Active Sensing: The Rat's Nose Dances in Step with Whiskers, Head, and Breath

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http://dx.doi.org/10.1016/j.cub.2017.01.034

Active sampling of touch and smell involves coordinated movements first observed in the rat half a century ago. A new study has unveiled the elegant choreography of this facial and head motion during tactile and olfactory exploration.

In the early 1960s, at the dawn of the Space Age, Wally Welker [1] conducted pioneering work on rodent orofacial behavior using cinematographic recordings of rats as they sniffed and explored surfaces with their snouts. His observations were largely qualitative given the rather limited technology available for behavioral tracking at the time — he used a stopwatch, 75W light bulbs and Kodak film — but nonetheless revealed that the rat's nose, head, and whiskers moved in an orchestrated manner during exploration [1]. In a new study reported in this issue of Current Biology, Kurnikova et al. [2] extend these early observations [1] on coordinated orofacial behaviors in rodents using cutting-edge, Silicon Valley Age methods. The results uncover a detailed choreography that links key rhythmic orofacial motor actions: nose twitching, whisking, head bobbing, and breathing [2].

Prior work by the authors' research group and others [3–5] had already begun to extend Welker's classical observations via careful delineation of the phase relationships between sniffing and

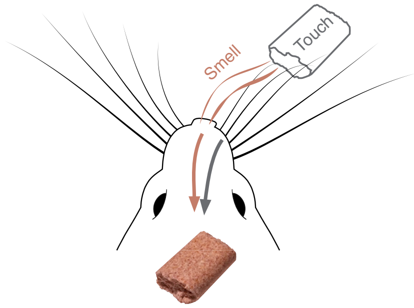

Figure 1. Touch and smell converge via coordinated sensory sampling.
Kurnikova *et al.* [2] have revealed precise spatial and temporal coordination among nose, head and whisker movements as animals explore their environment. This sensory-motor choreography may help 'bind' sensations from different modalities into a unified percept.

whisking. Whisking is controlled by coordinated action [6,7] of three main muscle groups, which together produce a rhythmic pattern of forward and backward motion (protraction and retraction, respectively) that rats and mice use to help locate and interact with objects [8,9]. Sniffing resets this cycle: each onset of inspiration brings a new protraction. The authors [3,4] have also recently conducted pioneering work to discover the brainstem oscillator that patterns whisking, and to define the neural circuitry that implements coordination of the whisking oscillator with the oscillator that controls breathing [10]. Until now, missing from this exciting body of work was a treatment of how rhythmic motion of the nose and head fit into this active sensing dance.

Kurnikova *et al.* [2] began by quantifying correlations between simultaneously measured motion of the nose and breathing. Rats were implanted with a thermocouple device in the nasal passage that measured the temperature fluctuations associated with the breathing cycle. The tip of the rat's nose was marked with a reflective dye, which was then tracked from above using a high speed video camera running at more than 200 video frames per second. Nose position in the third dimension was tracked with the aid of a well-placed mirror [11] beneath the rat's snout. The authors found that, when rats breathed at a low frequency or sniffed at higher frequencies, vertical, as well as lateral, excursions of the nose were synchronized with breathing. Nose position in the vertical and lateral directions peaked at the onset of inspiration, with the next peak occurring at a fixed delay during periods of relatively slow sniffing. These observations suggest rhythmic nose motions are driven by a neural oscillator that is reset by breathing, akin to what was found for whisking [3–5].

Kurnikova *et al.* [2] next investigated patterns of activity in the musculature [12,13] that underlies nose motion. Electromyogram recordings were targeted to the *deflector nasi* muscles, which sit on either side of the rat's snout and actuate the cartilage inside the nose. While head-restrained rats sniffed spontaneously, activity in each *deflector nasi* muscle was correlated with ipsilateral and upward motion of the nose. Frequently, muscles on both sides co-activated, canceling out lateral motion and resulting in nose motion only in the vertical direction. From these data, the authors propose a model in which rat nose motion results from a vector sum of *deflector nasi* muscle action.

Nose motion and whisking drive olfactory and touch sensing of objects near the rat's head. To measure the coordination of these two behaviors directly, Kurnikova *et al.* [2] simultaneously captured nose motion and whisking with high speed video, again in three dimensions, as well as electromyogram recordings from key whisking muscles [6]. Nose motion was highly coherent with whisker motion, with displacements ('twitches') of the nose slightly preceding whisker protraction.

Lateral mobility of the nose may be important for the rat's ability to localize odor sources, something for which rats show considerable talent and is likely to be of major ethological importance [14,15]. To investigate the link between nose motion and olfactory exploration, Kurnikova *et al.* [2] took advantage of rats' special interest in the smell of their home environment. When odor from cage bedding was presented to either the left or right side of the rat, its nose oriented strongly toward the odor source. *Deflector nasi* activity was weaker on the side contralateral to the odor and stronger ipsilateral to the odor, as expected from the vector sum model.

Was this nose orientating behavior a reflexive response to odor detection, or the result of more flexible behavior? Rats and other mammals engage in flexible odor localization behavior by smelling in stereo, using both nostrils [14–16]. Kurnikova *et al.* [2] devised a clever experiment in which rats, essentially, were given a precise, laboratory grade case of nasal congestion — that annoying kind where one nostril but not the other is clogged. After blocking one nostril with a small bead of silicone, the authors observed spontaneous nose motion directed mainly toward the unblocked side. This suggests that lateral movements of the nose are curiosity-driven motor actions, presumably under willful rather than reflexive control. Moreover, nose movements toward one side were accompanied by a change in orientation of the whisker pads (cheeks) toward the same side. These results indicate that rapid reorienting toward regions of interest [17,18] is multisensory in nature. Through coordinated movement of the nose and whiskers, olfactory and touch inputs are aligned both temporally and spatially. This alignment may be important for 'binding' the different senses together into a coherent percept (Figure 1).

In addition to nose twitches, the rat's head also 'bobs' in a rhythmic fashion while it sniffs [1]. Kurnikova *et al.* [2] next turned their attention to quantifying how head motion relates to the breathing rhythm. Rats were outfitted with miniature head-mounted gyroscopic sensors to track head motion in three dimensions. This is similar to the technology in modern smartphones, and would have been hard to imagine at the time of Welker's seminal study. As the rats peered over the edge of a platform, investigating the world around them, their heads bobbed in a manner coordinated with breathing. As the rats sniffed, their heads moved in the pitch and yaw axes, with head position peaking during the inspiration phase of sniffing. Electromyogram recordings in the neck muscle *splenius capitis* revealed that head bobbing is driven, at least in part, by rhythmic neck muscle contraction that is highly coordinated with breathing and that precedes inspiration.

So far Kurnikova *et al.* [2] had separately shown that nose motion and head motion were each coordinated with sniffing. This implies that nose and head movements are coordinated with each other, but the authors went on to pursue a direct demonstration. In an especially challenging experiment, freely moving rats were again equipped with gyroscopic head motion sensors, but now also with magnetic sensors to record nose motion. As expected, head movements were found to be coordinated with nose movements during sniffing.

Together, the results of Kurnikova et al. [2] provide further support for the intriguing hypothesis that orofacial multisensory input is perceptually bound together via rhythmic sampling of the environment, with the breathing rhythm as the master timekeeper [19,20]. Dancers learn to coordinate breathing and movement to produce works of art. Careful observation of the humble laboratory rat has begun to show us a dance of comparable elegance, perfected across millions of years of evolution.

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