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Sniffing and whisking in rodents

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Sniffing and whisking are two rhythmic orofacial motor activities that enable rodents to localize and track objects in their environment. They have related temporal dynamics, possibly as a result of both shared musculature and shared sensory tasks. Sniffing and whisking also constitute the overt expression of an animal's anticipation of a reward. Yet, the neuronal mechanisms that underlie the control of these behaviors have not been established. Here, we review the similarities between sniffing and whisking and suggest that such similarities indicate a mechanistic link between these two rhythmic exploratory behaviors.

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Introduction

When one observes rodents introduced in a new environment, one immediately notices that they are extremely curious [1]. They run about, stand up on their hind legs, crane their necks forward, and repeatedly explore the whole environment by sniffing and whisking vigorously. Psychologists have described curiosity as a drive like hunger and thirst, which implies that gathering information is rewarding. In experimental studies, sniffing and whisking are commonly considered as motor strategies for rapidly gathering detailed information about the location, texture, and scent of objects. Yet, it is intriguing that decorticated rats, or rats deprived of olfactory and vibrissa afferents, continue to sniff and whisk in a relatively normal manner. Therefore, beyond the obvious intuition that vibrissae are 'for touch' and noses 'for smell', it is not clear why rhythmic activity is associated with the use of these sensors. Here, we examine the dynamics of rhythmic sniffing and whisking, and how

they shape olfactory and tactile sensations in rodents. We place special emphasis on the behavioral significance of the apparent coordination of these patterned activities.

A link between sniffing and whisking

In a now classic paper published in 1964, Welker [2] provided the first descriptive account of the sniffing behavior in rats. Using cinematographic technique, he reported that sniffing consists of an integrated movement sequence involving: (1) bursts of polypnea, (2) recurrent protraction and retraction of mystacial vibrissae, (3) repetitive retraction and protraction of the tip of the snout, and (4) a rapid series of head movements and fixations. These four components occur at rates between 5 and 11 Hz, in bursts of various durations, and "exhibit a fixed temporal relationship to one another" (Figure 1b). Welker further made the little noticed remark that "Polypnea and nose movements together may occur independently of vibrissae and head movements, but rapid vibrissae or head movements were never observed to occur independently of polypnea and nose movements". In short, Welker noted that whisking was always coupled to sniffing. This temporal relationship is illustrated in Figure 1c,d, where whisking and sniffing were recorded as a rat explores the exit of a tunnel (Figure 1a).

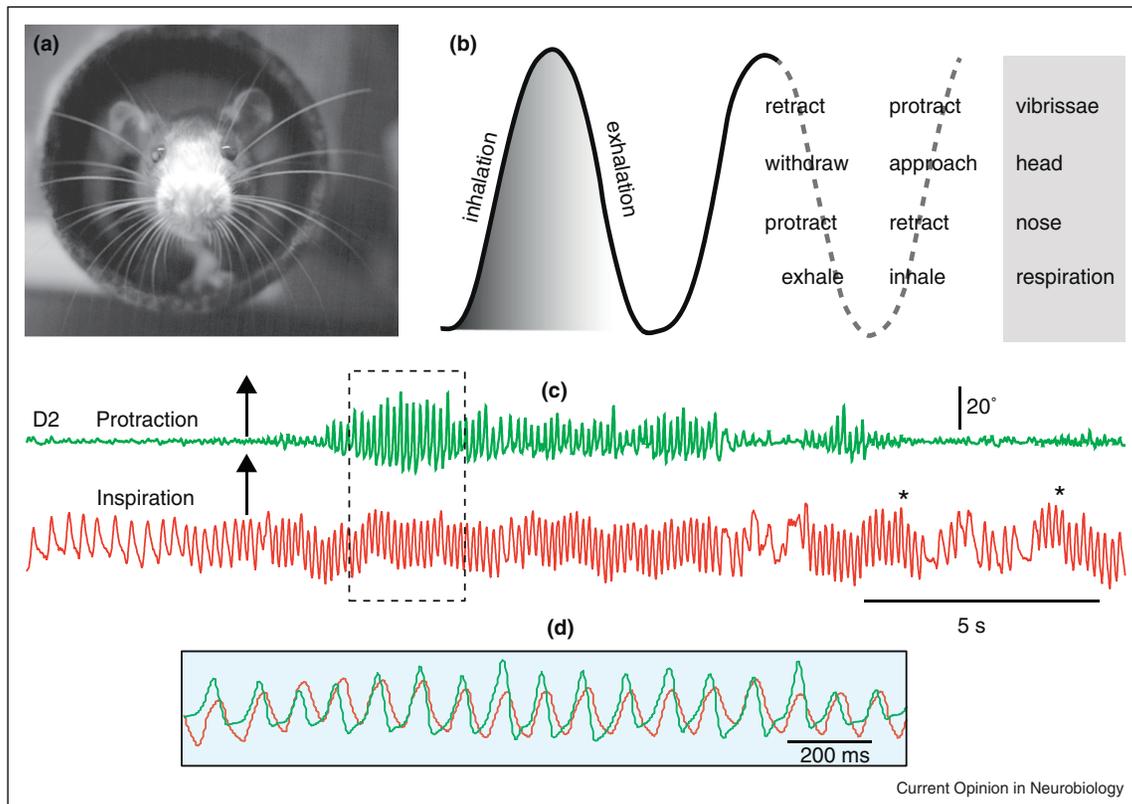
Welker's seminal observations did not raise immediate interest in the sensorimotor community as the rodent vibrissa (barrel) cortex had yet to be discovered [3], and most sensorimotor work at that time was focused on primates. Later studies in the field of respiratory physiology alluded to Welker's findings in reporting instances of facial nerve, muscle, or motoneuron activity that were time-locked to different phases of the respiratory cycle [4–6]. Interestingly, the nasolabial muscle, which contributes to flare of the naris during sniffing, also acts as a retractor muscle during whisking [7,8]. This dual role suggests an obligate neuromuscular coupling between whisking and sniffing that requires coordinated control to ensure that these behaviors do not interfere with each other.

Rhythmogenesis of sniffing and whisking

Sniffing in rats is usually defined as rapid, rhythmic respiration [2,9]. Rats, unlike humans, always breathe nasally, so lower frequencies (1–3 Hz) correspond to basal respiration while higher frequencies (4–12 Hz) correspond to 'sniffing' *per se*. Although rats and mice are commonly used in studies of respiratory rhythmogenesis, the neural mechanisms underlying the generation of sniffing remain unknown. One possibility is that sniffing relies on an increased rate of bursts in the central pattern

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Figure 1



Co-occurrence of sniffing and whisking in rodents. **(a)** Photograph of a rat whisking at the exit of a tunnel. Image was obtained in the dark under near infrared illumination. **(b)** Sniff and whisk cycles are coordinated with nose and head movements. Adapted from Welker [2]. **(c)** Whisking occurs in phase with sniffing, but sniffing can occur without whisking; asterisks denote sniffing bouts without whisking. Overlapping traces in **(d)** show the framed area in **(c)**. The motion of vibrissa D2 was monitored by high-speed videography (250 frames per second), and sniffing was recorded by means of a thermocouple implanted in the nasal cavity (unpublished data).

generator (CPG) that controls breathing, for example, the Böttinger/pre-Böttinger complex and the parafacial group [10,11]. Yet, a mechanism for generating rhythmic sniffing remains to be demonstrated.

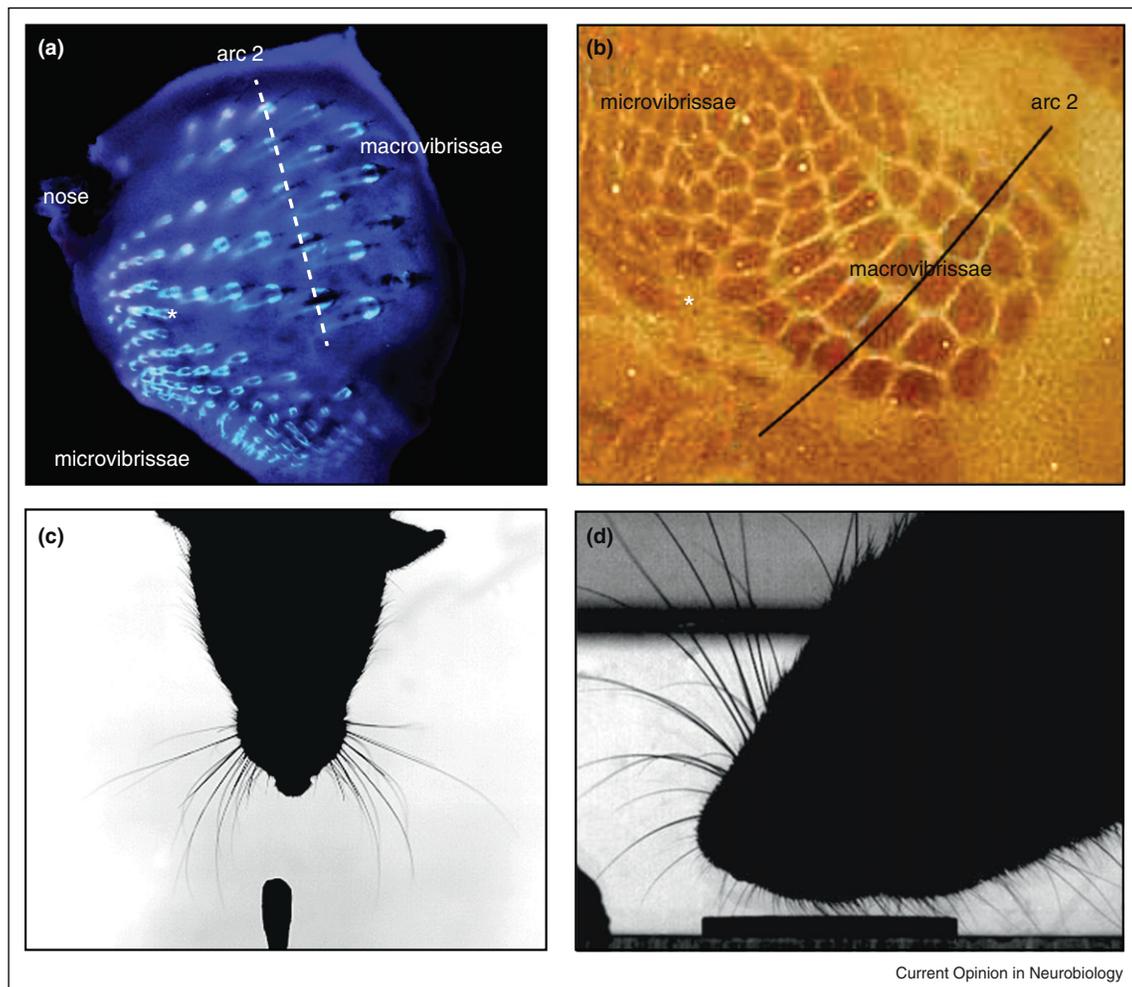
As with respiration, it has long been postulated that whisking is driven by a CPG located in the brainstem. This hypothesis is derived from the observation that whisking persists after decortication [2,12], and that bilateral section of the infraorbital branch of the trigeminal nerve, that is, sensory denervation, has only little effect on the generation, kinematics, and bilateral coordination of the normal whisking pattern [2,7,13]. Attempts to identify neurons that form the core of the whisking CPG have so far yielded unconvincing results. Beyond the obvious participation of facial motoneurons as downstream command neurons, the premotor whisking circuitry remains elusive. It has been proposed that facial motoneurons themselves generate whisking in response to modulatory input from serotonergic pre-motoneurons [14]. Yet, this hypothesis does not explain the synchrony of motoneuron discharges, nor how different pools of facial motoneurons

are activated both bilaterally, and in a multiphasic manner, to generate the protraction/retraction cycle [7,8]. Alternatively, and on the basis of Welker's description of the close phase relationship between sniffing and whisking [2], one might speculate that both rhythmic activities share a common neural circuitry.

The function of the vibrissae in sensation

It is necessary to first consider the anatomical organization and function of the vibrissa sensorimotor plant itself to understand the behavioral significance of whisking. Rats and mice are nocturnal animals with poor visual acuity. They have laterally placed eyes, which allows very little overlap of the visual fields. Panoramic vision gives them a wide field of view, which probably helps them detect predators but provides poor depth discrimination. At close range they rely on sniffing and whisking to sense objects and move about, search for food and shelter, and interact with conspecifics [15]. They are equipped with two sets of vibrissae (Figure 2); one set is the large macrovibrissae that form a matrix of approximately 25 motile sensors on each side of the face, while the other is a dense array of

Figure 2



Rodents have two sets of vibrissae. **(a)** Vibrissa follicles on the mystacial pad and perioral region. **(b)** The follicles are mapped in a one-to-one manner in layer 4 of the primary somatosensory cortex. Note the presence of small-sized follicles, that is, microvibrissae, that are represented by smaller sized barrels in cortex. Asterisks indicate the transition point between macrovibrissae and microvibrissae and their representation in cortex. **(c)** Photograph of a rat whisking upon presentation of a new odor on the cotton swab in the lower part of the image (unpublished data). **(d)** Photograph of a rat sampling a coin with its microvibrissae. Adapted from Fox *et al.* [50].

shorter vibrissae, or microvibrissae, around the mouth, chin and nose. Each of the macrovibrissae has a corresponding 'intrinsic' papillary muscle responsible for the protraction phase of the whisk cycle [16]. Microvibrissae do not have intrinsic muscles and do not protract, but they are distinguished from the surrounding pelagic fur by a thick shaft that is housed within a follicle–blood sinus complex. The entire mystacial pad, including the microvibrissae, is under active control of three major 'extrinsic' muscles that are responsible for pad translation [8,16].

Though both macro and microvibrissae are capable of detecting tactile features such as texture and shape, there appears to be specialization and complementarity of function. Macrovibrissae serve principally to locate objects in space (Figure 2c), whereas the microvibrissa array is

primarily used for close examination of shape and surface properties [17] (Figure 2d). The functional importance of both sets of vibrissae is reflected by their extensive representation in the primary somatosensory cortical area (Figure 2b). However, very little is known about the psychophysics and physiology of tactile sensation mediated by the microvibrissae nor about the anatomical organization of pathways that convey microvibrissa information from the trigeminus to cortical stations.

Sniffing and whisking shape sensory inputs

Sniffing and whisking affect both the encoding and central processing of sensory inputs. Sniffing and whisking *per se*, in the absence of odor or touch, modulate the activity of mitral cells and first-order vibrissa afferents respectively [18,19,20*,21] (Figure 3a). Though air flow

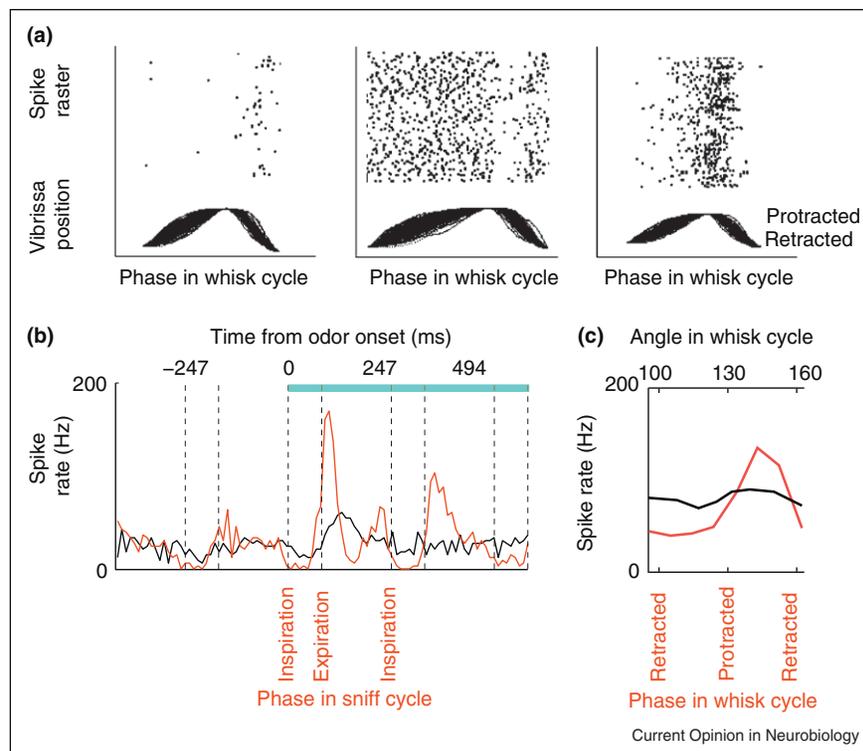
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varies in amplitude, velocity and frequency, individual mitral cells preferentially discharge at a specific phase of the sniffing cycle [21], such that odor evoked responses are normalized to the duration of the sniff cycle (Figure 3b). Similarly, there is analogous coding of touch information in terms of normalized parameters of whisking in the vibrissa system, where neuronal activity locks to the phase in the whisk cycle in primary somatosensory cortex [22,23,24^{••},25] (Figure 3c). This is thought to provide a phase reference signal for decoding object location independently of the amplitude, midpoint, and frequency of whisking [24^{••},26[•]]. The encoding of sensory inputs in a manner that is pegged to the rhythmic motor control of the sensory organs demonstrates the fundamental link of motor control of behavior to sensation for both somatosensation [24^{••}] and olfaction [27^{••}].

The modulation of touch sensation by motor activity has precedents from other studies as well. Whisking gates

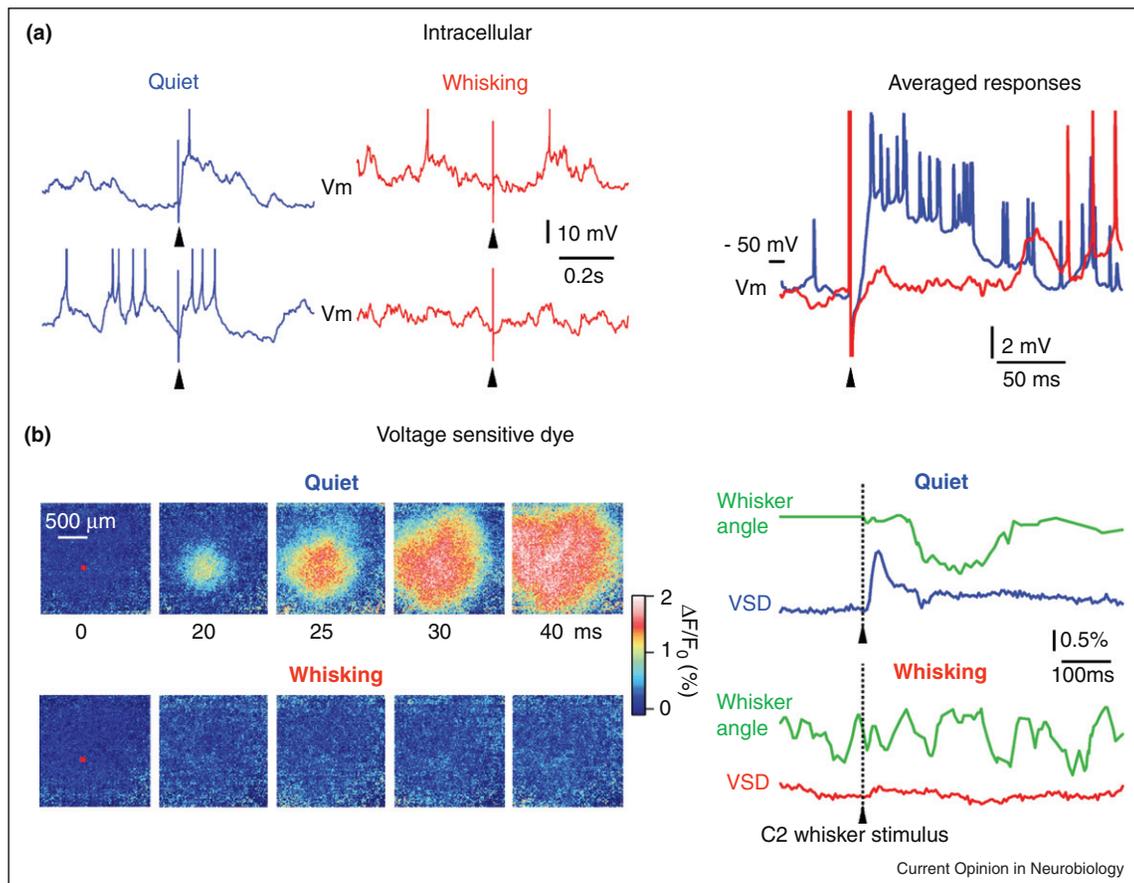
touch along afferent pathways of the vibrissa system [28–30]. The study of Ferezou *et al.* [28] is particularly interesting in this regard (Figure 4). Using voltage-sensitive dyes in freely moving mice, the authors find that in awake but otherwise sessile mice, an unexpected vibrissa deflection produces a large response in barrel cortex. When the same stimulus is delivered unexpectedly during a whisking bout, the evoked response is markedly attenuated. Finally, ‘expected’ contact of the vibrissae with an object during exploratory whisking leads to a pronounced cortical response. These results are clear indication that both the state of arousal and the behavioral context impact on the transfer of sensory messages along the vibrissa-to-barrel pathway. The results of anatomical and physiological studies indicate that gating occurs at the first relay station in brainstem, via inhibitory projections from the spinal trigeminal complex to the principal trigeminal nucleus [30,31]. In the olfactory system, however, there is no clear evidence that a central signal related to sniffing gates sensory inputs [32[•]].

Figure 3



Encoding of odorants and vibrissa contact during the sniffing and whisking cycles. **(a)** Whisking solely in air modulates the activity of trigeminal ganglion cells. Unit recordings were obtained from a head-fixed rat together with simultaneous optical tracking of vibrissa position. Vibrissa movements are aligned to protraction onset, retraction onset, and end. Raster plots the spike times above the movements. Adapted from Khatri *et al.* [19]. **(b)** Peristimulus time histograms for a mitral/tufted cell in response to an odor stimulus (blue bar, stimulus duration): synchronized by odor onset (black), and temporally warped to the phase in the sniff cycle (red). Note that mitral cell activity is modulated by sniffing before the odor presentation, and that odor-induced responses are more tightly time-locked to the sniff phase than to the time after odor onset. Vertical dashed lines indicate the beginning and end of inhalation intervals. Adapted from Shusterman *et al.* [21]. **(c)** Touch response in vibrissa sensory cortex is strongly modulated by the phase in the whisk cycle. The red trace shows the spike rate of a neuron in response to object contact parsed according to the phase in the whisk cycle at which the contact occurred. The black line is the same data parsed according to the angular position of the vibrissa where the contact occurred. Unlike the case for phase, there is no significant tuning for angle. Adapted from Curtis and Kleinfeld [24^{••}].

Figure 4



State-dependent gating of vibrissa responses in barrel cortex. **(a)** Vibrissa stimuli (arrowheads) were delivered randomly during recording from a layer 4 barrel neuron. Intracellular recordings show that the depolarizing sensory response is strongly reduced during active whisking (red) compared to during quiescent wakefulness (blue). Adapted from Crochet and Petersen [23]. **(b)** The above state-dependent reduction in sensory processing can be imaged with voltage-sensitive dye. Passively evoked sensory responses during quiescent wakefulness have large amplitude and spread across large cortical areas, whereas the response is almost suppressed during whisking. The red square on the images at 0 ms indicates the region of interest centered on the C2 cortical column from which voltage-sensitive dye fluorescence changes are quantified in the adjacent traces (lower right). Adapted from Ferezou *et al.* [28].

Context-dependent and state-dependent sniffing and whisking modes

There is evidence to suggest that the expression of both whisking and sniffing is dependent on the motivational state and behavioral goals of the animal. Analysis of sniffing in rats performing a go-nogo odor discrimination task reveal two modes of sniffing: a 7–8 Hz sniffing mode associated with odor sampling, and a 10–12 Hz sniffing mode in anticipation of reward delivery [33]. Correspondingly, several other studies report that sniffing is associated with reward anticipation. For example, sniffing becomes part of the conditioned response as rats learn to predict the occurrence of a reward based on a sensory cue [34,35]. Electrical stimulation of brain regions whose activation is intrinsically rewarding, such as the lateral hypothalamus, elicits exploratory behaviors as well as high-frequency sniffing

[36]. Although whisking was not quantified in these latter studies, the authors incidentally report that whisking was associated with sniffing. Further, in a situation where rewarding brain stimulation is repeatedly delivered at fixed intervals, regardless of response, rats eventually exhibit vigorous sniffing just before the delivery of the stimulation [37].

The context of exploratory behavior can shape how sensory input is processed in the nervous system. In a study in which rats whisked in air either spontaneously or for a reward, oscillations in the local field potential in primary sensory cortex showed drastically increased coherence with the whisking rhythm when the rats were motivated by the reward [38]. This occurred without an increase in field potential amplitude and thus implies a decrease in the variability of the cortical response under

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conditions of a near-term reward, possibly as a result of increased attention to salient features in the environment.

As with sniffing, different whisking frequencies could subservise different behavioral goals. First, a wide range of whisking frequencies, that is, 2–20 Hz, was reported in an early study of texture discrimination [39]. Later work showed that whisking could be divided into two overall frequency ranges, each with a different pattern and associated behavior [7]. Large amplitude whisks at 8–9 Hz are associated with exploration, while a second pattern of whisking, termed foveal whisking, occurs when the animal is perched and the vibrissae are thrust forward and stretched toward an object of interest. This latter pattern consists of relatively low-amplitude whisks in the frequency range of 15–25 Hz, and are reminiscent of 25 Hz oscillatory muscle activity that occurs during the hold period of a precision grip task in monkey [40]. For the moment it is unresolved whether fast whisks are part of a scanning motor strategy, or whether they are rhythmic events related to a strategy of maintaining vibrissae in a protracted position.

The above observations suggest that sniffing and whisking not only serve odor sampling and touch, but they also constitute activity patterns that are the overt expression of reward expectation, and thus serve to automatically sample and identify objects of potential interest. This motivates the question of whether there are specific behavioral contexts in which whisking and sniffing are related. When whisking and sniffing occur together, they appear to be synchronous [2] (asterisk in Figure 1c), yet no study has examined the precise conditions under which the two rhythms couple. Casual observations suggest that rats sniff without whisking when the object of interest is near the nose, and can be inspected with the microvibrissae in conjunction with head and forepaw movements. Beyond behavioral contexts, it is of theoretical interest to understand how two CPGs phase lock and decouple in a dynamic manner that depends on their synaptic interactions and the action of modulators that control emotional and motivational states [41]. Such an understanding of these mechanisms could provide insight into the nature of coupling of other rhythmic behaviors to respiration [42].

Why do rodents sniff and whisk?

Although sniffing clearly subserves olfaction and strongly patterns olfactory processing, several studies reported that basal respiratory rhythm is sufficient for delivering odorants to olfactory receptors, and that rats and mice can perform simple odor discrimination after a single sniff [32,43,44]. Likewise, rodents can locate objects and gauge aperture widths with a single whisk and, rather dramatically, severing the facial nerve to block whisking does not affect performance [45,46]. Lastly, rodents can perform many tactile tasks without whisking *per se*, either

by using head and body movements to move the vibrissae or by maintaining their vibrissae still in a region of interest where contact or stimulation is expected [46,47].

Given the above evidence that smelling can occur without sniffing and vibrissa touch can be effective without whisking, the questions remain as to why rodents sniff and why they whisk. There are likely to be multiple answers. First, since rodents have relatively limited visual capabilities and are the targets of predators, fast sampling of the immediate environment has clear survival value [48]. The few extra hundreds of milliseconds of warning that are gained by scanning the environment may be sufficient for escape. Second, since rodents live in burrows and locomote in a bumpy, cluttered environment, they must rely on tactile inputs to look ahead and avoid obstacles. The speed of locomotion could account for variability in the whisking frequency given the monotonic relation between whisking frequency and the speed of locomotion across species that whisk [49]. Finally, sniffing and whisking not only serve odor sampling and touch, but also represent the overt expression of an animal's interest in its environment. In this regard, casual observation suggests a marked difference in behavior between strains of rats, with Long Evans rats being much more enthusiastic sniffers and whiskers than their Sprague Dawley congeners. The use of transgenic mice, in which the effects of neuromodulators are up or down regulated, might be useful models to understand the neural basis of the drive to sniff and whisk.

Conclusions

Many rhythmic behaviors in rodents have been reported to alternately couple and decouple to breathing. These include whisking and head movements [2], licking, mastication, and swallowing [42]. These rhythmic activities are all generated by pattern generators located in the brainstem. The case of sniffing and whisking is of particular interest as these behaviors often occur spontaneously, are phase locked, and are related to the sensory exploration of the immediate environment. From a practical standpoint, they can be controlled by classical and operant conditioning. The accessibility of the vibrissa system for electrophysiological studies and the use of high-speed videography and indwelling sensors for electromyography, air flow, and related measurements make the rodent an ideal system to understand the neural mechanisms that underly the generation of these rhythms. Such studies may further provide a framework for the nature of the circuitry, the modulation of sensory inputs, and the computations that underly coupling between other brainstem-controlled rhythmic behaviors.

Beyond sensory coding, sniffing and whisking constitute overt expression of the emotional and motivational state of rodents. A detailed knowledge of these behaviors could provide simple metrics for assessing the animal's

subjective valuation of objects and experiences. Such metrics would be of particular interest, for instance, to assess motor and motivational deficits in animal models of neuropsychiatric disorders.

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