Neurobiology and Human/Animal Behaviour
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problem set #2 solutions

1. Cell bodies of primary afferent fibres are located in the dorsal root ganglia (or, in the cases of the cranial nerves, in the various cranial nerve ganglia).

2. Projections can be identified by tract tracing using chemical, viral, or radiological agents (*e.g.* horseradish peroxidase, tritiated thymidine); various agents move anterogradely or retrogradely along axons. Cutting an axon produces Wallerian degeneration of the axon's distal segment, and often cell death or other activity-dependent changes in the cells of origin as well as in the cells to which the axon projects. Axons can be traced by electrical stimulation: stimulating somewhere along the length of an axon causes action potentials to propagate both prodromically towards the axon's target and antidromically back towards the soma. Stimulation of entire tracts or regions can be accomplished non-invasively with the use of a magnetic stimulator. Other non-invasive methods use magnetic resonance imaging: diffusion-tensor imaging, which takes advantage of the fact that water molecules diffuse preferentially along fibre tracts rather than perpendicularly to fibre tracts, and correlative functional magnetic resonance imaging, which examines the covariance (and therefore the presumed functional linkage) of activity in separate brain regions.

3. Tactile receptors are often classed as either 'rapidly adapting' or 'slowly adapting.' These terms describe how the receptors behave in terms of <u>time</u>. An equivalent distinction, more common in the theory of signal processing, is that of 'high-pass' versus 'low-pass' filtering. This latter distinction is phrased in terms of <u>frequency</u>. Rapidly adapting receptors pass high-frequency signals but filter out low frequencies, whereas slowly adapting receptors pass low frequencies but not high. To see the relationship between these two ways of describing receptor selectivity, think about how a rapidly adapting receptor responds to a high-frequency vibration. Vibration consists of alternating periods of compression and rarefication of the tissue in which the receptor is embedded. The rapidly adapting receptor responds to the initial compression, but then quickly adapts to the compressed state. When the rarefication comes along, the compression-adapted receptor again responds vigorously. So in the rapidly adapting receptor there is a strong response to high-frequency

inputs, this response generally being phase-locked to the periods of the input waveform. Consider now how the same rapidly-adapting receptor responds to a low-frequency input, whose amplitude changes very slowly over time. The input simply doesn't change quickly enough to overcome the receptor's rapid rate of adaptation: by the time the input has risen or fallen to any appreciable degree, the receptor has already adapted to the input's new level, and thus the input that the receptor actually 'feels' is always zero. Thus the rapidly adapting receptor is a high-pass filter, preserving high frequencies and losing low frequencies. The case of the slowly adapting receptor is exactly complementary: it loses high frequencies selectively, since its lack of adaptation prevents it from following rapidly changing signals. The receptors listed in order of low to high frequency selectivity (slow to rapid adaptation) are Merkel's receptor, Meissner's corpuscle, and the Pacinian corpuscle.

4. Aδ fibres (medium diameter, lightly myelinated) convey tactile stimuli (including sharp pain) and proprioception. Primary afferents ascend in the ipsilateral dorsal columns (gracile and cuneate fasciculi) to the dorsal column nuclei in the medulla. Ascending from the medulla, fibres of the medial lemniscus decussate and then terminate in the ventral posterior thalamus. Fibres from the thalamus course through the internal capsule to cortical regions S1 and S2 in the postcentral gyrus.
C fibres (small diameter, unmyelinated) convey burning pain and temperature. Primary afferents synapse in the dorsal horn, from which secondary fibres decussate and then ascend contralaterally in the several tracts of the anterolateral system. The spinoreticular tract projects to the medullary and pontine reticular formations, the spinomesencephalic tract to the periacqueductal grey matter, and the spinothalamic tract to posterior, ventral posterior, and intralaminar thalamus. From the thalamus, fibres ascend in the internal capsule to S1 and S2 and to anterior cingulate cortex.

5. Thalamic input is received in layer 4, cortico-cortical projections originate from the pyramidal cells of superficial layers 2 and 3, and output to subcortical structures arises from the pyramidal cells of deep layers 5 and 6.

6. In a labelled-line paradigm, a computational unit (*e.g.* a cortical column or minicolumn) responds to only one type of signal (*e.g.* a single receptor type or a single point in the visual field or on the body surface). In population coding, each unit's receptive field is much larger than the discrimination

threshold of the system as a whole, and the signal is coded by the pattern of activity across all the units. While labelled-line coding is computationally simpler, population coding is more robust to localised damage or noise.

7. According to the simplest version of the gate control model, both nociceptive C fibres and tactile Aα and Aβ fibres have excitatory synapses on projection neurons in the dorsal horn. In addition, the C fibres inhibit inhibitory interneurons and the Aα and Aβ fibres excite the same inhibitory interneurons. Tactile activity, conveyed by the Aα and Aβ fibres, can therefore block the C fibres' inhibition of the inhibitory interneurons, resulting in less excitation of the nociceptive projection neurons.

8. Cingulotomy patients still feel pain as a sensation, but cease to feel the aversive, unpleasant aspect of pain. In a sense, they still feel pain but they don't care about it. The catch is, when you destroy someone's anterior cingulate there are *many* things that they cease to care about....

9. The periacqueductal grey and the septum.

10. Neighbouring regions invade the deafferented cortical territory. This double innervation produces sensation in the phantom limb during stimulation of somatotopically adjacent regions – hence VS Ramachandran's famous funny story about the woman whose orgasms spread to her phantom foot.