensory input that encodes the residual mismatch and (in itself relies on integration of motor information (Hill et al. 2011; Kleinfeld and Deschenes 2011; Lee et al. 2008)) and the (slowly changing) object position hypothesis that correlates with a stable modulation of the whisking pattern.

As a result of this modulation, contact parameters for contacts with a static environment are stabilized across whisk cycles, allowing for better fine sampling of exact position, surface texture, etc., while contacts with unexpected or moving objects are made more salient because they result in large changes in contact phase. This process is similar to eye movements that saccade to points of interest (Mitchinson and Prescott 2013).

Without constraining where or in what form the hypothesis is encoded in the neural substrate, we infer that 1) it must modulate the point of whisker protraction cessation, 2) it must react to sensory input while 3) remaining independent from sudden changes or absence of bottom-up information, and finally 4) it must be modified to compensate for self-motion. We propose that the representation of the slowly changing whisking amplitude (Friedman et al. 2012) and midpoint in vM1 (Hill et al. 2011) could play a central role in this computation, potentially through modulation of a central pattern generator circuit (Cao et al. 2012; Cramer et al. 2007; Cramer and Keller 2006; Moore et al. 2013; Ranade et al. 2013).

Taken together, our results indicate that mice localize objects by precisely matching their whisker protraction to expected object positions. This modulation of the motor pattern is anticipatory and does not depend on immediate sensory input. Consequently, tactile information carried by whisker contacts can be read as an error signal that is comparing the anticipated and true object position.

ACKNOWLEDGMENTS

We thank Mira Mehta, Christine Bui, Andrew Platt, and Timothy Vossler for help with data acquisition and review. We also thank Drs. Karel Svoboda, Christopher Moore, and David Kleinfeld for their feedback on a previous version of the manuscript.

REFERENCES


Vincent SB. The function of the vibrissae in the behavior of the white rat. Anim Behav Monogr 1: 845, 1912.
