

Mapping the Gates. Focus on "Relationship Between Physiological Response Type (RA and SA) and Vibrissal Receptive Field of Neurons Within the Rat Trigeminal Ganglion"

Marcin Szwed and Ehud Ahissar

J Neurophysiol 95:2729-2730, 2006. doi:10.1152/jn.00147.2006

You might find this additional information useful...

This article cites 18 articles, 5 of which you can access free at:

<http://jn.physiology.org/cgi/content/full/95/5/2729#BIBL>

Medline items on this article's topics can be found at <http://highwire.stanford.edu/lists/artbytopic.dtl> on the following topics:

- Veterinary Science .. Brain Stem
- Veterinary Science .. Thalamus
- Veterinary Science .. Ganglia
- Veterinary Science .. Trigeminal Ganglia
- Engineering .. Resonance Frequency
- Veterinary Science .. Rats

Updated information and services including high-resolution figures, can be found at:

<http://jn.physiology.org/cgi/content/full/95/5/2729>

Additional material and information about *Journal of Neurophysiology* can be found at:

<http://www.the-aps.org/publications/jn>

This information is current as of July 10, 2006 .

Mapping the Gates. Focus on “Relationship Between Physiological Response Type (RA and SA) and Vibrissal Receptive Field of Neurons Within the Rat Trigeminal Ganglion”

Marcin Szwed¹ and Ehud Ahissar²

¹Unité de Neurosciences Intégratives et Computationnelles, Institut de Neurobiologie Alfred Fessard, Centre National de la Recherche Scientifique, Gif sur Yvette, France; and ²Department of Neurobiology, The Weizmann Institute of Science, Rehovot, Israel

Four decades ago, Hubel and Wiesel demonstrated that cortical neurons show a response specificity that does not exist in the thalamus or retina and triggered a universal pursuit after cortical mechanisms of perception. Under this pursuit hid an implicit assumption that whatever is needed to be known about the input to the cortex is already known. Forty years later, we are realizing that actually we don't know what the sensory organs are telling the brain, and yet, this knowledge is crucial to discriminate between alternative hypotheses of cortical function. Specifically, recent studies on sensor-level encoding of natural-like or complex stimuli in vision (e.g., Olveczky et al. 2003; Puchalla et al. 2005) and touch (e.g., Andermann et al. 2004; Arabzadeh et al. 2005; Jones et al. 2004; Szwed et al. 2003, 2006) have shown that information conveyed to the cortex differs from what was assumed previously. At the same time, important foundations needed to guide experiments on sensory encoding are still missing, and that is why the article published in this issue of *Journal of Neurophysiology* (p. 3129–3145) in which Leiser and Moxon (2006) provide the first functional map of the trigeminal ganglion (TG) of the rat, is a significant step toward systematic characterization of tactile encoding.

So far, physiologists studying the TG (also abbreviated as Vg or NV) could rely only on the purely anatomical map of Schneider et al. (1981). It was also unclear if the TG has a somatotopic organization of receptive fields. Well-delineated somatotopic maps have been documented in the SI primary somatosensory cortex (“barrels”) (Woolsey and Van der Loos 1970), in the VPM thalamic nucleus (“barelloids”) (Van der Loos 1976), and in the trigeminal brain stem nuclei (“barellettes”) (Ma 1991). It would be tempting to assume that this organization originates with a somatotopy in the TG just like retinotopy in the visual system originates in the retina. However, studies on the TG done so far have reported either no somatotopy at all or weak tendencies in that direction (reviewed in Leiser and Moxon 2006). Because none of them was specifically aimed at mapping the TG, a possibility remained that a somatotopy exists in the TG, but is simply harder to detect.

Leiser and Moxon (2006) recorded from 350 sensory-responsive TG cells and found a gross somatotopy, mapping different facial areas onto different ganglion zones; for example, cells innervating the eyelid were positioned more medially than cells innervating the lower lips. However, they established also that in spite of this gross somatotopy, no “barellettes” exist in the TG and vibrissa-responsive cells are not arranged into any clear map resembling those at higher stations. A

question that arises is how brain stem nuclei show clear somatotopy, whereas the TG, the cells of which project to the brain stem, does not. The answer might be simple. TG cells are pseudounipolar; they “hang on” the fibers running from the whisker follicles to the brain stem. Thus even if the fibers are organized in a topographical manner, their cell bodies are not committed to a similar organization. Relative cell location might be affected instead primarily by factors such as size and energy consumption.

In addition to clarifying several previous contradictions, the paper by Leiser and Moxon (2006) is also an important voice in the ongoing discussion on how specialized the whiskers are in their functions. Do all the ~35 large whiskers sense similar stimulus features or are they tuned to different features, like auditory hair cells are sensitive to different frequencies? Recently, Hartmann et al. (2003), Neimark et al. (2003), and Andermann et al. (2004) have demonstrated that whiskers and TG neurons can act as frequency-specific band-pass filters. When a high-frequency (40–800 Hz) stimulus is applied to the whisker, the hair either amplifies it or dampens it, depending on its own intrinsic fundamental resonance frequency. Interestingly, the fundamental resonance frequencies of different whiskers create a neat spatial pattern on the whisker pad with the larger whiskers having lower frequencies (Neimark et al. 2003). Because vibrations at varying frequencies (“kinetic signatures”) are generated when rats actively sweep their whiskers across textures (Arabzadeh et al. 2005), it is possible that due to band-pass properties of whiskers, textures are encoded in the somatosensory system in a spatially distributed way (Neimark et al. 2003) in addition to kinetic encoding by each whisker (Arabzadeh et al. 2005).

Leiser and Moxon (2006) looked for specialization in another aspect of TG responses and asked whether TG neurons contain different proportions of slowly adapting (SA) and rapidly adapting (RA) cells. Adaptation rate and directional selectivity are arguably the most prominent response features of TG neurons during passive¹ touch (Zucker and Welker 1969). When a whisker is deflected passively with a ramp-and-hold stimulus of low frequency, its response will either be transient (RA) or prolonged (SA). Leiser and Moxon (2006) demonstrate that all TG neuron populations that receive input from the large whiskers have similar proportions of RA and SA cells and thus might be equipotent in the encoding of dynamic stimulus features. Equipotentiality is found also with active touch: whisking, touch, and whisking/touch cells distribute

Address for reprint requests and other correspondence: E. Ahissar, Dept. of Neurobiology, The Weizmann Institute of Science, 76000 Rehovot, Israel (E-mail: ehud@weizmann.ac.il).

¹ Passive vibrissal touch occurs when an external agent moves stationary whiskers or when the rat moves near objects without whisking (see Szwed et al. 2006).

similarly across different whiskers (Szwed et al. 2003, 2006). So, are the whiskers specialized or equipotent? The answer probably depends on the task. As the neuronal encoding machinery seems to be similar across whiskers, differences would emerge mainly due to mechanical differences, such as whisker's length and rigidity.

This multifaceted view of TG encoding, confusing as it might be, is probably not the whole story. Cockroaches use their whiskers to detect air currents caused by an approaching predator (Camhi and Tom 1978), and seals can use their whiskers in an analogous fashion in the aquatic medium (Dehnhardt et al. 2001). Rats could use their whiskers to detect air currents caused, for example, by large predators. Knowing the wind's direction would also help locating the source of odors simultaneously smelled by the rat. Another possibility is that rats can use the vibrissal system to detect loud sounds. The rat auditory system works poorly for frequencies of 50 Hz to 1 kHz (Kelly and Masterton 1977). By resonating at their intrinsic frequencies, the whiskers could capture acoustic information in that low part of the spectrum that their auditory system fails to grasp. Verification of these tempting hypotheses should start, again, at the level of first order neurons of the TG.

ACKNOWLEDGMENTS

We thank V. Jacob for suggesting the idea of whiskers as air current sensors and R. Keinan for suggesting the contribution of whiskers to odor source localization.

REFERENCES

- Andermann ML, Ritt J, Neimark MA, and Moore CI.** Neural correlates of vibrissa resonance; band-pass and somatotopic representation of high-frequency stimuli. *Neuron* 42: 451–463, 2004.
- Arabzadeh E, Zorzin E, and Diamond ME.** Neuronal encoding of texture in the whisker sensory pathway. *PLoS Biol* 3: e17, 2005.
- Camhi JM and Tom W.** The escape behavior of the cockroach *Periplaneta americana*. I. Turning response to wind puffs. *J Comp Physiol [A]* 128: 193–201, 1978.
- Dehnhardt G, Mauck B, Hanke W, and Bleckmann H.** Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* 293: 102–104, 2001.
- Hartmann MJ, Johnson NJ, Towal RB, and Assad C.** Mechanical characteristics of rat vibrissae: resonant frequencies and damping in isolated whiskers and in the awake behaving animal. *J Neurosci* 23: 6510–6519, 2003.
- Jones LM, Depireux DA, Simons DJ, and Keller A.** Robust temporal coding in the trigeminal system. *Science* 304: 1989–1993, 2004.
- Kelly JB and Masterton B.** Auditory sensitivity of the albino rat. *J Comp Physiol Psychol* 91: 930–936, 1977.
- Leiser SC and Moxon KA.** Relationship between physiological response type (RA and SA) and vibrissal receptive field of neurons within the rat trigeminal ganglion. *J Neurophysiol* 95: 3129–3145, 2006.
- Ma PM.** The barrelettes–architectonic vibrissal representations in the brainstem trigeminal complex of the mouse. I. Normal structural organization. *J Comp Neurol* 309: 161–199, 1991.
- Neimark MA, Andermann ML, Hopfield JJ, and Moore CI.** Vibrissa resonance as a transduction mechanism for tactile encoding. *J Neurosci* 23: 6499–6509, 2003.
- Olveczky BP, Baccus SA, and Meister M.** Segregation of object and background motion in the retina. *Nature* 423: 401–408, 2003.
- Puchalla JL, Schneidman E, Harris RA, and Berry MJ.** Redundancy in the population code of the retina. *Neuron* 46: 493–504, 2005.
- Schneider JS, Denaro FJ, Olazabal UE, and Leard HO.** Stereotaxic atlas of the trigeminal ganglion in rat, cat, and monkey. *Brain Res Bull* 7: 93–95, 1981.
- Szwed M, Bagdasarian K, and Ahissar E.** Encoding of vibrissal active touch. *Neuron* 40: 621–630, 2003.
- Szwed M, Bagdasarian K, Blumenfeld B, Barak O, Derdikman D, and Ahissar E.** Responses of trigeminal ganglion neurons to the radial distance of contact during active vibrissal touch. *J Neurophysiol* 95: 791–802, 2006.
- Van der Loos H.** Neuronal circuitry and its development. *Prog Brain Res* 45: 259–278, 1976.
- Woolsey TA and Van der Loos H.** The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex. The description of a cortical field composed of discrete cytoarchitectonic units. *Brain Res* 17: 205–242, 1970.
- Zucker E and Welker WI.** Coding of somatic sensory input by vibrissae neurons in the rat's trigeminal ganglion. *Brain Res* 12: 138–156, 1969.