Natural Whisking: Focus on “Variability in velocity profiles during free air whisking behavior of unrestrained rats”
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Running head: Exploring Natural Whisking

The rat whisker system is inherently an active sensory system (Mehta et al., 2007). The whiskers move through space to locate and palpate objects in the environment, varying amplitude, frequency and angular direction as they do so (Fee et al., 1997). The earliest studies by Welker (1964) described coordination between vibrissae, nose, head and sniffing movements. Importantly, Welker suggested that the animal’s whisking behavior is dependent on the task and that whisking during exploratory behaviors was different than whisking during discriminative behaviors. Discrimination is an important sensory task and several studies have examined whisking behaviors during tactile discrimination tasks that necessarily require intense training of the animals and constrain the way in which the animal contacts the discriminandum (Harvey et al., 2001; Carvell and Simons, 1990; 1995; Guić-Robles et al., 1989). Therefore, the type of stimulation presented to the animal was far more limited than the broad range of trajectories, amplitudes, and velocities in which rats might typically move their whiskers (Brecht et al., 1997, 2004; Sachdev et al., 2001, 2002, 2003; Bermejo et al., 1996, 2002, 2005; Gao et al., 2001, 2003; Mitchinson et al., 2007; O’Connor et al., 2002; Berg and Kleinfeld, 2003a,b; Hattox et al., 2003; Simons, 1983, 2003). This in turn limits the information conveyed to the brain, limiting our understanding of neural encoding strategies. The relationship between the design of sensory organs, the kinematics of how those sensory organs are used by the organism and the neural substrates within the brain that process this information are not well understood. A major reason for this is a lack of understanding of how animals naturally explore their environment. In an article published in this issue of Journal of Neurophysiology (p. x-xx), Towal and Hartmann (2008) provide an important examination of natural whisker movements as a significant first step to understanding the kinematics of how the rat uses its whiskers in space to find targets.

Importantly, Towal and Hartmann (2008), rather than training the animals to repetitively make a particular movement, embraced the variability in the velocity profiles of whisking during natural exploratory behavior. They examined the velocity profiles of 325 distinct whisks made by freely moving rats attempting to find a rewarding target in the space. Because the animals were freely moving, it was necessary to develop a method to track the position of the whiskers. An important achievement of this work was their ability to track head angle and angular positions of the whiskers in order to classify the whisks as single, delayed (meaning that there was an inflection point somewhere in the whisk’s velocity profile) or double-pumped (slight retraction in the middle of whisk followed by protraction to complete the whisk cycle) whisks. Previously, these types of movements were documented and qualitatively studied (Wineski, 1983), but no quantitative kinematics had been done. The ability of Towal and Hartmann (2008) to track head positions allowed quantitative assessment of kinematic parameters of the whisk movement and
quantification of asymmetries and asynchronies between whiskers on either side of the face. This information is critically important to understand what information is available at higher levels of processing (Ganguly and Kleinfeld, 2004).

In addition to clarifying the fundamental kinematics of natural whisking, Towal and Hartmann (2008), provide important insight into the role of central pattern generators for whisking. They demonstrate that delayed and double pumped whiskers allow for velocity variability within a whisk, while reducing variability in the average whisking velocity across whiskers. This is important for two reasons. First, it means that the rat can control where, along the whisk cycle, the maximum velocity occurs. Since velocity is the greatest determinant of neural responsiveness in the cortex, by shifting the phase of maximum velocity, the rat can shift the phase of the whisk when the largest activity is induced in the cortex. If one is trying to find an object in space, this would be essential. In fact, during exploratory whisking, neurons within the trigeminal somatosensory system can follow whisk frequencies from 5-15 Hz. Since it has been shown that the whisker motor cortex does not convey information about whisker position to the sensory cortex via some type of collorary discharge (Fee et al., 1997), it is important to understand where the system gets this information regarding whisker position (Kleinfeld et al., 2006). It is well documented that at the neural ensemble level spike timing conveys sufficient information for perception of complex tactile features by downstream neuronal circuits (deCharms and Merzenich, 1996; Nicolelis et al., 1998; Fanselow and Nicolelis, 1999; Ghazanfar et al., 2000; Foffani and Moxon, 2004; Jones et al., 2004a,b; Foffani et al., 2004). By directing its whiskers to the spot where they are most needed and at the optimal speed, the animal can influence the responsiveness of single neurons within the trigeminal somatosensory system. In this way, the rat employs a broad range of whisker movements during natural whisking to maximize the probability of activating many cells and thus optimize the ability to encode the features of the environment. Our studies recording activity from trigeminal ganglion cells during natural whisking supports this view by demonstrating that small changes in whisk kinematics produce different responses from the cell (Leiser and Moxon, 2007). These results are also supported by the conclusion of Zucker and Welker (1969) and Gibson and Welker (1983a,b) stating that a population of trigeminal sensory neurons is capable of encoding many parameters of the stimulus delivered to the vibrissae.

How then does the rat encode whisker position? It was first reported during fictive whisking, that cells within the trigeminal ganglion can behave like whisk cells, responding when the whiskers were stimulated to move through the air but not responding when the tips of the whisker passed an object in the path (Szwed et al., 2003), suggesting that these cells responded to the position of the whisker but not when that whisker contacts an object. In awake rats the conditions are a bit more complicated but the same idea holds. We have reported evidence that during certain behavior conditions, cells within the trigeminal ganglion respond during a particular phase of the whisk (Leiser and Moxon, 2007). Of course, if the contact stimuli are strong enough, these cells will also respond to contact. However, it is clear that the awake, freely moving rat has several mechanisms available to change the state of the whisker follicle and thereby modulate the sensitivity of cells in ganglion to whisker movement. Behaving rats may modulate biomechanical parameters that affect damping of the vibrissae and the time course of this damping varies depending on the individual whisker and the phase of the whisking cycle (Hartmann et al., 2003). For example, it appears likely that during natural whisking the response of cells can be modified by changes in blood flow to the whisker follicle (Ebara et al., 2002). The effect of the blood sinus on activation of a receptor is dependent on the parameters of movement (i.e. decreasing receptor isolation for increased acceleration, see Szwed et al., 2003). This is supported by our data documenting the variability of trigeminal cell responsiveness during whisking in air from freely moving rats. For example, during free
whisking in air, trigeminal ganglion cells do not fire during every whisk. In fact, we documented periods of whisking in air that lasted more than four seconds when a cell did not fire. These non-spiking periods occurred in about a third of the cells tested but were always much less than 10% of the total recorded time of each cell (Leiser and Moxon, 2008). Observation of these non-spiking periods in awake rats whisking in air could explain why during previous studies in anesthetized rats cells were observed not to respond during artificial whisking (Szwed et al., 2004).

The Towal and Hartmann study presented here clarifies how the rat may take advantage of its whisker system to identify whisker position during exploratory behaviors. Double-pumped whisks, first described by Wineski (1983), now assume an important role. Moreover, control over where along the whisk trajectory maximum velocity occurs appears to be part of the motor plan. Towal and Hartmann (2008) suggest that this is likely due to fine motor control of the whisk protractions. However, control over retraction may also play an important role. The CPG could have important agonist/antagonist coupling between the intrinsic and extrinsic muscles in the whisker pad. In this way, the command signal from M1 would request a restart of the whisk, as in a double pump, and both the protraction and retraction muscle groups would be engaged to optimize the response of the whiskers. It has recently been demonstrated that retraction as well as protraction are under muscular control (Berg and Kleinfeld, 2003). This is important and highlights the fact that retraction is not just a relaxation back to the set point for protraction during exploratory whisking. Moreover, neural circuitry in this muscle system, consisting of the extrinsic muscles for protraction (Carvell et al., 1991; Berg and Kleinfeld, 2003) and the intrinsic muscle, for retraction (Wineski, 1985; Berg and Kleinfeld, 2003), has been shown to work in antiphase, to produce full control of the whiskers. This will need further study to fully identify the role of active retraction in the control of whisker movements.

Finally Towal and Hartmann (2008) raise an intriguing question regarding the origin of these double pumped whisks. They suggest that a double pumped whisk is a single whisk with similar starting positions and ending positions to other whisks but a unique velocity profile. This is important because if the rat uses its starting position and velocity profile to identify the position of the whisker in space during the whisk, then the double pumped whisk would suggest that there is no unique position of the whisker in space relative to the starting point. However, if double pumped whisks are two separate whisks with different starting points then there is always a unique position of the whisks in space along the whisk trajectory. In fact, short whisker movements often occur during nonexploratory states and are sometime referred to as twitching (Nicolelis et al., 1995). These movements have been shown to last for up to a minute (Fee et al., 1997). They often occur before a bout of exploratory whisking in a freely moving animal and could be necessary for calibrating whisk position in preparation for motor planning. Therefore, double pumps could be two separate whisks. The short, fast whisks could be initiated during a particular phase of the whisk to improve the sampling. As Towal and Hartmann (2008) point out, whiskers need to move at a velocity relevant to the spatial structure of the environment. Interspersing long whisks with short-fast whisks enables the systems to change the whisking velocity in real-time to modify the flow of incoming sensory information and enhance the detection of an object in space. These are important issue that will require further analysis of the cortical control of whiskers and responses of cells within the trigeminal ganglion during natural whisking behaviors. The study presented here brings us closer to being able to ask the right questions.

REFERENCES


