Tactile object localization by anticipatory whisker motion

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Voigts J, Herman DH, 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.

sensorimotor; barrel cortex; active perception; whisking

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; Deschênes 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 retractions, 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 a 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 protraction 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

- **Whisker base angle**: Vibrissa angle measured at the whisker base (follicle) in the horizontal plane.
- **Vibrissa tip protraction**: Horizontal distance of the whisker tip (located via whisker tracking) relative to the animal’s nose.
- **Target distance**: Horizontal distance of the target platform from the animal’s nose.
- **Virtual whisker tip protraction**: Estimate of the whisker tip protractions 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).
- **Mismatch of virtual tip and target**: 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.

### 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 platform while the animal is permitted on the edge of a second (i.e., home) platform (Celikel and Sakmann 2007; Harris et al. 1999; Hutson and Masterton 1986; Voigts 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 (Voigts 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 Motion-Scope M1) at 1,000 frames/s (fps) with a resolution of $\sim 0.20$ 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 $\sim 5$ mm at a speed of $\sim 13$ 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 $\sim 0.13$ mm/pixel (Pipe 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 Voigts 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 (pre-retraction contacts: trial count, 0:4, 1:13, 2:7, 3:1). Data analysis was carried out with custom software in MATLAB (MathWorks). Whiskers and their contacts with the target platform were tracked as described previously (Voigts 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 (Voigts et al. 2008), and the distance between the nose and the target platform 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 plane of the animal’s face (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.
(Gaussian filter, $\sigma = 25$ ms) as previously described (Voigt 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, $\sigma = 8$ ms) mean whisk angle and aligned to the nearest rostral/caudal set points in the raw unsmoothed trace.

**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. 6, B and C)], we computed the information gain as the Shannon entropy between the distributions:

$$\text{Information gain} = H(\text{base}) - H(\text{test})$$

$$= \sum_{i \in \text{bins}} P(\text{base}) \log_2 P(\text{base}) + \sum_{i \in \text{bins}} P(\text{test}) \log_2 P(\text{test})$$

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 throughout, reported numbers are means ± SD, or medians and interquartile range (iqr) for non-Gaussian data.

**RESULTS**

Using high-speed infrared videography (Voigt et al. 2008), we observed mice ($n = 6, 179$ trials) search for a target platform on the gap-crossing task (Celikel and Sakmann 2007; Harris et al. 1999; Hutson and Masterton 1986; Voigt et al. 2008), using their whiskers. In each trial, the target platform was placed at a randomly selected distance (range: 30, 40,
or unilateral C1 whisker (N = 46), or 60 mm (N = 7.4) C1 whiskers occurred at 4.5 mm whisker contact depended on the gap width: the first contact of 10 mm of the target platform (Fig. 4A1) contacted the target for the first time when the nose was within the distribution with the higher median. The distribution with the lower median is larger than a sample from as AUC that specifies the probability that a sample from the

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target distance (i.e., “target distance”) was quantified as the horizontal span between the nose tip and platform (Fig. 2B). The angle of each whisker was measured at the base of the whisker shaft. C: a polynomial was used to predict a “virtual whisker tip protraction” from the whisker base angle for each whisker. Because contact with the target does not deform the base of whiskers (see Fig. 5 and RESULTS) the position of this “virtual whisker tip” reflects the animal’s motor pattern. D: representative data as a mouse approaches the target platform (see Fig. 3 for more example raw data).

The overall rate of change was 48.5 ± 38.3°/s (slope of linear regression in the same 79 whisker traces). This change in protraction amplitude coincided with a reduction of protraction duration (Fig. 4C). Decreased protraction duration led to an increased whisking frequency (P < 0.05, AUC = 0.29, N = 3.342; Fig. 4E). Retraction duration was also reduced slightly (P = 0.40, AUC = 0.41, N = 3.342; Fig. 4D).

This modulation of the whisking pattern shows that mice reduce the amplitude of their whisker protractions as they approach the target platform, in agreement with previous studies in a variety of other behavioral paradigms (Carvell and Simons 1990; Deutsch et al. 2012; Grant et al. 2009; Mitchinson et al. 2007; Sherman et al. 2013). To study the effect of this modulation on the sensory information carried by whisker contacts, we next examined whether the observed reduction in protraction amplitude was due to whisker deformations or due to a change in the motor pattern.

**Whisking 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

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Fig. 2. Sketch of experimental setup, basic data analysis procedures, and representative data from freely behaving animals during haptic object localization. A: mice were trained on the gap-crossing task to locate a tactile target while standing on an elevated platform. B: whiskers were traced as previously described (Voigts et al. 2008). The angle of each whisker was measured at the base of the whisker shaft. C: a polynomial was used to predict a “virtual whisker tip protraction” from the whisker base angle for each whisker. Because contact with the target does not deform the base of whiskers (see Fig. 5 and RESULTS) the position of this “virtual whisker tip” reflects the animal’s motor pattern. D: representative data as a mouse approaches the target platform (see Fig. 3 for more example raw data). E: the distance between the virtual whisker tip and the target quantifies how well the whisker protraction is matched to the
target distance.

50, 55, and 60 mm). The distance between the animal and the target (i.e., “target distance”) was quantified as the horizontal span between the nose tip and platform (Fig. 2A). To facilitate unsupervised whisker tracking, most whiskers were plucked, sparing bilateral C rows (N = 35 trials), unilateral C row (N = 36), unilateral C1 and C2 (N = 79), or unilateral C1 whisker (N = 29). This whisker deprivation protocol does not affect the kinematics of spared whisker use (Voigts et al. 2008).

Data are reported as means ± SD, and effect size is reported as AUC that specifies the probability that a sample from the distribution with the lower median is larger than a sample from the distribution with the higher median.

**Whisking amplitude is progressively reduced in gap crossing.** We first examined how whisking patterns changed as mice approached and made contact with the target. Whiskers contacted the target for the first time when the nose was within ~10 mm of the target platform (Fig. 4A1). Onset to the first whisker contact depended on the gap width: the first contact of C1 whiskers occurred at 4.5 ± 1.6 mm, 6.9 ± 1.3 mm, or 7.4 ± 2.8 mm when the gap width was 40 (N = 38), 50 (N = 46), or 60 mm (N = 84), respectively. The position of the whisker within the whisker pad, and the target distance, also affected time of whisker contact, with the longer, caudally located whiskers contacting the object at larger distances than shorter, rostral whiskers (Fig. 4A1). As mice approached the target, but before the first contact, they increased their whisker protraction amplitude (Fig. 2B) with an average rate of 1.4 ± 1.2°/mm (r = −0.31 ± 0.23; Fig. 4B; amplitude change between >20 mm and 10 ± 1 mm from object: P < 0.05, N = 485, AUC = 0.246). This increase in whisker protraction during exploration of the space above the gap suggests that the mice expected to find the target platform as they explored the gap.

At distances where the animal made contact with the target, whisker protraction angle decreased as the animal approached the object (r = 0.66 ± 0.23, P < 0.05; Fig. 4B). This modulation was large [the most protracted whisker angles (at rostral set points) had a large range of 27.9 ± 9.1° at −10 to 0 mm distances (corrected for head rotation)] and relatively slow, with a median cycle-to-cycle change of 5.3°/cycle (75% under 9.5°/cycle, analyzed in 235 cycles in 79 whisker traces at distances of 0–10 mm with at least 5 consecutive protractions).
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 $\pm 0.03^\circ$, $N = 30$ protractions). We found the same results when analyzing pairs of whisker protraction in which the target object is suddenly retracted (see Protraction amplitude 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: $-0.04 \pm 1.93^\circ$, $N = 434$).

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 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 (protration 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...
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 \( \text{C1} \), \( r = 0.611 \) for \( \text{C2} \) in \( \text{animal 1} \); 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 \( \text{animal 1} \) (whisker \( \text{C1} \)) and 0.15 mm/mm for all data from whisker \( \text{C1} \) 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 \(-0.75\)–1 mm (\( \text{C1} \) quartiles: 0.101, 0.75, 1.54 mm; \( \text{C2} \): \(-0.12, 0.77, 1.54 \) 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 (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 \( \text{animal 1} \), \( \text{C1} \) 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 \( \text{animal 1} \), \( \text{C1} \) whisker [difference between \(-15 \) mm to \(-10 \) mm (far) and \(-5 \) mm to 0 mm (near); \( \text{AUC} = 0.27, * P < 0.05 \)]. D: whisker retraction duration in respect to distance to the target (\( \text{AUC} = 0.41, P = 0.40 \)). E: whisking frequency increases as animals approach the target. Frequency is computed from the time between caudal set points. (quartiles for: 14.4, 16.9, 18.8 Hz; near: 17.2, 19.2, 22.2 Hz; \( \text{AUC} = 0.29, * P < 0.05 \)). In \( B–E \), box plots depict the quartiles (25%, median, 75%).
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 ± 0.33 bit (P < 0.05, N = 16) vs. 0.71 ± 0.29 bit for only protractions with contacts], although the decrease in SD was no longer significant [0.19 ± 0.67 mm (P = 0.85, N = 16) vs. −0.70 ± 0.32 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 protrusion phase (87% of contacts), with a fraction of touch events happening within ±0.5 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, slope = −0.03/s/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 protrusion 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 for right C1 of animal 3 at 5.5 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. 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 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 receded 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 protractions 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
significantly deform the whisker. In the opposite case, when the whisker protraction barely reaches the target (i.e., the modulated whisk amplitude “underestimates” object location relative to the average whisker deflections), the whisker contact will be a light touch closer in time to the point of maximal protraction (rostral set point). In each case, the time or strength of whisker contact should encode the mismatch between whisking amplitude and target position (Fig. 2E). Similarly, the deflection amplitude and contact velocity could also encode information about the mismatch.

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 “overshot” or “underestimated” 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 \( -0 \)). 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 angle (\( r = -0.20 \pm 0.21, P < 0.05, N = 13 \)). 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 whisks. 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).
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.
position and to compensate for self-motion, using sensory input such as the contact phase as feedback (Fig. 10C). Because the whisking pattern modulation predicts object position (Fig. 6) and does not depend on immediate sensory input (Fig. 8), it can be interpreted as a correlate of a (slowly changing) hypothesis about the egocentric object position. The residual mismatch between the predicted and the true position mechan-ically correlates with contact characteristics such as the phase, which can be read as error signal (Fig. 10) and combined with the prior hypothesis to form an updated, “posterior” hypothesis for target location (Fig. 11B). As the animal approaches the target, it uses its knowledge of self-motion together with the updated estimate of the object position to adjust its expectation of object location and with it refines the modulation of its whisking pattern (Fig. 11B). 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; Kleinfield and Deschenes 2011; Lee et al. 2008)] and the (slowly chang-ing) 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.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: J.V., D.H.H., and T.C. conception and design of research; J.V. and D.H.H. performed experiments; J.V. analyzed data; J.V. and T.C. interpreted results of experiments; J.V. prepared figures; J.V. and T.C. drafted manuscript; J.V. and T.C. edited and revised manuscript; J.V., D.H.H., and T.C. approved final version of manuscript.

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