

PERSPECTIVES

Observing without disturbing: how different cortical neuron classes represent tactile stimuli

Dirk Schubert

Department of Cognitive Neuroscience,
Section of Neurophysiology and
Neuroinformatics, Radboud University
Nijmegen Medical Centre, Geert Grooteplein
21, 6500 HB Nijmegen, the Netherlands

Email: d.schubert@science.ru.nl

How does our brain translate sensory information that has been acquired by receptors in our periphery into information that is relevant for behaviour and decision making? Currently we are only beginning to understand the basic neuronal mechanisms that allow such signal processing. A crucial step forward to reveal general intracortical sensory network functions is to unravel the details about how specific neurons classes in the different layers of a cortical functional column respond to sensory stimuli. Whereas in this respect *in vitro* investigations can deliver detailed anatomical and functional information about the theoretical range of capabilities that different neuron classes possess, only *in vivo* approaches can tell how neurons might actually react to a specific sensory stimulus in real life.

Important questions that arise in this context are: (i) which neuron class(es) in which layer(s) may be the first to respond to sensory activation and thus initiate intracortical processing of a given stimulus, (ii) at which temporal sequence are different neuron classes activated, and (iii) which class delivers what kind of cortical output? The challenge here is to 'observe' activity of single neurons, which means to record the activity of morphologically classified neurons without manipulating their intrinsic properties.

In this issue of *The Journal of Physiology*, De Kock *et al.* (2007) address these questions by investigating stimulus related suprathreshold activity of a large range of morphologically identified excitatory neurons in the rat primary somatosensory cortex (barrel cortex) *in vivo*. Using whisker stimulation in combination with intrinsic optical imaging the authors detected the localization of the activated barrel in cortical layer 4 and the related cortical column in the barrel cortex. Subsequently they used juxtosomal *in vivo* recordings which allow 'observer-like' recordings of a neuron's

activity and subsequent staining to define the neuron's structure (Swadlow & Hicks, 1996).

A general notion about intracortical processing of sensory information is that in primary sensory cortices activity typically starts in only one layer, namely the granular layer 4, from where the intracortical signal processing initiates a sequential activation of the other layers of a cortical column in a hierarchical fashion. According to the findings of De Kock *et al.* (2007) at least for excitatory neurons in the somatosensory cortex this notion must now be reconsidered.

Following a tactile stimulus, they could observe early activity simultaneously in several layers, namely layer 4, 5b and 6 – all of them layers that are known to be targets of thalamocortical afferences originating from the ventral posteromedial thalamic nucleus. Such a notion is in line with other recent *in vivo* studies (e.g. Derdikman *et al.* 2006). In only two layers excitatory neurons seem to lag behind: in the supragranular layers and in presumptive layer 5a. For their activation the pyramidal neurons in these layers seem to rely mainly on excitation by either subsequent intracortical inputs or inputs of a parallel sensory pathway from the posteromedial thalamic nucleus. The obviously differing responses of layer 5a and layer 5b neurons are in line with other recent *in vitro* and *in vivo* studies (Manns *et al.* 2004; Schubert *et al.* 2006) and once more stress the necessity for future studies to distinguish these two infragranular layers.

Surprisingly, in the sample of De Kock *et al.* (2007) the different morphological classes within a cortical layer respond in a comparable way to a single tactile stimulus. However, for layer 4 of the barrel cortex (Schubert *et al.* 2003) and layer 6 of the visual cortex (Zarrinpar & Callaway, 2006) it is known that in terms of their functional integration into intracortical networks, the excitatory neurons show distinct cell type-specific capabilities. This raises interesting implications for possible context-dependent contributions of defined neuronal populations to intracortical signal processing. A single tactile stimulus might initially activate the different neuron classes within those layers in a similar way. However, Derdikman *et al.* (2006) could demonstrate that during complex tactile stimulation in layer 4, the population responses change dramatically over time.

Thus it is likely that more extensive physiological stimuli or prolonged sensation is needed to recruit intralaminar cell type-specific networks.

What kind of output can be expected to emerge from the different neuron classes? De Kock *et al.* (2007) convincingly demonstrate that a sensory stimulus does not initiate an avalanche of action potentials in masses of cortical neurons, as one might have assumed, but in contrast follows the concept of sparse coding. By correlating the average number of elicited action potentials with the estimated total number of cells within a cortical column, the authors calculated cell type-specific numbers of action potentials per stimulus and column. Such numbers are of significant value for a more comprehensive understanding of general features of signal processing and transmission. This calculation gives direct evidence for the notion of layer 5b thick tufted pyramidal neurons being capable of dominating spontaneous as well as stimulus related cortical output.

Consequently, the approach of De Kock *et al.* (2007) bears interesting implications for possible general concepts of intracortical signal processing. It shows that the model of strictly hierarchically organized intracortical processing of sensory information might be too much of a simplification. It has, however, still to be investigated how different stimulus protocols may affect the presented concept of intracortical activity. And finally intracortical activity is tuned by numerous classes of inhibitory neurons as well. In the future it will be interesting to learn whether these neurons react to sensory stimuli in a layer or even cell type-specific manner as well.

References

- De Kock CPJ, Bruno RM, Spors H & Sakmann B (2007). *J Physiol* **581**, 139–154.
- Derdikman D, Yu C, Haidarliu S, Bagdasarian K, Arieli A & Ahissar E (2006). *J Neurosci* **26**, 9538–9547.
- Manns ID, Sakmann B & Brecht M (2004). *J Physiol* **556**, 601–622.
- Schubert D, Kötter R, Luhmann HJ & Staiger JF (2006). *Cerebral Cortex* **16**, 223–236.
- Schubert D, Kötter R, Zilles K, Luhmann HJ & Staiger JF (2003). *J Neurosci* **23**, 2961–2970.
- Swadlow HA & Hicks TP (1996). *J Neurophysiol* **75**, 1753–1759.
- Zarrinpar A & Callaway EM (2006). *J Neurophysiol* **95**, 1751–1761.