Neurobiology and Human/Animal Behaviour
Matthew Belmonte
problem set #5 solutions

THE CHEMICAL SENSES

1. Population coding, it's all about population coding. The olfactory system in particular uses an interesting form of population coding. Unlike other perceptual systems, its representations rely not simply on a single focus around which activity is maximal, but on complex distributed patterns having many separate foci of activation. This form of distributed coding is known as pattern coding.

2. The olfactory bulb relies on overlapping pattern codes, while the pyriform cortex exhibits more specific responses.

3. Anosmia following closed head injury may result from the shearing of olfactory axons by the cribriform plate, or from damage to olfactory bulbs, olfactory tracts, or inferior frontal cortex. These inferior frontal regions (as well as temporal regions) are particularly susceptible to damage from closed head injury since the inner surface of the skull within which they're enclosed is rough and can easily abrade the brain when brain and skull are differentially accelerated. Anosmia after occipital blunt force trauma is an example of contrecoup injury (French, 'opposite the blow'): mechanical energy is transmitted as an impulse that propagates all the way through the head, and is absorbed at the interface between brain and skull on the opposite side of the head. Anosmia due to shearing of trans-cribriform axons is temporary, since the olfactory receptors that produce these axons are regenerated. Anosmia due to other types of inferior frontal damage is generally permanent.

4. Pyriform cortex has strong connections to the hippocampus and adjacent cortex of the medial temporal lobe, which govern the encoding of episodic memory. Engrams laid down in the presence of a strong olfactory stimulus may thus be tied to the same olfactory cue.

5. Making a salt receptor is simple: just place a sodium channel in contact with the oral cavity. Sourness receptors are only a bit more complicated: protons from dissolved acids block voltage-gated potassium channels. Other

gustatory receptors, in contrast, are rather more complex: bitterness depends on a G-protein-activated phosphodiesterase which hydrolyses the second messenger cAMP, resulting in the opening of channels, and sweetness depends on G-protein-activated adenylate cyclase which produces cAMP and thereby closes potassium channels.

6. Monosodium glutamate. (Mm, glutamate.)

7. The nucleus of the solitary tract sits anteriorly in the hindbrain, and has a rather long rostrocaudal extent.

EMOTION

1. Antonio Damasio's somatic marker hypothesis distinguishes primary emotions and secondary emotions. In this view, secondary emotions are learnt responses that interpret autonomic responses and other aspects of the body's physical state in light of explicit knowledge about the situation. The central idea is not a lot different from the James-Lange theory of emotion perception which, simply stated, posited that emotions were interpretations of physical states – in other words, we feel sad because we cry, and not *vice versa*. The James-Lange theory, however, interpreted *all* emotions in this way and did not distinguish between primary emotions and learnt emotions.

4. The sexually dimorphic nucleus of the preoptic area (SDN-POA), a part of the hypothalamus, is smaller in women and homosexual men than in heterosexual men.

5. The stria terminalis courses around the horn of the lateral ventricle to the bed nucleus of the stria terminalis, the nucleus accumbens septi, and the hypothalamus. The ventral amygdalofugal pathway projects ventrally to the hypothalamus, the dorsomedial thalamus, and the anterior cingulate cortex.

6. The central nucleus of the amygdala can be selectively lesioned by stereotactic injection of ibotenic acid – a method that is particularly useful because it destroys cell bodies without damaging axons that merely pass through the targeted region on their way to distant termini. Rats so lesioned, when exposed to tone-shock conditioning stimuli, fail to exhibit behaviours associated with fear in response to the tone alone.

7. Klüver-Bucy syndrome, in humans and in other primates, arises after

extensive bilteral damage to the temporal lobes affecting the hippocampus and amygdala as well as higher-order cortical areas involved in mnesis and in visual perception. Klüver-Bucy syndrome's characteristic hyper-orality may be explained by a failure of visual gnosis: if one can't identify an object and doesn't understand what it's for, one is more likely to treat it as food. In humans, Klüver-Bucy syndrome is a rare complication of meningitis, which often preferentially damages temporal lobes. In the past, a few cases of Klüver-Bucy syndrome arose following overzealous bilateral surgical resection of the temporal lobes.

NEUROMODULATION, AROUSAL, AND SLEEP

1. Acetylcholine: nucleus basalis of Meynert and peribrachial pons, deficient in Alzheimer's disease and in normal aging.
Norepinephrine (a.k.a. noradrenaline): locus coeruleus, likely has some involvement in depression.
Dopamine: substantia nigra, depleted in Parkinsonism.
Serotonin: raphé nuclei, depleted in obsessive-compulsive disorder and also has some role (perhaps an indirect one) in depression.

2. The current thinking is that the pharmacologically mediated increase in serotonergic activity may indirectly induce an up-regulation of norepinephrine receptors. This change in noradrenergic transmission has a time course more closely matched to the therapeutic effect.

3. The suprachiasmatic nucleus of the hypothalamus, so named because it sits atop the optic chiasm, seems to implement the circadian rhythm. It receives input from the retina. Lesioning it abolishes the circadian rhythm, whilst grafting new suprachiasmatic cells into its place restores the rhythm. The tau gene, which codes for casein kinase 1ϵ, is strongly expressed in the suprachiasmatic nucleus, and knocking out this gene in golden hamsters shortens the cycle to 22 hours in heterozygotes and 20 hours in homozygotes.

4. The reticular nucleus is a thin layer of cells that forms a rind around the rest of the thalamus. Thalamic axons on their way to cerebral cortex send collaterals into the reticular nucleus, and feedback from the reticular nucleus seems to help determine the response mode of thalamic neurons. In single-spike mode, neurons in the thalamus are at resting potential and tend to respond to a single input spike with a single output spike. This mode

preserves the maximum amount of information about the input, transmitting it verbatim to cerebral cortex. In bursting mode, thalamic neurons are hyperpolarised, and when they fire spikes they fire in bursts. This is thus a low-fidelity mode, discarding the details of the input spike pattern but evoking a maximum of cortical excitation. Although thalamic neurons switch between single-spike and bursting modes during wakefulness, in sleep more of them tend to be in bursting mode. This mode switching may be important in disconnecting the cerebral cortex from its inputs during deep sleep, and in exciting the cerebral cortex to wakefulness in response to very salient stimuli. (See work by Steriade *et al.*)

5. The electroencephalogram depends on the fact that cortical pyramidal cells are orientated with their apical dendrites perpendicular to the cortical surface. Since all of the pyramidal cells in a local patch of cortex are arranged parallel to each other, the minute electromagnetic fields generated in each apical dendrite are additive. (Were the cells randomly orientated, the fields would tend to cancel each other.)

6. An evoked potential, also known as an event-related potential, is the average brain electrical response surrounding a sensory, motor, or cognitive event.

7. For decades, the conventional wisdom in electroencephalography was that all of the information in the event-related brain response was present in the averaged evoked potential. However, the evoked potential is a time-domain phenomenon, in which averaging all the individual trials together discards information concerning the brain's event-related frequency response. If an event alters the frequency spectrum of the electroencephalogram without altering its phase-locking, this frequency spectral information will be available only by analysing the trials in the frequency domain.

8. The information capacity of a neural network depends on the degree to which individual neurons can activate independently of each other – this capacity is known in information-theoretic terms as entropy. The entropy of a neural system is equally low when none of the neurons are active as when all of the neurons are active at the same time. As an analogy, think of the two extremes of a blank chalkboard and a whited-out chalkboard: neither can represent any information. During non-REM sleep, the brain is not representing much information, and cortical activity consists largely

of synchronous oscillations which summate to yield a high-amplitude, low-frequency electroencephalogram.

9. A sleep spindle is a spike in the electroencephalogram reflecting synchronised cortical activity, evoked by thalamic bursting.

10. PGO spikes propagate through the pons, the lateral geniculate nuclei, and the occipital cortex. It has been suggested that these events may aid memory consolidation by activating engrams unselectively.

11. Early work by Frederic Bremer demonstrated that whilst transecting the cat brain between the colliculi induced continuous sleep, a transection between the medulla and the spinal cord left the normal sleep cycle intact. In the mid-twentieth century, Moruzzi and Magoun found that transection at the level of the pons left the animal unable to sleep. Using selective anaesthesia of brainstem regions, they confirmed the existence of a rostral brainstem centre inducing wakefulness and a caudal brainstem centre inducing sleep.

12. Lesioning the locus coeruleus, the primary source of noradrenergic innervation, abolishes sleep paralysis and leaves the animal acting out its dreams during REM.

13. People (and animals, including dogs who've been bred for narcolepsy) who suffer fromn narcolepsy go unpredictably from wakefulness directly to REM sleep. These episodes can be precipitated by strong emotion. Secondary injuries often occur during falls produced by sleep paralysis.