1. Why is it difficult to understand olfactory neural encoding compared to other sensory modalities, such as vision or audition?

It is difficult to understand olfactory neural encoding since odors cannot be represented, or classified by some simple parameters, such as wavelength or frequency in vision and audition systems. Olfactory system uses numerous different odor receptors to detect odors. In order to discriminate different odors, the combinatorial coding and circuit-level interactions at multiple steps of olfactory processing are significant. Also the discrimination can be affected by olfactory learning. Since there are many different parameters to determine/discriminate odor, it is complicated to study it systematically. (p45)

2. Explain the relationship among physical space, neural space, and perceptual space in olfactory processing.

The physical odor space describes the physiochemical properties of odorants. Different descriptors of the odor structure are different in physical space. The neural space describes how an odorant is represented in the olfactory system. It is associated with the response pattern of the olfactory neurons. Perceptual space is related to how people think of the odor. In the paper they use pleasantness of the odor for this space. The experiment found that all three spaces are related. Specifically, physical odor space is able to predict perceptual space, and the neural space is related to perceptual space in a way that neurons close in neural space also close in perceptual space. (p55)

3. Enumerate three ways in which the olfactory system limits the temporal extent of neural response to an odorant. What are the advantages and disadvantages of this temporal limitation?

The first way is that odorants loosely bind with olfactory receptors. Bind is mediated by hydrophobic and van der Waals interactions. Since binding is loose, the dwell times of the odorant is also very short. Secondly, the olfactory transduction is also consistent with short odorant dwell time. The olfactory receptor is activated by a concatenation of events, and only one G-protein needs to be activated, as compared to phototransduction where many G-proteins are activated. Third, expeditious signal termination is required for olfactory system to work. Experiments find that the inhibition of the cyclic-nucleotide gated channel, activation of phosphor diesterase, and other processes might be the reason for signal termination, and the receptor might not be the target. Therefore the signal is terminated very fast. One advantage of the temporal limitation is that it can enhance the temporal resolution. The adaptation of the background odor will also result to acuity in discriminate the new odor with the background one. The disadvantage is that the noise would have larger affect when the time is limited. (p50)
4. (Extra credit) What is combinatorial encoding? Where is it found in the olfactory system? What are the computational advantages and disadvantages of combinatorial encoding.

Combinatorial encoding means that odorants are identified by the pattern of receptors that are activated, rather than by a single receptor. It is found in activation of glomerular clusters in the olfactory bulb with primary odor neurons. The advantage is that it can be used to represent a large amount of odors using not that many receptors. If it is not combinatorial coding, one odor requires one type of receptor, and the receptor numbers can be numerate. The disadvantage is that the signal is more complicated and needs to be decode when interpret information. (p49)

5. (Extra credit) What is "sparse coding" and how is it achieved in third-order neurons?

Sparse coding is a coding form that only a small subset of neurons activated by the stimuli and the responses of neurons only consist of few action potentials. In olfactory system, cortical pyramidal neurons are much more narrowly tuned than their presynaptic neurons. It is illustrated by Figure 3 in Page 53 in the paper. An odor activates multiple second order neurons, and the third order neurons are activated only when they receive synchronized inputs from multiple second order neurons. Therefore, only a few third order neurons are activated. (p53)

6. (Extra credit) What is "pseudogenization"? Give two examples in different species.

Pseudogenization is a process by which genes nonfunctional is caused by mutation. V2R genes in human are one example of pseudogenization. Class II olfactory receptors in dolphin is another example. Class I ORs are tuned toward water-soluble odorants and Class II is for hydrophobic odors. (p48)