Review

The mathematical whisker: A review of numerical models of the rat's vibrissa biomechanics

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ABSTRACT

The vibrissal system of the rat refers to specialized hairs the animal uses for tactile sensory perception. Rats actively move their whiskers in a characteristic way called "whisking". Interaction with the environment produces elastic deformation of the whiskers, generating mechanical signals in the whisker–follicle complex. Advances in our understanding of the vibrissal complex biomechanics is of interest not only for the biological research field, but also for biomimetic approaches. The recent development of whisker numerical models has contributed to comprehending its sophisticated movements and its interactions with the follicle. The great diversity of behavioral patterns and complexities of the whisker–follicle ensemble encouraged the creation of many different biomechanical models. This review analyzes most of the whisker biomechanical models that have been developed so far. This review was written so as to render it accessible to readers coming from different research areas.

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1. Introduction

Numerical modelling is an excellent tool to explain the basis and the internal processes of complex mechanisms. When a numerical simulation is able to reproduce the results of real experiments, the scientist can apply it to predict different behaviors in new situations. By using such models, scientists not only can reproduce experimental results but can also predict results not obtainable experimentally because of the lack of appropriate techniques. This idea was already known at the time of Lagrange (circa 1780). However, only after the revolution in computer science, computational numerical modeling became common scientific practice. Biological systems and, specifically the vibrissal system, are examples of complex mechanisms.

The vibrissal sensory system is present in many mammals but is especially developed in rodents and particularly in rats (Prescott et al., 2011). Rats depend on the sensory input from their whiskers as primates depend on visual input (Krubitzer et al., 2011). Spatial orientation, localization, food discrimination and even social behavior such as courting or fighting, are some of the tasks rats can do with this sophisticated system (Carvell and Simons, 1990). Many scientists from biology, bioengineering, biomechanics and mathematics have focused their attention on trying to understand the way this sensorial system works, for different purposes. Some teams have studied internal processes by analyzing the whisker, the follicle, the mystacial pad and the neuronal circuits (i.e. Maravall and Diamond, 2014). Scientists close to bioengineering have directed their attention to the development of biomimetic devices (i.e. Prescott et al., 2009). They use this system to run applications such as object detection in robotics or enhancement of human haptic sensory systems, just to name a few.

The mechanical signals are generated from the body of the whisker to the follicle.. These signals will be later transduced by mechanoreceptors. The rat actively moves the whisker, which is deformed elastically by interactions with the environment. It gets stuck and released with a complex inertial behavior which includes velocity and acceleration profiles as well as rotation about different axes. In addition, the follicle is oblong and has different and varied structures and mechanoreceptors at different levels (Rice et al., 1993). The shape of the follicle suggests that more than one mechanical variable of the whisker is codified by the vibrissal system per each vibrissa (Mitchinson et al., 2004).

Computational models predicting certain aspects of the vibrissal system behavior appeared at the beginning of the XXIst century thanks to four facts: (i) Mathematical tools of mechanical modeling and computational neuroscience reached sufficient levels of maturity for use by the end of the XXth c. (ii) Computer systems evolved in a way that made it possible for personal computers to be used to process models in a matter of hours or minutes at low cost. (iii) Technological advances allowed events to be recorded in time and space according to the vibrissal system information processing. For example, high-speed cameras or single-unit recordings allowed the validation of the models. (iv) Great advances in vibrissal system physiology occurred at the end of the 1990s.

In order to understand how the whisker-follicle complex works, many mechanical models were published in scientific journals; these models differed not only in their conception but also in their objectives. This review aims to analyze most of the biomechanical models of the whisker that have been developed so far. It has been conceived from a general point of view in order to be accessible to readers coming from different research areas.

1.1. The input of the vibrissal system

The rat, as many mammals, has a sensory system of specialized hairs called vibrissae. They are arranged in an organized facial structure, called the mystacial pad (Dorfl, 1985). The distribution pattern is genetically determined for each species (Van Der Loos et al., 1984). In the rat, it consists of five horizontal and one vertical lines (caudal to the horizontal rows) on both sides of the snout, which makes about 30 macro-vibrissae (Fig. 1A) (Albarracín et al., 2006).

The characteristic movements of the vibrissae or "whisking" are part of the rat's "sniffing behavior" (Welker, 1964). The whiskers are often actively swept back and forth at high speeds (5–25 times/s) (Prescott et al., 2009). The animal coordinates head, nose and vibrissae movements and uses this exploratory behavior to gather information about object features in the environment such as location, shape, texture and size (Albarracín et al., 2006; Boubenec et al., 2012; Vincent, 1912).

The whisker's shape is practically a linear truncated cone with a tapered tip and a circular cross section with a hollow medulla near the base (Carl et al., 2012; Quist et al., 2011). In adult rats, the typical length varies approximately from 10 to 50 mm (Haidarliu and Ahissar, 2001) and depends on the location in the mystacial pad; the shortest are localized at the rostral part of the snout. Diameters range between 20 and 50 μm at the base of the whisker and about 5 μm at the tip (Pearson et al., 2007). Also, it has an intrinsic curvature which fits a quadratic function (Knutsen et al., 2008). Between 50 and 70% of the whisker lies in a single plane and the out-of-plane curvature increases towards the tip, but this out-of-plane curvature is relatively small compared to the typical length of a whisker (Towal et al., 2011). The vibrissa has three layers: (1) internal, the medulla, which is mostly hollow (Carl et al., 2012); (2) middle, the cortex; and (3) external, the cuticle (Fig. 1B). The medulla tapers from base to tip and disappears in the distal half of the vibrissa; the cuticle decreases in thickness from the base to the distal third, and is constant near the tip (Quist et al., 2011). The cuticle consists of flat scales with the free end pointing in the distal direction. The scales are set in an irregular pattern, which is the same in all of the whisker parts. However, the size of the scales does vary in different parts (Voges et al., 2012). The whisker has an inhomogeneous structure that produces different levels of elasticity in different sections, as reflected in Young's modulus. In a longitudinal analysis of the whisker, the average modulus is approximately 4 GPa at the base section and approximately 3 GPa at the tip (Quist et al., 2011). Radially, the cuticle, the cortex, and the medulla, have on average ∼3.6 GPa, ∼4.8 GPa and ∼4 GPa respectively, the cuticle being the most variable (Adineh et al., 2015).

Each vibrissa is anchored in a complex structure called the follicle–sinus complex (FSC) (Rice et al., 1986). The follicle is composed of two concentric layers, the internal root sheath, next to the hair shaft, and the external root sheath surrounded by the glassy membrane (Fig. 1C) (Rice et al., 1993). The follicle is surrounded by a blood sinus and an outer collagenous capsule (Kim et al., 2011). The FSC complex is embraced by the vibrissal capsular muscle, which originates on the facial muscles, thereby enabling voluntary movement (Kim et al., 2011). The whisker movement exerts pressure both in the blood sinus and in the multilayers of tissue, producing the activation of the different mechanoreceptors distributed around the follicle (Ebara et al., 2002; Mosconi et al., 1993; Rice et al., 1997). All these physical properties of the FSC and other related ones, like resonance and damping, will be among the critical determinants of the signals generated when a whisker contacts a surface (Prescott et al., 2009).

Over the last few years several scientific teams have studied the mechanical behavior of the whiskers (e.g. Quist and Hartmann, 2012),
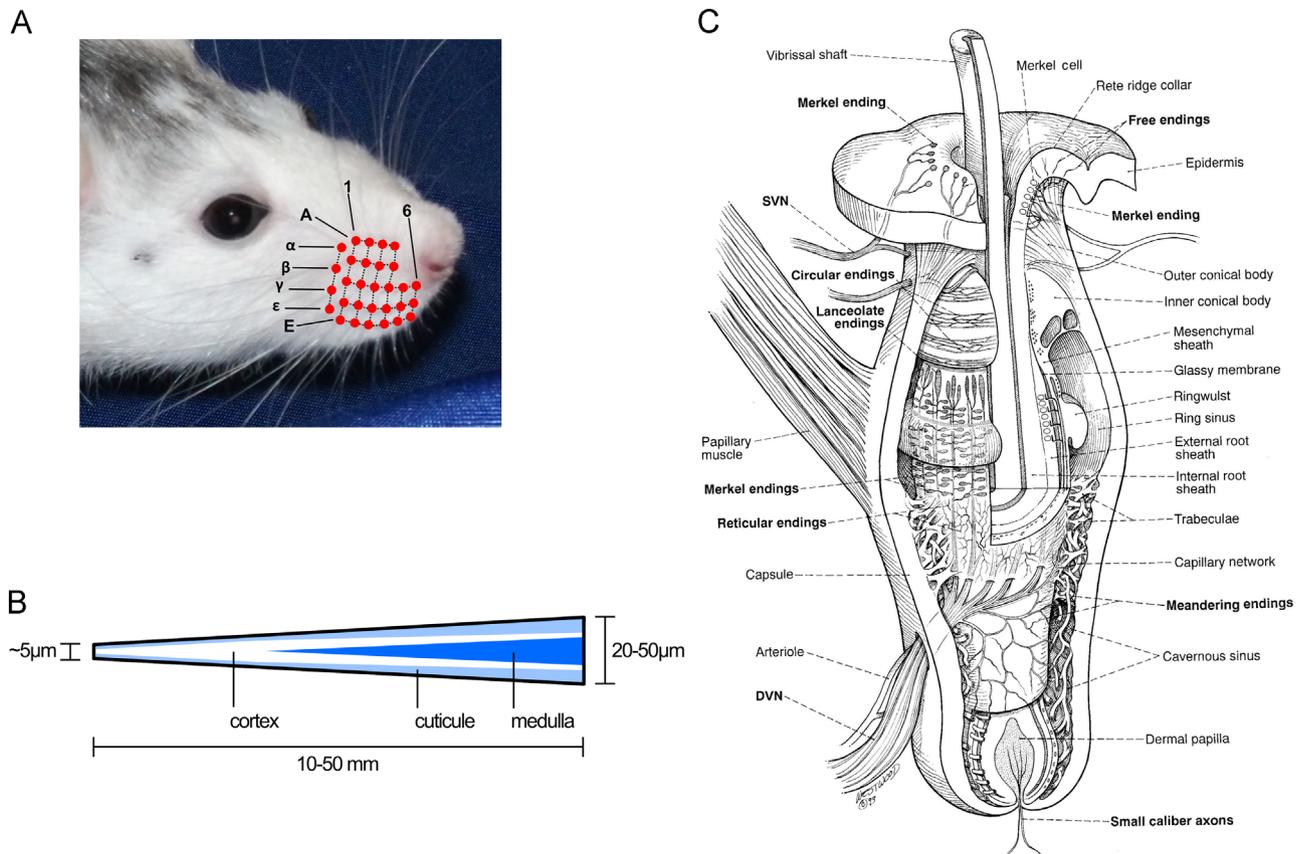
Fig. 1. (A) Mystacial pad: **s**tructure that contains the follicles, which are placed at both sides of the rat's snout. In the rat, this pad consists of approximately 30 follicles with five horizontal lines and a vertical line. Vibrissae are identified by positional coordinates. (B) Scheme of the internal structure of the whisker with typical geometrical measures. Three inner layers, i.e. medulla, cortex and cuticle (not to scale). (C) Internal structure of the follicle–sinus-complex. This diagram presents the number of layers and structures of the FSC. The highlighted ones are the muscles in the external part of the FSC, which allow the rat to make the characteristic whisking; the blood sinuses (cavernous sinus and ring sinus) enclosed by multiple layers of connective tissue; and the large amount and variety of receptors placed at different heights (Circular endings, free endings, lanceolate endings, among others). Figure reproduced with copyright permission from Rice et al. (1993) obtained from John Wiley and Sons.
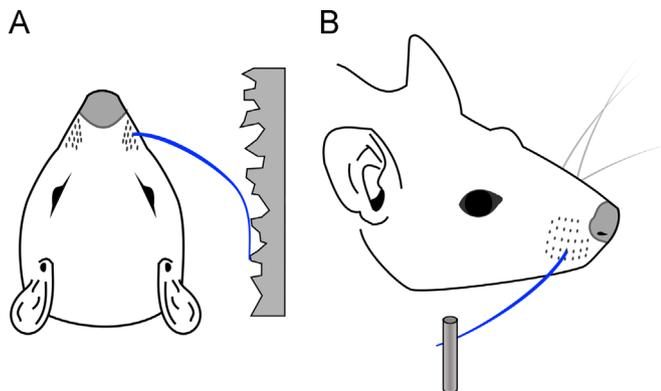
Fig. 2. Typical behavioral test of the rat using one whisker. (A) Texture Perception. The rat makes one or more sweeping movements over a rough surface. The dynamic behavior of the shape of the whisker is observed. (B) Object localization. The rat moves its whisker and, in its cycle, it encounters a peg. Once contacted is done, the change in form of the whisker and the moments and forces generated at the base are observed.

the transduction mechanisms (e.g. Mitchinson et al., 2008), neural responses at peripheral level (e.g. Pizá et al., 2014) or at higher levels (e.g. Garion et al., 2014) in the vibrissal system. These approaches consider two different tasks that rats perform by using their vibrissae. One is texture perception (Fig. 2A). There are three hypotheses regarding the mechanical signal codification of the whisker: (i) the mean speed theory, where the parameter codified by the vibrissal system is the mean speed of the surface-induced vibrations of the vibrissa (Jadhav and Feldman, 2010); (ii) the differential resonance theory, which postulates a multi-vibrissal codification where the texture is codified by the relative amplitude of sustained vibrations across the different whiskers in a row (Andermann et al., 2004); and (iii) the slip–stick theory, also known as the kinetic signature theory (Arabzadeh et al., 2009). This is the most accepted hypothesis; it states that the trajectory of the whisker on a surface is characterized by an irregular skipping motion made up of intermixed low and high velocities, called stick/slip events (Diamond, 2010; Diamond and Arabzadeh, 2013). Discrimination occurs because each texture is associated with a distinct trajectory of sticks and slips and the coarser the texture, the greater the rate or magnitude of slip-stick events (Arabzadeh et al., 2009; Diamond, 2010; Diamond and Arabzadeh, 2013). It should be noted that some experiments have suggested other kinematic parameters, besides the slip-stick events, associated with the identification of textures (Maravall and Diamond, 2014; Zuo et al., 2011). The rat with a single vibrissa can relatively accurately discriminate different surfaces (Diamond, 2010) but when it uses more than one, its discrimination is more accurate (Morita et al., 2011). Another important task that rats perform is the objects' localization in a 3D space (Fig. 2B). There is currently no consensus on this topic, even though there have been proposals on how the vibrissal system carries out this task (e.g. Ahissar and Knutsen, 2008). The main concern about object detection is related to the dependences of the sweeps on motor patterns (Sherman et al., 2013). It has recently been found, that the whisking motor patterns are anticipatory more than a reaction to an object contact; the whiskers make contact with the object at the end of the whisking cycle and with minimal deformation. Evidence has been found that the rat codifies the objects'

location by means of whisking pattern modulations with the sensory inputs working as feedback in a control system that uses the difference between the real and the expected location of the object (Voigts et al., 2014). Rats can accurately localize objects along the horizontal axis with just a single whisker (Ahissar and Knutsen, 2008; Knutsen et al., 2006; Mehta et al., 2007). However, it was observed that radial object localization with a single whisker presents a challenge for mice, suggesting that under natural conditions, they tend to rely on signals from multiple whiskers (Pammer et al., 2013).

2. Numerical modelling of the whisker–FSC complex

The signals transduced in the FSC are inherently mechanical. The whisker is a beam with a particular shape that is deformed by the interaction with the environment and the oscillatory movement on its base. Therefore, modelling has been developed by using the mathematical tools of Structural Engineering. The mechanical complexity of the whisker–follicle complex requires mathematical models that can accurately represent the biomechanics of the whisker movement, as well as the existing electrophysiological observations. Such models should also contemplate the different behavioral strategies that rats use to solve different tasks, such as morphological object recognition or discrimination of textural surfaces. The ideal model would take into account all these details. It would also facilitate testing of the different hypotheses under consideration or any new hypothesis about the biomechanics or transduction mechanisms of the whisker–follicle complex. But it is not necessary for a model to be so complex; in fact, a simpler model (e.g. linear equations, in 2D space with simple boundary conditions) may produce results that could be easily implemented. Then, it would be possible to refine the model with more complex mathematical structures.

As mentioned by Behn et al. (2013), two kinds of models have been used to analyze the mechanical behavior of the vibrissa: rigid body models (RBM) and continuum models (CM). In the framework of RBM, the component bodies do not suffer deformation. The pieces are attached with springs–dampers and the deformation is measured as the relative position of the different bodies. On the other hand, CM evaluate in every infinitesimal part of the continuum. Examples of RBM are those developed by Huet et al. (2015); Quist et al. (2014); Behn et al. (2013); Quist and Hartmann (2012); Solomon and Hartmann (2011); Hill et al. (2008); Birdwell et al. (2007); Solomon and Hartmann (2006); Berg and Kleinfeld (2003). Among examples of CM are the publications of Boubenec et al. (2014, 2012); Hires et al. (2013); Bagdasarian et al. (2013); Pammer et al. (2013); Yan et al. (2013); Towal et al. (2011); Williams and Kramer (2010); Kim and Möller (2007); Clements and Rahn (2006); Scholz and Rahn (2004); Neimark et al. (2003).

2.1. Continuum models

2.1.1. Neimark et al. (2003)

The paper by Neimark et al. (2003) was one of the first published numerical models of the whisker. The authors proposed one fundamental hypothesis about texture perception, called "differential resonance theory" (as it was called by Jadhav and Feldman (2010)), which relates the resonant frequency to the whisker length. Whiskers were represented as thin elastic beams in a 2D space, assuming a conical shape and linear damping. The differential equation that governs this problem was obtained by equating the shear and the bending moments; and it was solved using separation of variables (Weaver et al., 1990). The solution (vertical displacement in terms of horizontal position and time) was computed as a sum of spatial modes.

The outstanding contribution of this paper was that the authors provided the first proposal for the mechanism of tactile sensory encoding. Further significant progress was achieved on vibrissa resonance and psychophysical capabilities. The relevance of these biomechanical observations was demonstrated by experimental tests, which showed that vibrissae resonance is transduced into neural activity.

2.1.2. Yan et al. (2013)

Yan et al. presented a model in 2013 to analyze the vibration frequency of rat whiskers. They used the Bernoulli–Euler beam theory and model the whisker as a truncated cone with a circular cross-section. The radius of the beam cross-section varies linearly along the axial direction, i.e., the x-direction. They did not consider the intrinsic curvature and damping effects. Also, the rat whisker material was assumed as isotropic and homogenous, in other words, density and Young's modulus were both constant. They added at both ends translational springs and rotational springs to constrain the transverse deflection and the angular movement, respectively. They considered that in this form the attachment of the vibrissa to the follicle is more accurately represented than when fixed (as was used by Neimark et al. (2003)). For the tip, the stiffness constants of the springs allow simulating different cases, like free vibration in the air or touching an object. For the different model parameters such as length, density, etc. of the vibrissa, they used means of different vibrissae measures from Neimark et al. (2003). They analytically solved the equation using Bessel functions (Conway et al., 1964) in a generic form. As the solution is generic, they could simulate two kinds of situations: freely whisking in air and with the tip making contact with and sticking an object; without having to obtain a new solution for each boundary condition.

2.1.3. Boubenec et al. (2014, 2012)

In 2012, Boubenec et al. developed one of the first numerical models including inertial dynamic behavior of the whisker. The authors analyzed the case of the vibrissae sweeping through a rectangular obstacle and later, in 2014, they included the interaction with textures. They combined the use of micropatterned substrates with high-resolution videography during tactile exploration to study how texture information is mechanically encoded in the whisker motion. This study was aimed at providing a comprehensive description of the process of texture transduction during tactile exploration in whisking rodents, from the whisker tip to the somatosensory cortex.

The vibrissa was modeled as a slender tapered rod with non-intrinsic curvature, linearly elastic with a uniform Young's modulus and uniform density. The whisker profile is described using curvilinear coordinates, defined as the normalized arc length of the non-truncated whisker (Fig. 3A). The anchorage at the base was assumed to be strictly rigid, while the whisking process was modeled by imposing a rotation around the base at a constant rate. When the whisker contacts an object or texture, it supports a frictional force applied to a single point. The imposed constraints are tangent to the object surface. The orientation of the force with respect to the normal direction of the whisker at the contact point is set by the friction angle, depending on the friction coefficient. The whisker dynamics are divided into two superimposed parts: (i) the movement in rapid small-amplitude resonant oscillations and (ii) a slow sequence of deformation called a quasi-static sequence. The oscillating term was also decomposed into a series of resonant modes with spatial and temporal properties.

Regarding numerical aspects, the differential equations of quasi-static movement were computed and whisker stationary profiles for given values of the base and friction angles were obtained. The quasi-static movement sequence is expected to be
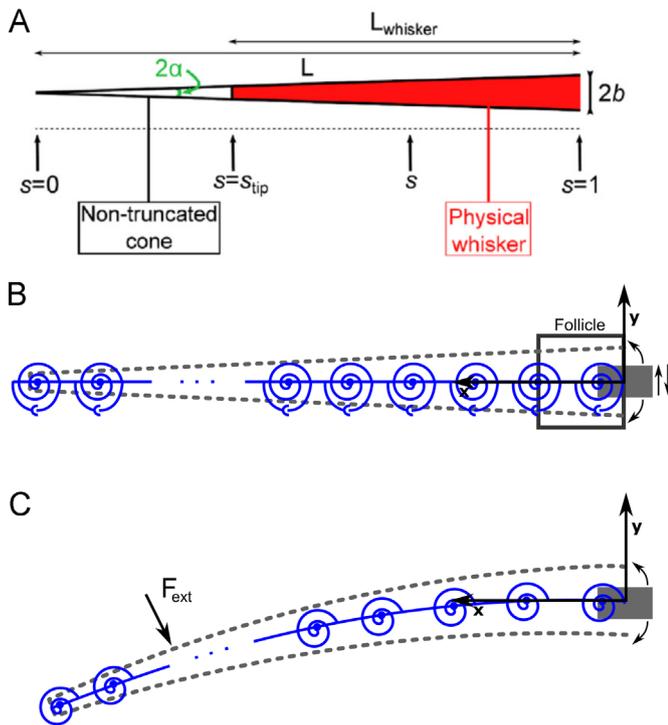
Fig. 3. Schematic visualizations of different whisker models (not to scale). (A) Boubenec et al. (2014, 2012). The vibrissa has been modeled as a slender taper rod. The reference system used here has as its origin what should be the tip of the cone if it were not truncated. Figure reproduced from Boubenec et al. (2012) licensed under Creative Commons Attribution licence (CC-BY 3.0). (B) Quist et al. (2014). The model is composed of links with nodes formed by torsional springs and torsional dampers in blue. The first link is rigidly controlled and it represents the part of the whisker that is inside the follicle. The reaction forces and moment are measured in the first link and the change of shape is measured as the angle between the different nodes. (C) Huet et al. (2015). It is very similar to the model by Quist et al. (2014), but it is in 3D and with an intrinsic curvature. It is here simplified.

valid only for a massless whisker or at infinitely slow scanning speeds; however, inertia effects will induce significant deviations. The fast dynamic movement was modeled as a small displacement, normal to the quasi-static profile sequence. Using the limitation of small approximation, the authors modeled the dynamic contribution using the classical Euler–Bernoulli equation (Gere and Timoshenko, 1990) that governs the equilibrium problem. The solution of this equation gives a sum of eigenmodes regarding the whisker clamped at the base and pinned at the contact point. Each mode is associated with a resonant angular frequency; and the sum gives the oscillation of the whisker.

2.2. Rigid body models

2.2.1. Quist et al. (2014)

Quist et al. developed in 2014 a vibrissa model with a general dynamic behavior. It includes the effects of inertia, damping and collisions. With the authors' assumption that trigeminal ganglion neurons are sensitive to several force and moment combinations at the vibrissal base, the model generates a set of predictions of those mechanical variables.

The vibrissa has been modeled as a series of rigid links in a 2D space without intrinsic curvature, with a linear variable Young's modulus (based on Quist et al. (2011)), and with uniform density, using the discrete method of Lagrange (Johnson and Murphey, 2009). Each link consists of a conical frustum, modeled as a point mass at the mass center of the link. The joints between links were defined as nodes, containing a torsional spring and a torsional damper (Fig. 3B). The first link represents the part of the vibrissa

rigidly supported inside the follicle. The assessment of the model parameters, i.e. masses, springs, and dampers, was based on a D1 vibrissa by Hartmann et al. (2003). The vibrissa movements are described by a generalized coordinate composed of the linear translation at the *y*-axis and the angles between two links.

First, the smooth trajectory of the rat vibrissae in free air without collisions was modelled; in this case, using continuous Lagrangian mechanics. When the collisions were incorporated, the Euler–Lagrange equation could not be solved because the assumption of smooth trajectories was broken. Therefore, a discrete Euler–Lagrange equation of the system was obtained using discrete Lagrangian mechanics. To include the collision surface, the authors defined a function of the system state that included the boundary of the objects. Two algorithms were specially designed to solve these equations. The first was applied to the free dynamics of the vibrissa, in order to find the time when the collision occurred. The second consists in a discrete three time step procedure, to find (i) the energy of the collision, (ii) the constraint force required to prevent the vibrissa from penetrating the object surface, and (iii) to compute the configuration of the system. Following this procedure, the solution for different kinds of collisions can be obtained: elastic, inelastic, or any intermediate type.

The model allows the quantification of time-dependent forces and moments at the vibrissa base during non-contact ("free-air") whisking and when the vibrissa taps against an object ("collisions"). With these results, the authors deduced implications for the rat's exploratory behavior.

2.2.2. Huet et al. (2015)

This is the most recent publication by a scientific work team (Huet et al., 2015; Quist and Hartmann, 2012; Solomon and Hartmann, 2006, 2011; Birdwell et al., 2007) about quasi-static models that study the relationship between the bending of the vibrissa and the forces and moments at the base. Huet et al. (2015) quantified the variation in the vibrissa curvature in the case of slow collision against a peg in a 3D space.

The authors modelled the vibrissa as a series of rigid links connected by nodes. The motion of each of these nodes is constrained by rotational springs (Fig. 3D). They assumed that the total force applied always acts normal to the vibrissa, which means that there is no friction. The vibrissa is modeled with its intrinsic curvature, just as it was described by Knutsen et al. (2008). As model parameters, they used typical geometrical values by Hires et al. (2013) and Williams and Kramer (2010), constant Young's modulus obtained from Quist et al. (2011) and Poisson's ratio from Etnier (2003).

To validate the model, the authors tracked the whisker motion as it hits a peg, using 3D video recordings. During this process the rat's body movements were restrained except for those of the head. In each video frame, the shape of the experimentally measured whisker was compared with the shape of the one modeled. If the shapes coincided, then the forces and moments were correctly determined. This corresponds to an indirect validation, since it is not possible to measure in-vivo the forces and moments at the base of the vibrissa.

3. Discussion

This review documents the numerical models that several scientific teams have developed so far to understand the biomechanical events that occur in the whisker. Table 1 summarizes the characteristics of the revised models.

Table 1
Principal characteristics of the models analyzed in this review.

Model	Type	Objective	Theory	Brief description
Neimark et al. (2003)	CM[a]	Texture information	Bernoulli–Euler beam theory	A thin elastic beam with conical beam shape. Linear damping. Linear density. Constant Young's modulus. Small displacements.
Yan et al. (2013)	CM	Vibrational behavior of the whisker	Bernoulli–Euler beam theory	A circular cross-section truncated-cone with non-intrinsic curvature. Small displacements. No damping, Linear density. Constant Young's modulus.
Boubenec et al. (2014, 2012)	CM	Mechanical behavior of the whisker	Bernoulli–Euler beam theory	A truncated cone with circular cross-section with non-intrinsic curvature. Uniform density and Young's modulus. Small displacements. Linear damping.
Quist et al. (2014)	RBM[b]	Mechanical behavior of the whisker	Discrete Lagrangian mechanics	A series of rigid links connected by torsional springs and torsional damper with non-intrinsic curvature. Large displacements. Linearly variable Young's modulus.
Huet et al. (2015)	RBM	Object localization	Bernoulli–Euler beam theory	Series of rigid links connected by torsional springs with quadratic intrinsic curvature in a 3D space. Small displacements. No friction. Constant Young's modulus and constant Poisson's ratio.

[a] CM stands for continuum model.
[b] RBM stands for rigid body model.

3.1. Vibrating the whisker

Understanding the vibrating nature of the whiskers is crucial to comprehend their behavior in object localization, particularly when colliding, as well as during exploration and texture discrimination. The publications by Neimark et al. (2003) and Yan et al. (2013) analyzed the frequency responses of the whiskers. Both papers, together with those by Adineh et al. (2015); Quist et al. (2014); Boubenec et al. (2012) and Williams and Kramer (2010), subjected their models to vibrational tests and observed their frequency responses. All these publications present results that are within the set of tests with real vibrissae, but they do not coincide. This is mainly due to the simplifications assumed by each model.

Particularly, Yan et al. (2013) made a thorough analysis of the vibrating nature of the whiskers. They found that natural frequency not only depends on the geometrical and material characteristics of the whisker, but also on the boundary conditions (fixed-free, fixed-fixed, etc.). Yan et al. indicated that the animal could modify the natural frequency as a strategy when exploring the environment, mainly modifying the rotational constraints of the base. So far, there are neither behavioral nor physiological works showing evidence that the rat controls the anchoring of the whisker.

3.2. Object localization

Quasi-static models are used mainly for the biomechanical analysis of object location. We regard quasi-static models as those in which the movement is infinitesimally slow or the whisker has no mass (Boubenec et al., 2012). As was proved by Boubenec et al. (2012) and Quist et al. (2014), the inertial phenomena due to the vibrissa mass is relevant only during the collision with an object. After the collision, whisker bending can be analyzed using quasi-static models.

Quasi-static models are the most common in the literature, mainly because of the large amount of works developed by one scientific team, the latest of which was Huet et al. (2015). They started with a single vibrissa model in 2D space without curvature for the case of small displacements (Solomon and Hartmann, 2006), that later extended to 3D space with inherent curvature and large displacements (Huet et al., 2015). The main characteristic that renders these models easily identifiable with respect to the others is that the vibrissa is simplified into a series of links connected by nodes. This simplification may seem excessive, but its excellent results in quasi-static models as in dynamic ones (Quist

et al., 2014) demonstrate that it is a convenient and easy-to-use approach. Among other quasi-static models, those by Bagdasarian et al. (2013); Hires et al. (2013); Pammer et al. (2013) and Williams and Kramer (2010) must be mentioned. These are continuous models which share similar simplifications, namely, constant Young's modulus, the whisker as a 2D truncated cone, and small displacements.

All these models have simulations, from simple experiments such as one in which the whisker is attached to a galvanometer and makes contact with a peg (Quist and Hartmann, 2012) to complex ones such as making the rat contact a peg with its whisker (Huet et al., 2015). They have focused on the relationship between the change in the whisker's curvature and the forces and moments generated at the base. Some papers have also included the rate of change of these variables (Huet et al., 2015; Birdwell et al., 2007).

Dynamic models must be used in order to analyze the fast-dynamic phenomena produced by the collision between an object and the whisker in the object localization task, just as it was done in the publications by Boubenec et al. (2012) and Quist et al. (2014). It is found in these works that the collision with the whisker is inelastic. That is, the whisker does not bounce against the object. Boubenec et al. (2012) found that just as the collision happens, a shock wave travels axially trough the whisker. This shock wave leaves a "characteristic frequential signature" at the base of the whisker (Hartmann, 2016). The magnitude of the signature depends on the speed at which the whisker rotates. However, it is small compared with much larger, but slower, components dominated by the effects of whisker bending and deceleration (Hartmann, 2016). Quist et al. (2014) found that these components do not depend on whisking speed. Immediately after the collision, Quist et al. (2014) found that the dynamic effects are often negligible compared to the static effects. Because of this, they conclude that for the analysis of object location tasks, quasi-static models provide a good approximation, but in certain cases (i.e. for certain values of rotation angles) the contribution due to dynamic phenomena reaches the values of the quasi-static order. To summarize, a dynamic model would be necessary if a complete analysis of the biomechanics of the whisker in the object localization paradigm has to be done.

The paper by Huet et al. (2015) showed the importance of using 3D models in this behavioral task. They proved that in the same experiment, a 2D model- that works in a single plane- is not able to analyze the forces and moments at the base that occur out of this plane. Besides this, the 3D model includes a "twisting" moment, which is missing in the 2D analysis. However, the

remaining variables in a 3D model are very similar to the ones obtained in the 2D model. Another advantage of 3D models is that they considerably increase the number of experimental situations of whisker collision with an object. The 3D models can include all the types of collision analyzed in Quist and Hartmann (2012).

The latest behavioral experiments in object localization have questioned the relationship between the whisking motor patterns and object contact (i.e. Voigts et al., 2014); in these cases the whisker suffers little deformation. These experiments might show that the collision plays an important role, in which the "characteristic signature" observed by Boubenec et al. (2012) might be the cue the animal uses to detect the contact. It would be interesting to see a complete biomechanical analysis of this situation described by numerical modeling.

3.3. Texture perception

Boubenec et al. (2014) and Neimark et al. (2003) are the only papers that have proposed models for texture analysis. However, Neimark et al. (2003) only analyzed the resonance frequency of the whisker when it sweeps sandpaper of different roughness, while Boubenec et al. (2014) present a more thorough analysis of the whisker, analyzing a complete scenario of whisker motion when it sweeps micropatterned substrates.

The mode decomposition of the fast-dynamic part used by Boubenec et al. (2014) allowed them to separate the spatial and temporal components of the texture-induced whisker kinetics. Thanks to this, they could analyze the behavior of the different harmonics of the vibrissal kinematic, and found that fine textural features are mechanically encoded by the whiskers through a vibratory amplitude modulation scheme. Boubenec et al. (2014) provide details of this modulation scheme. They found that the scanning speed does not play an important role in textural analysis, while the angle between the vibrissa and the surface considerably affects the harmonic components of the vibration. Also, they found that the distance between the base of the whisker and the surface weakly impacts first-mode resonance frequency. This may ensure texture profile transduction to be robust to changes in sampling condition while an animal is palpating a surface.

The team of Boubenec et al. (2014) has claimed that their model has two simplifications that limit its use to situations in which these are valid. One is to assume small displacements and the other is not to include the intrinsic curvature of the whisker. They are improving their model to solve these limitations. The authors also note that it would be necessary to use 3D models if the goal is to analyze torsion around its axis, because it results in different circumferential pressure profiles on the follicle (Boubenec et al., 2014). To this, we add that to model a vibrissa sweeping an irregular rough surface (i.e. sandpaper), the section of the whisker that contacts the surface would not necessarily follow a straight line that is within the plane of the whisker's sweeping. The whisker could take an irregular path that offers less resistance, and this could make the whisker suffer torsion and be partially out of the plane of the sweep. Modeling this would require the use of 3D models since 2D ones are unable to simulate movements outside the plane. Nevertheless, as models about texture analysis are developed, shortly it will become clear when they are sufficiently refined.

Conflict of interest statement

The authors have no conflict of interest regarding the material discussed in this manuscript.

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