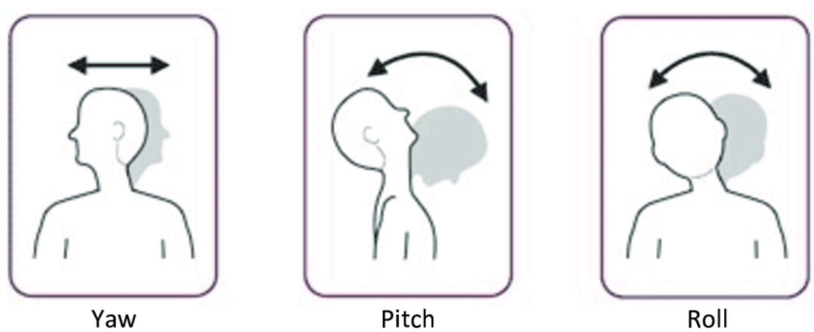
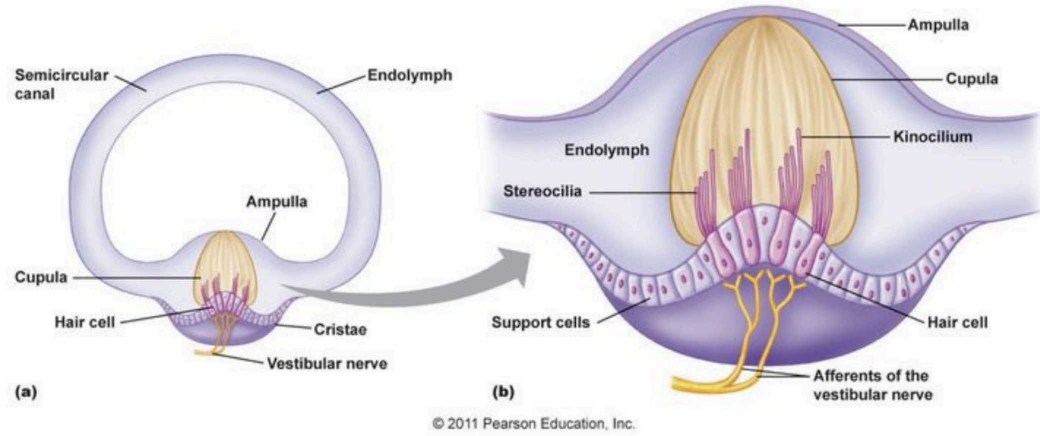
Detects movements of the head, detect orientation of the head

Vestibular sense is used to estimates where the body is in spaces, stabilise eyes during head motion, to maintain balance, silent sense

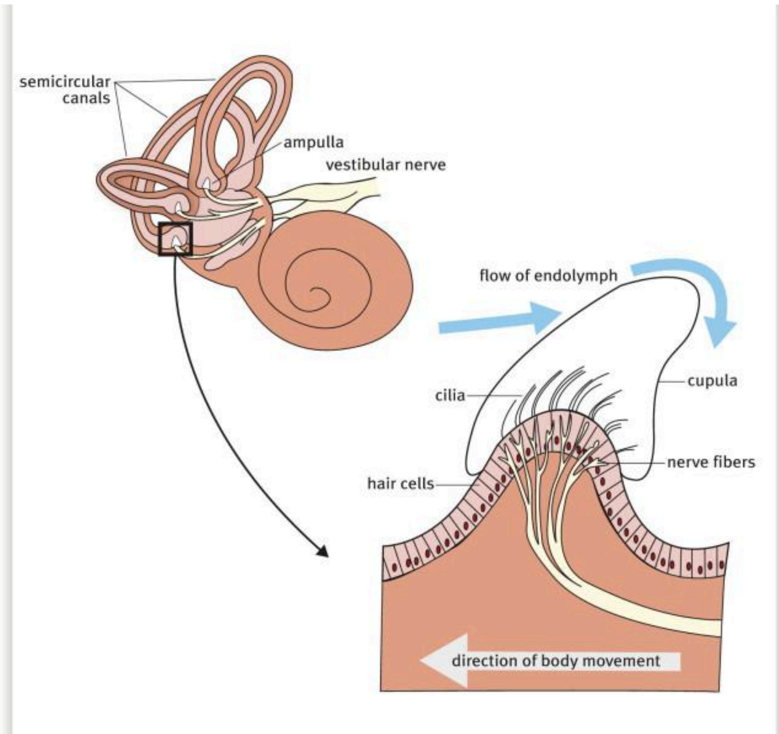
Semicircular canals:

- Angular sensors
- Set of 3 orthogonal body canals (semicircular canals)
        - Superior
        - Posterior
        - Horizontal
- Detects head rotations
    - Rotational accelerations
        - Yaw (turning left and right)
            - Horizontal semicircular canal
        - Pitch and roll: PItch is nodding, Roll is just rolling your head
            - Superior and Posterior semicircular
        - 

- Inertia sensors
- Each canal is filled with endolymph fluid
- Ducts end in an enlarged area called the ampulla, which contains the receptor
    - Within ampula, hair cells are embedded in a gelatinous merbane called cupula
    - Hair cells located on cristae ampullaris
        - Larger: kinocilium
        - Small: stereocilia



- Tip links guard mechanically gated potassium channels
    - Stretching causes opening of gates → depolarisation
    - Compression causes closing of gates → hyperpolarisation
- Endolymph pressure causes hair cells to deflect
    - Inertia = resistance of any physical object to any change in its state of motion
    - During motion the inertia of the endolymph causes it to lag behind, deforming the cupula and bending the hair cells



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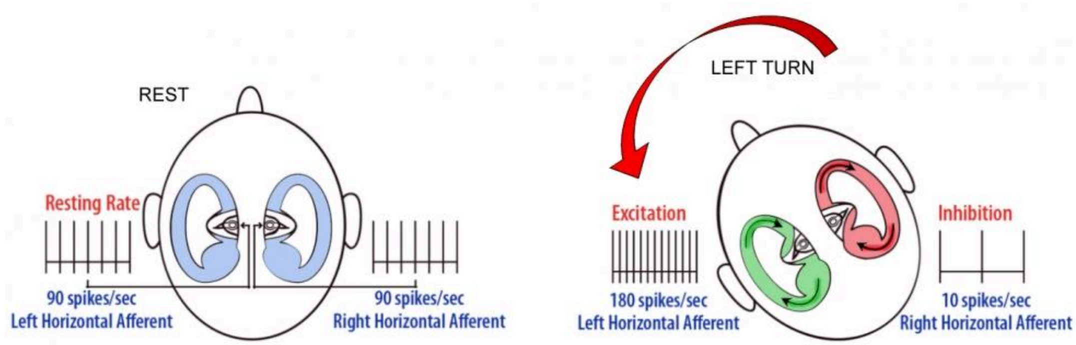
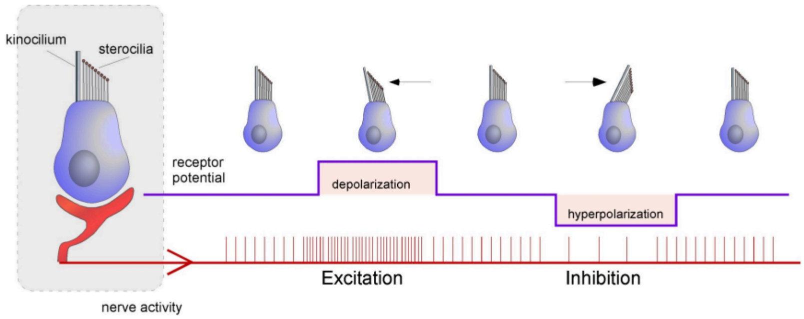


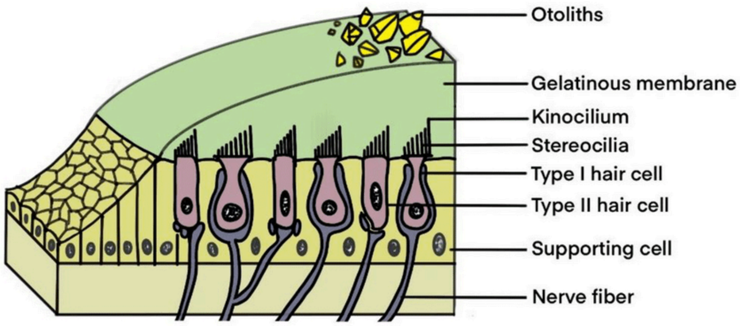
- Stereocilia bend:
  - Towards kinocilium → opens gates
    - More K^+ influx
    - Depolarisation of memrabne
    - Voltage-gated Ca^+ channels open
    - Release of neurotransmitters
    - Increase vestibular afferent firing rates
  - Bending away from kinocilium → closes gates
    - Less K^+ influx into cells
    - Hyperpolarisation of membrane
    - Closing of Ca^+ channels
    - Less release of neurotransmitter
    - Decrease afferent firing rates
- Peripheral vestibular sensors transmit motion to the brain through frequency encoding

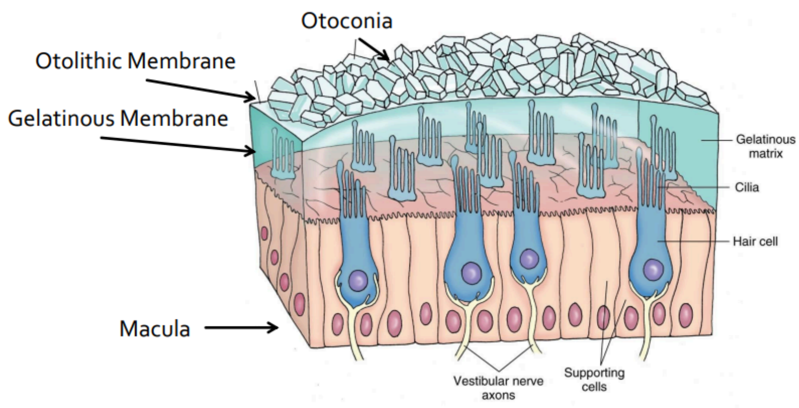
Otolith Organ

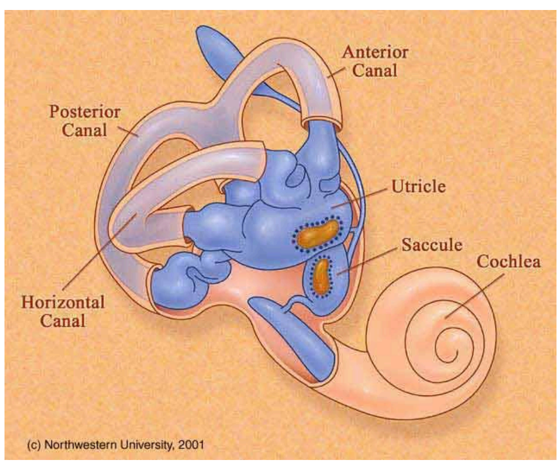
- 

- Bilateral
  - Right is mirror of left, vice versa
  - Bilateral canals are a reflection of each other and they work as antagonistic pairs
  - When one canal is excited, its pair is inhibited (push-pull organisation)
    - Canal on the side toward head rotation increase firing rate, the opposite decreased firing rate
    - Amplifies strength of a signal
- Hair cells and vestibular afferents
  - Hair cells detect fluid movement and convert this to nerve impulses
  - 2 types of afferents:
    - Regular
    - Irregular afferents have
      - Less regular resting discharge rate
      - Larger diameter axons and faster conduction velocities
      - Preferentially carry info from Type 1 or both type 1 and 2 hair cells
        - Type 1 hair cells tend to have more stereocilia than Type 2
- Limitation: Rotational signal decay
  - Mechanism
    - Friction between endolymph and canals slows fluid
    - Endolymph and canal move at same speed eventually
    - Less hair cell deflection
    - Nerve firing rate decreases
    - Rotational motion signalled incorrectly
      - Brain thinks you're still despite you are moving
  - **Post-rotary activation** (stop rotating after prolonged rotation)
    - Prolonged rotation causes endolymph and canal to move at the same speed
    - Fluid continues to move after rotation stops, but head is no longer moving
    - Hair is deflected
      - Perception: rotation in opposite direction
    - Decrease in firing, then slow recovery back
- Vestibular sense primed for small amplitude, high frequency motions
    - Not adapted to continuous rotational motion

Otolith Organ

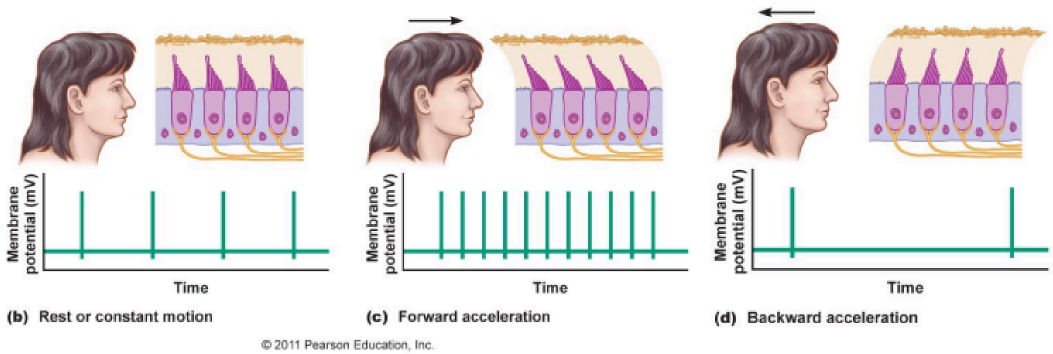
- Structure:
    - 

    - 

    - 

    - Utricle
        - Horizontally oriented
        - Encodes left/right and forward/backwards
        - Deflection toward striola = depolarisation
    - Sacule
        - Vertically oriented
        - Encodes up/down and forward/backward
        - Motion away from striola = depolarisation
    - Hair cells project from the neuroepithelium (**macula**)
    - Striola divides otolith organ in half
        - It is a curvilinear line through the middle of the macula

        - Lower density of hair cells
    - Otoliths
        - Calcium carbonates crystal glued together with a jelly-like membrane
        - Detect head movements, they lag behind (intertial lag) → bends hair cells, resulting in depolarisation / hyperpolarization of vestibular nerve
- Otolith organ detect linear acceleration and head tilt
    - Linear acceleration



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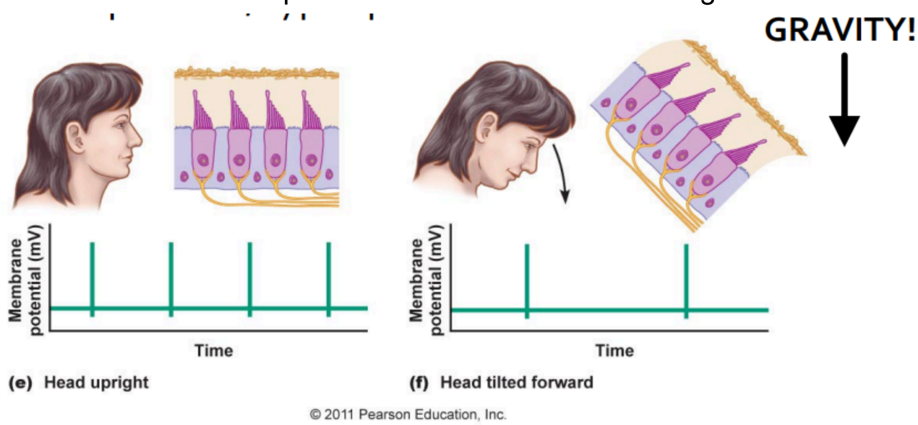
    - Otoliths are sensitive to gravity
        - Head tilt forwards comrpesses hair cells → less AP firing



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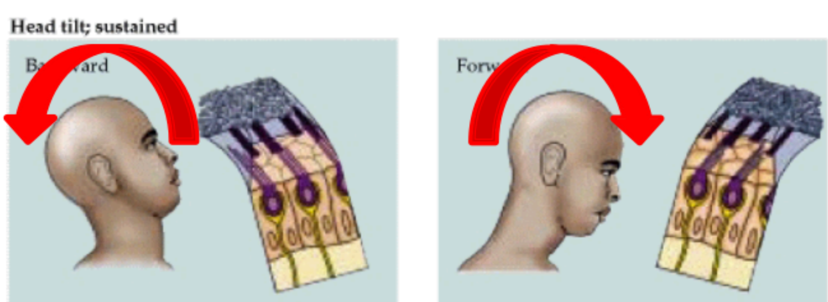
- Forward acceleration of head and gravity pulling head forward ⇒ hair cells bend similar way
    - Einstein's Equivalence Problem
    - Head uses semicircular canals to solve the ambiguity
        - Head tilts also have pitch properties



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Cortical Projections

Vestibular projections to:

- Vestibular nuclei (located in brainstem)
    - Projections are loosely grouped by function
    - Projections from vestibular organ
        - Utricles project to lateral, medial and descending nuclei
        - Saccule projects to lateral, medial and descending nuclei
        - Horizontal and superior canals project to superior and medial nuclei
        - Posterior canals project to superior, medial and descending nuclei
- Cortex
    - Perception of self-motion, external motion and gravity
    - Single-unit recordings in non-human primates suggest that there is more than 1 vestibular cortex → very diverse network
        - Parietoinsular vestibular cortex
        - Parietal areas and intraparietal sulcus
        - Temporal areas: visual posterior Sylvian and email superior temporal
        - Somatosnesory area
        - Premotor area
        - Vestibular cingulate region
    - Activation is stronger on side of stimulated ear and in the non-dominant hemisphere
        - Righ ear stimulated, stronger response in right hemisphere in right-handed people (right-handed dominant hemisphere = left cortex)
- Oculomotor neurons
    - Vestibular ocular reflex
        - Stabilise images on retina during head motion
        - Acts rapidly
            - Lateny = less than 10 ms
- Cerebellum
    - Multi-sensory integration
- Vestibulospinal tract
    - Posture and balance
    - Stimulated by vestibulospinal reflex
        - Galvanic vestibular stimulation evokes perception of head movement (stimulate reflex)
            - Applied electrical stimulation behind the ears, passing small current through electrodes behind the ear to stimulate vestibular afferents
            - Interpreted by brain as an unplanned whole body movement

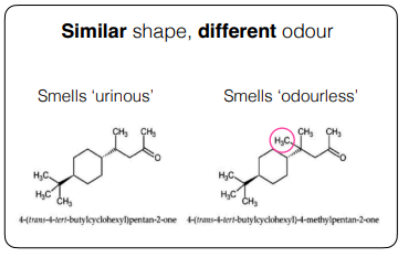
Olfaction

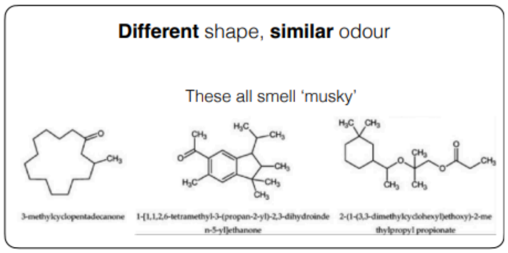
Olfaction is conserved across vertebrates → olfactory bulb/olfactory circuits (processing structures) are conserved across vertebrates

Stimulus space is very complex → has more than 400,000 odorous molecules, most odours are complex mixtures

- Scent of jasmine is very complex, a lot of odorous molecules

Odour is an unreliable stimulus → needs more integration / sampling in time
Temporal correlations may carry information about same/different source





Olfactory sensory neurons reside in the main **olfactory epithelium**, septal organ, vomeronasal organ and Gruneberg ganglion.

The olfactory epithelium is envoluted → larger surface area
Sensory transduction happens in the olfactory cilia

Olfactory genes are on end of chromosome in error-prone region

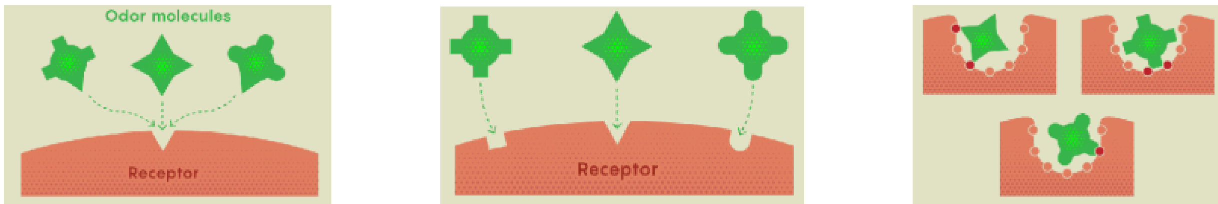
- ➔ High mutation rate
- ➔ Lots of duplications, resulting in pseudogenes

Monoallelic expression - one receptor = one neuron
Insetcs may have multiple receptors per neuron

Olfactory code is a dimensionality problem

- Stimulus space is >400,000
  - All molecules are different
- Receptor space is ~1000

Option 1 | Option 2 | Option 3

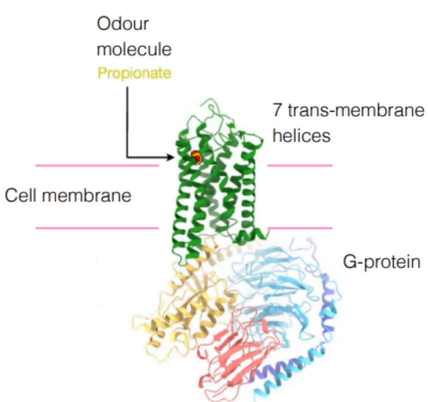


Single binding site for a functional group | Binding sites for multiple functional groups | Binding pocket with diverse weak affinities

Specialised membrane proteins, olfactory receptors

- 7 transmembrane helice
- GPCR

G-protein coupled receptor



Billesbolle … Manglik, Nature 2023

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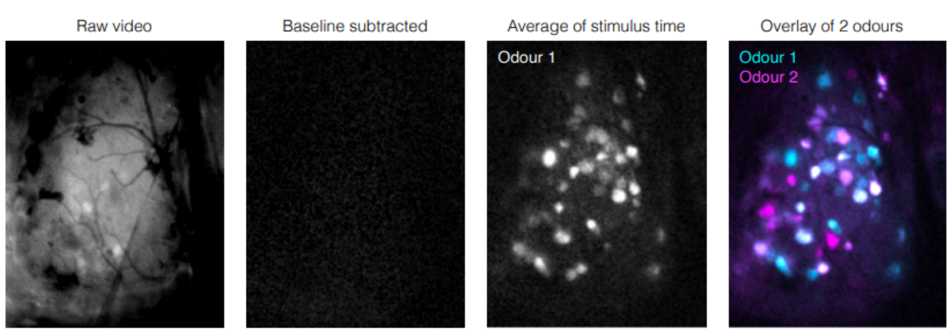
- Different odour molecules interact with different parts of the binding pocket
- Each odour will evoke a particular glomerular activation pattern
  - Most odour receptors will respond to multiple odours
  - Olfactory receptors have broad receptive fields
  - 

    - White = detects both odors
  - Combinatorial code → receptor reponds to various different odours
    - A given odour moeluclе leads to a characteristic olfactory receptor activation pattern
- Odour identity = a pattern of olfactory reception activation, and a pattern of active glomeruli

-
    -
- Glomeruli activate
    - Major number of cells in olfactory bulb are inhibitory
    - Transform glomerular patterns
- Particular glomerular activation pattern leads to particular mitral cell response pattern
    - Mitral and tufted cells are projection neurons in the olfactory bulb
- This signal is send to the piriform cortex

Olfactory Bulb Circuit

SARS-CoV2 can transduce ACE2 receptors

Performance = detection + discrimination
- More olfactory sensory neurons = better detection
- More olfactory genes = better discrimination

Size of olfactory brain and othe brain areas involved in olfactory processing also important

Olfactory system shave evolved to take arbitrary patterns of receptor activation and endow them with meaning through learning and experience

Important processing tasks for olfactory system
- Detect faint odours in strong background
- Represent important odours with more activity
    - Learning
    - Synaptic plasticity during learning is important
    - Mice
        - Reward certain odour
        - Over learning, the mice can learn the distinction between odours that are reward and not reward
        - Record activity of cell over learning, rewarded odour leads to greater activity in the olfactory bulb
        - Lateral inhibition enhances contrast between similar stimuli
            - In olfactory bulb there is only a distributed glomerular pattern
            - Receptors which are activated by multiple odours are useless, cannot be used to distinguish between different cells
- Form predictions about odour scnes
- Link odours with spatial information
- Identify odours across many orders of magnitude in concentration (deteceting something even if it is weak)
- Represent odour concentration
- Represent temporal odour statistics

2 photon calcium imaging

Tufted cells are concentration sensitive (response increases as concentration increases)
Mitral cells are not responsive to concentrations

Motivation and Learning

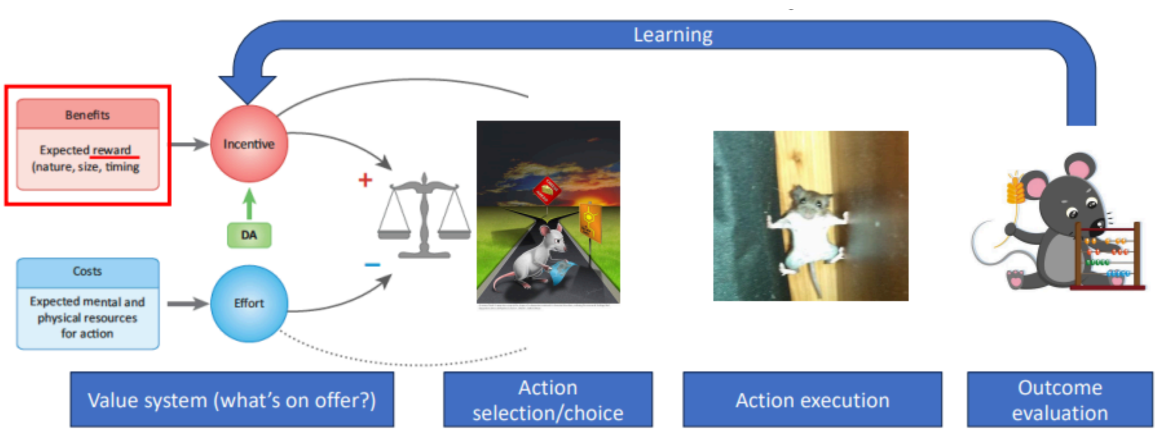
- Homeostatic account → motivation to drive action that satisfies a basic need (e.g. thirst, hunger)
  - Need ⇒ Drive ⇒ Drive-reducing behaviours
- Affective account → motivation to do a certain thing because it feels good. These accounts see emotions/affective reactions as important factors which explain behaviour and direct learning

Limitations of drive-reduction theory (homeostatis account):
- Cannot explain why there is overindulgence or underindulgence
- For many motivated behaviours, expressing motivation increases the original al drive rather than decreasing it (this is opposite to the drive-reducing behaviour)
- Intravenous or intra-gastric food delivery does not eliminate need to put food in mouth (mroe to eating than satisfying hunger)
- Difficult to explain the role of secondary reinforcers (those that are not directly linked to drive satisfaction e.g. money) in motivation

Motivation is based on the affective account.
- 1960 experiment demonstrates that sites in the brain which induced eating after stimulation were same sites that were stimulated by reward electrodes (rats pressed lever to deliver electrical stimulation to that area)
- Drive-reduction theory of motivation is wrong, because according to this theory animals are motivated to do a certain thing (e.g. eating) reduce aversive feelings (e.g. hunger)

Motivation is directed towards positive incentives (rewards) and hunger/thirst modulates incentive values of the rewards (e.g. thirst increase value of water, rather than inducing drinking via its aversive quality)

Motivation Processes:



- Value system computes subjective value of events, potential costs and can compare value of different stimuli/events
- Outcome evaluation → evaluates whether the initial computed value was correct (was the predicted value obtained?), supports learning

Emotions

Physiological responses and emotional responses to a situation are processed parallelly and independently. (Our emotions are not an interpretation of our bodily state)

Limbic structures mediate emotions
- Kluver and Bucy (1937)
    - Bilateral temporal lobectomy in monkeys resulted in marked changes in emotional behaviour
- Papez-circuit:
    - Cingulate cortex
        - Anterior cingulate cortex (ACC)
            - Value, action selection and curiosity
            - fMRI studies show rostrocaudal gradient in dorsal ACC between motor tasks and reward tasks
            - dACC encodes choice between exploration and exploitation in a patch foraging experiment. Not just about encoding the value of the current stimulus, but also consider the value of another choice which has not yet been explored.
    - Hippocampus
    - Anterior thalamus
    - Hypothalamus
    - Mammillary bodies
- Papez-circuit (limbic system) important roles in memory and spatial navigation, rather than emotion
    - Shruken mammillary bodies lead to diencephalic amnesia
    - Hippocampal formation contains neurons encoding key spatial signals (e..g distance travelled, direction, place)