17/1/22

BI 3234 - Animal Behaviour

Lecture 01

Behaviour of digging bee : male digs and waits for the female to emerge, then mates with her.

We can ask different type of questions -
  proximate : how questions
  ultimate : why questions

Evolutionary approach to Natural Selection

- Nothing in biology makes sense except in light of evolution.
- Natural selection is the differential survival and reproduction of individuals due to differences in phenotype

For it to occurs we need 3 things -

Variation   Differential fitness   Heritability

- Differential fitness is because of various selection pressures

Hypothesis - an idea that you can test
  it comes about from previous knowledge about the system.

Digger bee behaviour
  Why that mating routine?
    1. Found more females there
    2. Digging as a signal of male's strength
    3. Less predators / lesser competition at the site
    4. To avoid inter-specific mating
    5. This species were susceptible to sunlight, so they buried

\# Why think behaviour is adaptive? Could be a spandrel.
  Eldredge & Gould paper

AN
BE

\# Usually, the ability to learn is more successful than the thing that's learned.

Critique of Adaptationist programme - Gould & Lewontin 1979

1. Critique adaptationist programme for -
   a) Failure to distinguish utility from reasons for origin
   b) Failure to consider other factors -
      - Random fixation of alleles
      - Non-adaptive structures by developmental correlation with other selected features
      - Separability of adaptation & selection
      - multiple adaptive peaks
      - current utility as an epiphenomenon of non-adaptive struct
2. The Panglossian Paradigm
   a) An organism is atomised into it 'traits' — but an individual is so much more than a collection of discrete traits.
   b) Since each trait can't be optimised, independently, the notion of tradeoff is introduced.
      "A trait is suboptimal because that's what is needed for the best possible design of the whole"
3. 'We should cherish Darwin's consistent attitude of pluralism in attempting to explain Nature's complexity.
4. Alternative mechanisms - expansion of 1b. [Box 2 of P&K2000]
5. Constraints upon evolutionary change are not stressed enough. (Phyletic, Developmental)

Pigliucci & Kaplan 2000

a) The main critique was: what kind of evidence is acceptable to support adaptations?

b) Changes since spandrels - (in theory)
   - The idea of fitness/adaptive landscape has changed
   - Selection acts on more than just genes alone
   - 'Genetic' and 'epigenetic' constraints. Selection & Constraints become two major players.
   - Effects of environmental heterogeneity is seriously being considered.
   - Lande & Arnold - quantifying selection
   - Lot of empirical & experimental studies

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Lecture 02

Possible hypothesis for digger bee behaviour : females mated one are no longer receptive

Predictions : 1) a mated bee, if put in a burrow will not mate with a male - behaviourally less receptive

2) Anatomically less receptive - females can mate multiply.

3) Male-male aggression at digging sites

4) Compare with related bee species and how they mate.

Another behaviour: Infanticide in Hanuman Langur (New?)

Langur troops - multifemale - single-male group. Males attack and kill infants of females in their own group.

Possible hypothesis -

1) Not adaptive, but aggressive response to overcrowding due to feeding by villagers

Not true - it occured in troops of all numbers, far from villages

2) Males do this to induce ovulation in females so they can mate, & increase chances of reproductive output

Predictions - Males that take over kill infants, not their own

Females should ovulate after death of infant

Also occurs in other species with similar social structure.

Related observations: already pregnant females mate with new male soon after takeover. (langurs)

Similar thing with horses.

Its important to not attach morality to Natural Selection, it doesn't act 'for good of the species'.

Adaptations

A hereditary trait that has spread or is spreading by natural selection and replaced alternative traits.

Has more fitness benefits than fitness costs.

Fitness benefit : positive effects of trait on reproductive success

④

Adaptationist view

That every behaviour is a result of natural selection and provides some reproductive advantage.

Darwinian puzzles – behaviours that don't appear to increase reproductive fitness

Eg: Altruism, eusocial insects, infanticide (at first glance).

Gould & Lewontin critique the adaptationist programme for not being plural enough.

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Lecture 3

Proximate and Ultimate Questions

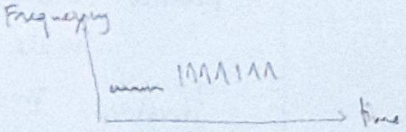
Tinbergen's 4 Questions

Proximate – within one generation

1. How is the behaviour produced?
   - Mechanisms (neurons, genes, hormones..)
2. How does it develop?
   - Innate or learned? How do genes, environment etc shape its development

Ultimate – across generations

3. Why is the behaviour produced
   - Function? Adaptation?
   - Important to remember difference b/w current & past function
4. How did it evolve?
   - Do related organisms have the behaviour? Evolutionary history



Spectrogram

Birdsong – questions at multiple levels

Basic : ~ 4000 types of song birds

Songbirds have dialects – same species sing different songs depending on location. (in White crown sparrows)

★ What is the cause for differences across geographical location?

→ It could be a result of genetic differences between birds in different locations – but there were no genetic differences.

→ Result of social environment? – a chick was transplanted from one location to another, it would sing the songs of adoptive nest and not natal nest. When grown in isolation, it sang some key songs, but not all

Songbird are vocal learners – white crown sparrows exposed to strawberry finch can learn their song

Songbirds learn their songs as human children learn language.

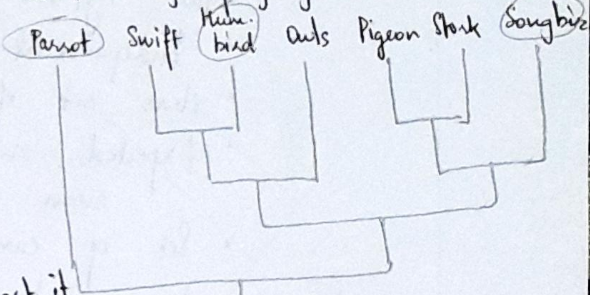
But there is a genetic component – untrained birds still produce specific songs.

★ How does the songbird learn and produce songs?

Multiple brain regions are very important in production of songs.

★ When did this ability evolve?

We can answer this by constructing phylogenetic trees.



Some birds can exhibit vocal learning. Based on trees constructed, either it evolved independently multiple times or they inherited from common ancestor while other birds lost it.

Comparison of brain structure doesn't support independent evolution of song learning.

★ What advantage does vocal learning provide?

→ Song learning could allow songbirds to match their songs to the environment for better communication

Eg: Great tits produce songs with different freq. tone etc. in dense forest vs. open grassland

→ Song learning could allow them to match their songs to those of their neighbours – to maintain territory

Eg: Songs of song sparrows are similar in some song-types (relating to aggression) and not in others

Its important understand the difference b/w proximate and ultimate questions to understand that multiple hypotheses can explain the same phenomenon.

Eg: Infanticide – males are agitated by rivals & redirect their aggression to infants

makes the female available for mating

Song bird singing in spring – increased testosterone in song control areas

To attract females

Its also important to have mutually exclusive hypotheses and understand the level

Also, they complement each other and help hypotheses generation at each level

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Lecture 4

Elements of a grant proposal

1 A good research question - focused and interesting (to the target audience)
  - why is it interesting?
  - Give background - why should this be next step
2. A clear testable hypothesis
3. Address 3 specific aims that test the predictions of the hypothesis
  - Independent aims, not interdependent
  - clear set of experiments with controls
  - Expected outcomes and interpretations - what does it mean to be successful with the experiment?
  - Set of caveats / pitfalls : "what if something else happens?"
4. Budget for instruments, consumables, travel etc
5. Preliminary data to show that these experiments will work (for some (2) aims).

Example of grant proposal : How does brain control the ordering of sounds to produce complex vocal sequences?

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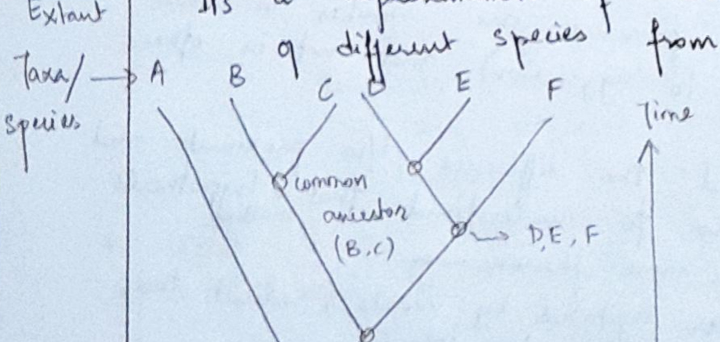
Lecture 5

Phylogenetic trees

Its a representation of lines of evolutionary descent of different species from a common ancestor



To find the relationship between any 2 species, we trace the the distance b/w them.
Longer the distance, farther long ago the common ancestor lived

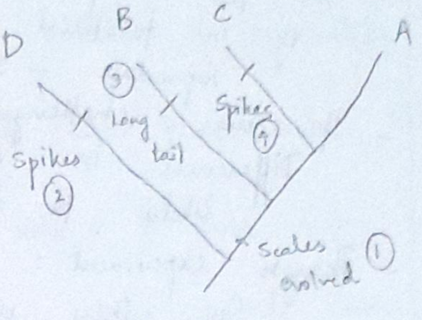
Clade (monophyletic group)
Group of organisms composed of a common ancestor and all its lineal descendents on a phylogenetic tree

The order in which taxa are written is not relevant, it carries no information. d(C, E) = d(C, D)

Constructing a tree

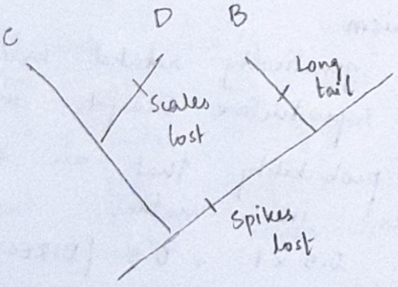
	Crest	Scales	Spikes	Long tail
A	Y	Y	N	N
B	Y	Y	N	Y
C	Y	Y	Y	N
D	Y	N	Y	N

4 evolutionary events



Ancestor
Crest, NO spikes, scale, LT

We choose a tree which has least numbers of evolutionary events is the correct tree - method of parsimony.



: 3 evolutionary events.

YES Crest Scales
Spikes NO Long tail

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Lecture 6

Social behaviour, kin selection, Altruism

Honey bees, Ants, Wasps, Termites – Eusocial insects

there, workers are sterile and work to protect queen and her offsprigs. Altruism : self sacrifice.

This is a Darwinian puzzle – natural selection should select for selfishness and not altruism.

How could altruism evolve?

Initially speculated to be designed by an intelligent designer

→ Group selection theory

- for the benefit of the group.
  Eg: in territorial species, only birds with territories reproduce – supposedly to prevent depletion of resources
- It was challenged by the book "Adaptation & Natural Selection".
  Differemes in rep. success b/w individuals are more likely to drive persistance of a hereditary trait
- Though experiment : Southern emu-wren
  Say, there were 2 types of males – selfish breeding and altruistic non-breeding male. Over time, the proportion of non-breding male should go down, although group selection should favor non-breeding.

Q: When would groups benefit from having altruistic individuals?
What is the unit of selection – individual or group?

Darwinian explanation for altruism

Idea of relatedness – helping genetically related individuals would also provide reproductive benefits indirectly.

Coefficient of relatedness (r) – probability that an allele in one individual is present in another.

1 offspring on its own : 0.5 × 1 = 0.5 [DIRECT FITNESS]

3 offspring of it's sibling : 0.25 × 0.25 × 3 = 0.75 [INDIRECT FITNESS]

So, the allele for altruism will persist if –

$r_B \times B > r_c \times C$

B : no. of relatives who survived becz of help

C : no. of offspring not produced by the altruist.

Hamilton's Rule.

Are <u>eusocial insects</u> related more to each other?

This depends on if the queen is monogamous and the haplodiploidy of eusocial insect.

In these insects, sons are haploid whereas daughters are diploid. Thus, sisters are related more to each other ($r = 0.75$) than to their mother ($r = 0.5$).

So they help raise their sisters than have their own

This supports the kin selection / inclusive fitness theory

Did haplodiploidy contribute to the evolution of eusociality or altruistic behaviour?

- Hymenoptera – female workers help raise their sisters rather than their offspring.
- Female workers are more closely related to their sisters (0.75) than their brother (0.25)
  - They are predicted to bias their help towards sisters.
  - female workers are also more related to their sons (0.5) than their brothers – so we predict them to have sons as compared to helping brothers
- Queens are equally related to sons and daughters – expected to produce 1:1 sons & daughters.
- In ant colonies, weight of females : males = 3:1

  If males are rare, then benefit of taking care of 1 male is greater than taking care of 1 female
- Doesnot fully support haplodiploidy as the driver of altruistic behaviour.

Phylogenetic relationships b/w hymenopterans

- Ancestral state was monogamy – which might have played an important role in evolution of altruism because sisters are more related to each other.
- Polyandry evolved independently later in multiple lineages
- Termites are diploid & are eusocial.

Kin Selection Theory also explains social conflict

- In many species, workers decide which larvae become queens - provisioning differently, placed in different sized cells.
- In Melipona bees, work larvae decide whether to become queen or worker. A worker on avg is related more to sister's son (0.375) than to Queen's son (0.5 × 0.5 = 0.25)
- So, becoming queen would be more costly when sisters produce more sons than the queen.
- Because - queens are overproduced
  workers kill excess queens
  too many queens reduce workforce & reduced care of larvae

Social behaviours in vertebrates

* Group living has benefits - increased foraging success, increased security, indirect fitness
* Costs - spread of parasites

Categories of social interactions

1. Cooperation
Both A and B gain direct fitness.
Eg: Male lazuli buntings - their plumage can be bright blue, intermediate or dull.
Bright male allow dull ones to establish territory next to them but not intermediate ones.
Dull males get mating opportunities; bright males get extra mating opportunity with females of dull males and they rear the offspring of bright males in their clutch

2. Cooperation after with delayed fitness.
Eg: Long tailed manakin display - two males have to work together to produce the courtship display
Only the alpha male courts with all females, the beta male is next in line & takes over when alpha dies
Other male birds still cooperate with the new beta
So, beta male gains direct fitness after delay.

3. Reciprocity

Immediate benefit for A, who might pay back B for it in a different way

Eg: Grooming in macaques – in return, groomer gets protection and may get groomed later

Experimental example

3 pairs of pied flycatchers were kept in a cage. A was presented with a tawny owl – C was allowed to go out of the cage and help mob the predator along with A, while B was caged. When B was presented with the predator, A didn't help B, because they remembered that B hadn't helped them.

Game Theory to understand cooperation

Prisoner's dilemma

Prisoner A

Prisoner B	Cooperate	Defect
Cooperate	1 year in prison for both	0 years for A 10 years for B
Defect	0 years for B 10 years for A	Punishment for mutual defection – 5 years for both

Strategies

Payoffs

Here, they cooperate with each other & remain silent or defect against each other and confess.

If A cooperates or if A defects, the better option is for B to defect – to get the lesser sentence

So what is the evolutionarily stable strategy?

Lecture 8 3/2/22

Example of applying kin selection to helpful behaviours

→ Belding's ground squirrel

Gives alarm calls when a predator is spotted.

Why? – • Benefit : alerting others could save relatives
reciprocity, sign of strength, could distract the predators

• Cost : attracting the predator

Experiment : marked population in California (over 3 yrs ~3000 hrs)
102 observations of predator - prey interactions
9 squirrels killed
22 cases where squirrels were chased – 14/107 callers were chased
8/168 non-callers were chased

So, there's a significant cost to the calling.

Also, among the callers – adult females were the largest fractions
Females are philopatric and males migrate to other areas.

Also, females are more parental than males.
Based on demographic, they showed that females call out more than expected & males less than expected

Reproductive females with relatives were more likely to call.

→ Helpers at the nest – Pied kingfisher

These birds live on banks of large lakes / rivers

1 year old males that don't have a territory can be –
- primary helpers : associate with parents & help them
- secondary helpers : help unrelated pair
- remain solitary (delayers) – wait out the year alone

1° helpers – associated with only one nest, almost always their parents
they were accepted before hatching & helped before too.

2° helpers – accepted only after hatching

Each nest had at most one 1° helper and could have many secondary helpers.

After years of observation, we could calculate costs, & benefits.

* Primary helpers help more than secondary helpers – they spend more time guarding the nest, and brought more food.

What is the cost for helpers – compare with 1 year males who bred
fraction of helpers that survive

★ % surviving to the next season

50% of primary. 78% of secondary and 70% of delayers returned / survived to the next season.

83% of females w/ 2 helpers & 45% of females with 1 helper survive to the next breeding season

★ More offsprings survived when helpers were present

No helper	1.82	⇒ 1.85 more fledling with 1° helpers
1° helpers	3.57	1.89 more with each
2° helpers	3.71	1.45 2° helpers.
1°+2° helpers	4.57	

★ Secondary helpers benefit by getting a mate in the next season

★ Calculations of inclusive fitness for male pied kingfishers —

n 52 mins

	1st year (indirect fitness)	2nd year (Direct benefit)
1° helper	0.58	0.41
2° helper	0	0.84
Delayer	0	0.29

2° helpers get direct fitness, but delayed, for helping

7/2/22

Lecture 9

Alternate hypothesis for helping at the nest

Could parental behaviour be triggered by begging calls of the young & late dispersal from nest could expose young adults to begging calls — so this could be a non-adaptive beh.

Are mechanisms of parental care same in species with helpers and without?

Mexican & <u>Florida scrub jay</u> — have helpers

<u>Western scrub jays</u> — no helpers

If its just a response to begging calls, then the parental care should be same in both species.

Prolactin is hormone that promotes parental care behaviour.

~~It~~ Prolactin level goes up in breeders after laying of eggs before hatching.

It also goes in non-breeding helpers but not non-breeding birds in Western scrub. This shows that helping is an adaptive phenomenon.

Helping is beneficial in other species too

Eg: Carrion crows – helpers are related to each other.

No. of fledlings produced and the proportion of successful breeding groups increases with

Experimental benefits of helping

Florida scrub jay population – helpers experimentally removed

No. of offsprings increased if there were helpers.

Young were lost to starvation or predation.

Presence of helpers increases hourly feeds of nestlings, so the nestlings gain more weight.

Similar results in Superb fairy-wrens

But here, the nestling weight is not affected by presence of helpers.

Less investment into the egg – lesser mean egg volume, lesser yolk wet mass / dry mass – if the helpers are present.

The female invests less in the eggs if helpers are present, because it can be made up with extra food

What ecological factors determine if birds help or reproduce?

Eg. Seychelles Warblers

Helping emerged in ~1970s, around the time when habitat was saturating.

All territories had similar predation levels, but the insect (prey) availability differed in high, med & low quality of territory.

Some of these birds were moved to other islands for protection.

Territories increased ⇒ helping slightly decreased in the first island initially when birds were removed

In other islands, mean age of breeders increased with time, and as territories saturated, helping emerged.

Habitat quality
- Birds born in high t. continue as helpers, even when low quality territories are available.
- This is because the proportion of survival and life expectancy is greater in high quality territories.
- Birds with high t. are often born in high t. themselves.
- So, habitat quality, mate availability, helper availability all play a role in decision to help.

Eusocial mammals - Naked mole rat

They are eusocial ⇒ single queen with multiple mates, where all other workers are sterile because of aggressive interactions which reduces production of sex hormone

9th Feb - prey capture videos.

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Lecture 10

Toad prey capture in common toad (Bufo bufo)

- Its prey - insects, beetles, earthworms. Predators: snakes, birds, small mammals
- Prey capture has fixed action pattern -

* Orienting, Approaching, Fixating, Snapping, Cleaning *

This is innate behaviour. Also fixed: during 'f' phase, if prey disappears, toad continues to 's' & 'c'. Its not dependent on feedback after a certain point.

Each action pattern has a particular set of stimuli RM (Releasing Mechanism)

For instance presence of prey and/or prey in lateral feild triggers RM for orienting.

Prey + Frontal visual field + far afield = Approach

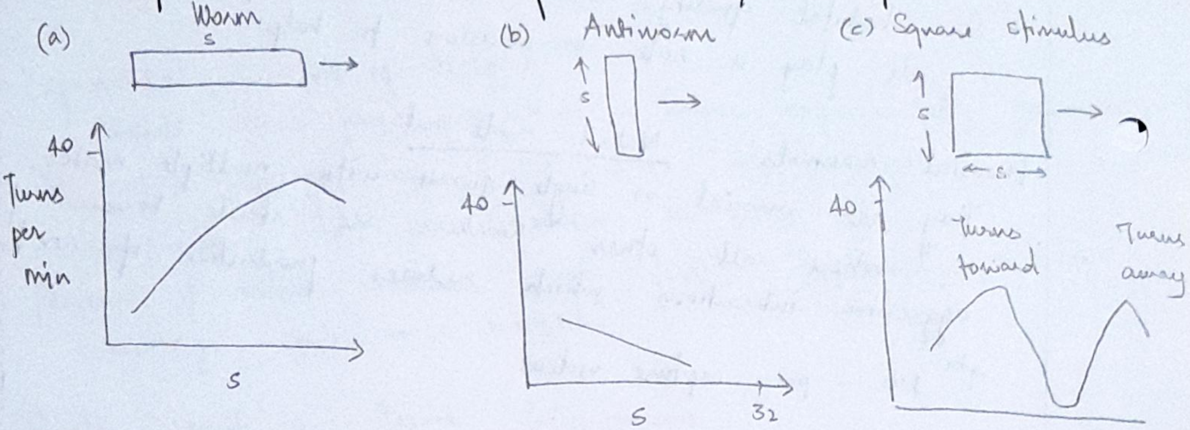
——— 〃 ——— + closer to eyes = Snapping

Prey + Binocular fixation field + within snapping distance = Snap

- So, there are not necessarily sequential –
  if prey is moving : o-a-o-a ....
  right in front of it : f-s
- So each pattern has particular sign stimuli, but its modified by motivation i.e. if its not hungry, it won't ~~hea~~ eat

Prey detection in the lab : Jorg-Peter Ewert

- Frog placed in glass cylinder, with cardboard stimuli moving in the periphery
- Cardboard were in different shapes & sizes
- They counted the no. of orientations / turns per min



- More turns/min for worm stimulus (axis of movement is parallel to its long axis) ↳ considered prey
- Antiworm is ignored
- Square stimulus – first turns towards (small square = prey)
  later turns away (large square = predator)

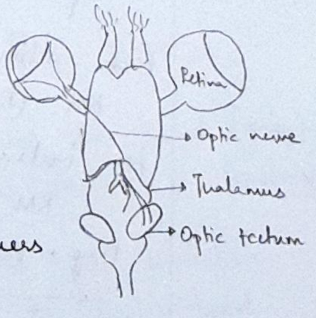
* So, shape and direction of movement are both important for prey capture mechanism

Visual pathway – Neural basis for prey detection

Visual stimuli are detected by retina

Optic nerves from retina have 2 projections :-

- Optic tectum on the contralateral side
- Thalamic projection : pretectal region



To identify the pathway we could use synaptic tracers which are transported across synapses, or by anteriograde & retrograde neurons

The activity of neurons was recorded while it was being presented with worm, antiworm & square stimulus.

They hypothesized that there would be feature detector neurons that classified orientation & movement.

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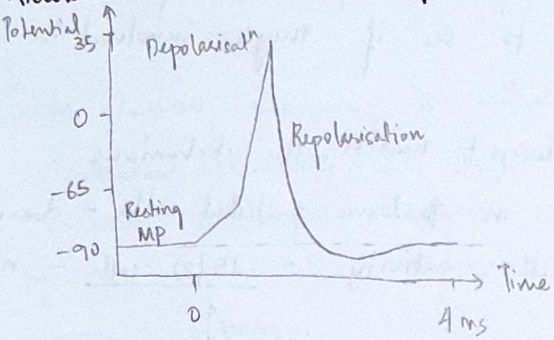
Lecture 11

Extracellular recording of neural activity

Neurons communicate using electrical potentials

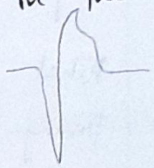


Neural activity can be recorded over different length scales (synapse - neuron - brain) and times scales (ms to days)

We put an electrode close to the neuron and record potential differences. Reference electrode is on brain surface

Since voltages are small, we need an amplifier.

What we get is the activity of many neurons in the vicinity of the electrode. If neurons are farther away, then the amplitude of waves will differ.



Waveform outside the cell

Perfect superimposition. of waveforms tells us that the APs are from a particular neuron.

Shape of AP is reproducible. Even if 2 neurons have same AP, individual neurons have refractory period (1-2 ms) (because of inactive state of Na⁺ channels & slow acting closing of K⁺ channels)

We can verify by making sure that interspike duration is never less than 1-2 ms.

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Lecture 12

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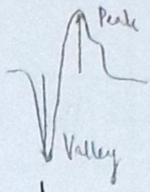
Different features of the recording (peak, valley) are plotted and this is used to sort multiple single units.



The time of APs is used to get spike train and that is used to study the activity of the neuron.

Raster and PST - used to correlate neuronal activity with behaviour

This can also be used to study sensory processing

Going back to toad prey capture.

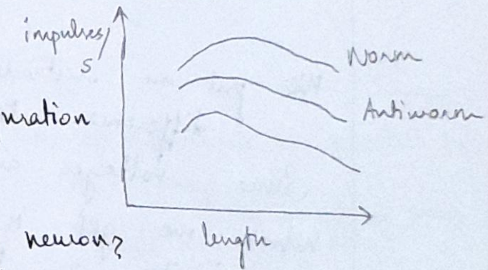
Recording neuronal activity while toad is exposed to worm or antiworm response to see if they're involved in prey capture

Response of retinal cells doesn't match the behaviour

So they recorded neurons in thalamic pretectal cells - doesn't match

They found that tectal cells' activity - T5 (2) cells - matches the behaviour

The cells didn't show variation with direction - it only responds to configuration of movement of the object



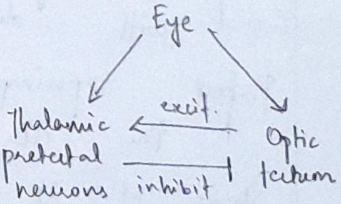
What determines 'prey-detecting' response of neuron?

- Timing and magnitude of excitation & inhibition generally determine a neuron's response

T5 (2) = T5 (1) - TH3

Tectum Thalamic pre-tectum

$$T5(1) \rightarrow T5(2) \leftarrow T3$$



- TH3 cells fire at a constant rate even when worm l. increases, whereas T5 (1) neurons fire faster as length increases.

→ Look at the graphs!

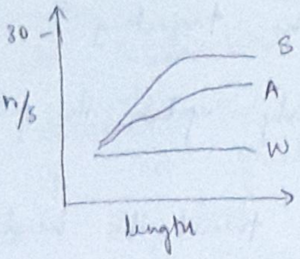
* Removing TH3 input should abolish selectivity to worm over antiworm

The no. of turns to other stimuli (antiworm, square) increases and they snap at other toads & hand & its extrimities

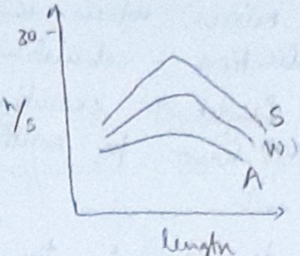
So when TH3 is legioned, T5 (2) respones are greater and less selective.

* When T5(2) cells are stimulated, the toad orients to the appropriate location in visual space

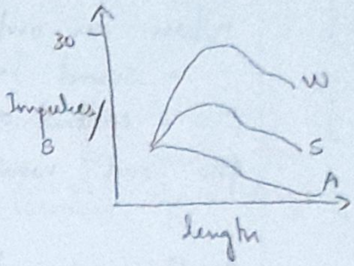
Then we can study how these cells connect to motor output cells.



TH3



T5(1)



T5(2)

Such sensory processing is called feature detection (CRS)

Command elements (ind. cells) make up command releasing systems which modulates response

Eg: T4 - stimulus moving in visual field } Orient towards prey.
T5 - prey

Neurons are tuned to a feature range within a stimulus continuum

Combinatorial coding, hierarchal organisation

Sign stimuli → innate releasing mechanism → fixed action pattern.

Feature detectors and invariance.

- Extreme form of single neuron / group of neurons that recognise a highly specific configuration of stimuli
  Eg. grandmother cell
- But toad responds to a continuum of stimuli that satisfy some configurational relationship, under a variety of conditions - shows invariance.

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Lecture 13

Owl catching prey

Barn owl : Nocturnal hunter, hunts small mammals on ground in open areas & found in all parts of world.

Neuroethology studies careful & quantitative features of a behaviour and then decipher its neural mechanism

- Not IR to detect prey - vitreous humor is opaque to IR & IR doesn't evoke pupil change

Owl typically attacked when mouse was stationary

Prey catching behaviour is complex

Owl uses auditory cues to localise the prey - not visual (dark) or smell (tissue used). In fact owl attacked the tissue attached, not mouse

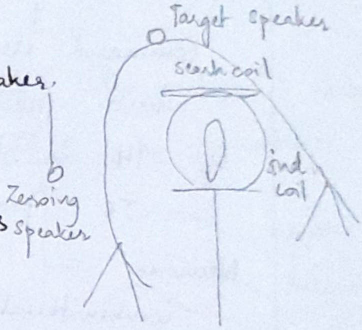
As its flying down towards the mouse, it extends the talons at the last minute, to catch the prey. It first turns towards the sound, flies down with talons at the back and at the last minute, extends to catch the prey

When an owl misses, where is the error?
- sound localization - calculating the trajectory
- control of flight & execution

Also owl would have to continuously update its path.

Anytime sound is played, the owl turned its head - it's a natural response to sound.

This is an important simplification - does the head turning accurately reflect the detection? Yes.



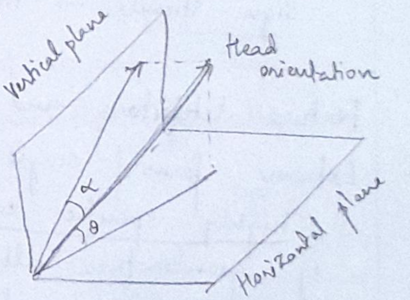
There was a Zeroing speaker and target speaker. Search coil and induction coil was used to measure the turning of head.

It was calibrated to make sure this works

It was measured in terms of -

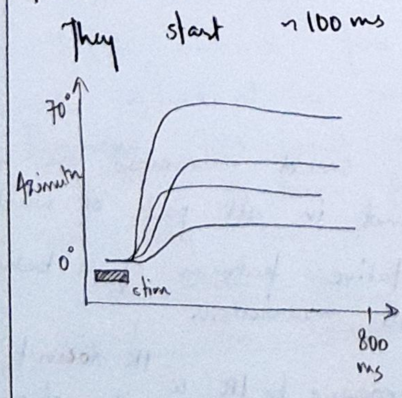
Azimuth - left / right side of owl's head

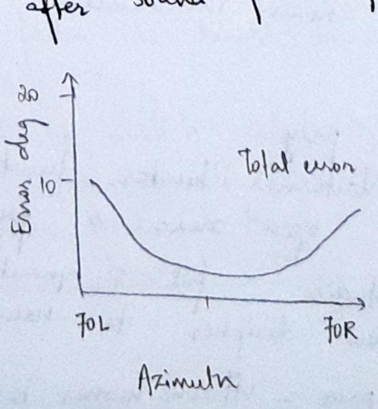
Elevation - up and down in the vertical plane

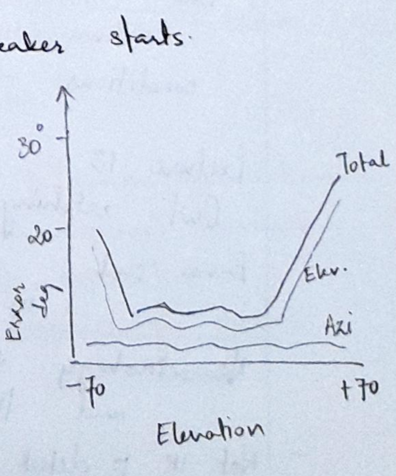


The targets can be superimposed on a 2D plane

Head movements are fast after sound from speaker starts. They start ~100 ms







ILD - interaural level difference.

Owls were trained to turn their head

Error is greater in the vertical plane than in the horizontal

Head movements are v. fast - suggests that these movements are 'open-loop': feedback is not involved i.e. continued stimulus is not ~~dire~~ required to direct the head for accurate localization

They decreased the duration of stimulus - and the accuracy is not greatly affected. The decision for turning the head is done in ~75 ms after stimulus starts playing

↓ Open loop

→ 1s stimulus

Closed loop (with feedback) accuracy is better only at angles >30°. i.e owl updates the info once it has turned its head

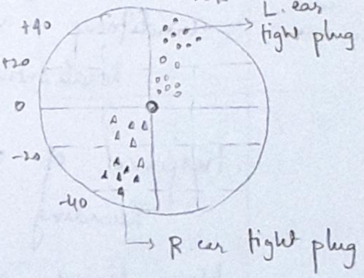
What cues can be used to locate the sound?

It doesn't move its head to localise a sound, it compares the sound detected b/w its two ears - either inter-aural time difference (ITD) or intensity difference (IID)

Plugging one ear affects sound localization ability, specifically in elevation

They plugged one ear with either loose or tight ~~plat~~ plug, which affects intensity of sound recorded and not the time of arrival

ITD - mainly used to locate sound in azimuth.



When L. ear is plugged, it looks up and slightly right. But horizontal error is smaller

ILD is mainly used to detect elevation due to anatomy of ears - R.E is lower & points up, LE is higher & points down. Feathers on the face (ruff) also contribute to directional sensitivity.

Microphones implanted in both ears to simulate sound coming from any position in the place.

You can map contours on a globe based on differences in ILD and ITD.

When ILD = 0 and ITD was varied, owl turned its head horizontally and when ILD was varied, it looks up/down.

The difference in ITD is ~ 100 μs whereas AP is 1-3 ms long. So how is localisation possible?

21/2/2022

Lecture 14

Prey capture by Barn owl : Neural mechanisms

How is location of a sound source encoded in the brain?

- Population based code
  - One population of neurons sensitive to sound from right and another to sound from left
  - Relative activity across these 2 populations decide where sound is coming from
- Individual neuron based 'place' code
  - Ind. neurons are sensitive to sound from specific place

Similar experimental set up as before - owl was anaesthetised and electrodes recorded brain signals

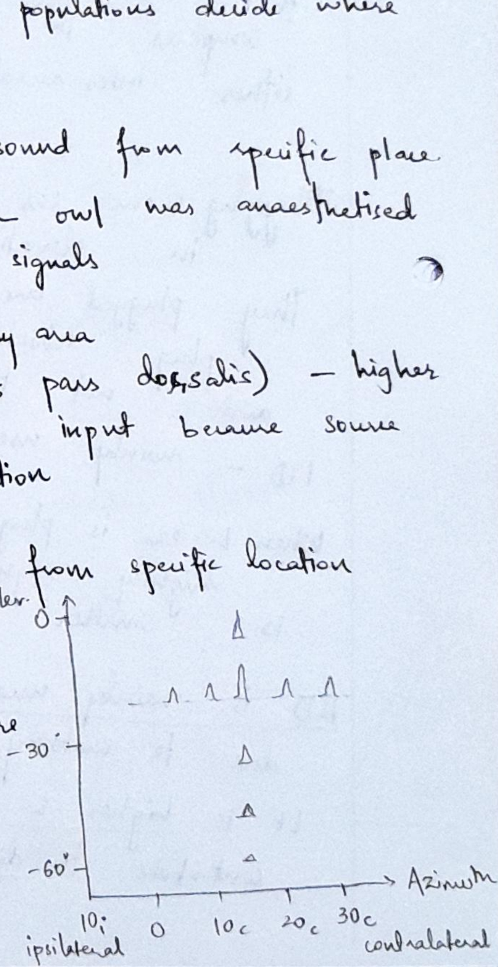
Inferior colliculus (MLD) - midbrain auditory area

MLD (nucleus mesencephalicus lateralis pars dorsalis) - higher auditory area that recieves bilateral input because source localization requires complex computation

Response of a neuron in MLD to sound from specific location

Recording from left side of the brain.

Max firing rate is b/w 5-15°c and -10° to -40° elevation - it fires much more if sound comes from these locations.



Neurons are confirmed by passing current and burning the neuron

---

We can map the firing to a contours field

Left MLD has a map of the right side of space

Neurons closer to one another localise corresponding space of the owl's surroundings. Neurons one below the other varied along the elevation, more than azimuth.

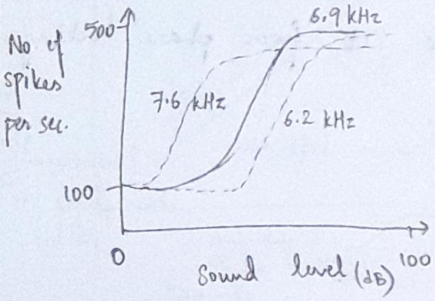
One section varies from 40°c to 15° i. So which smoothly progress in space — map is continuous and represents contralateral side more than ipsilateral

How does the computation happen?

Auditory nerve first projects to angular and magnocellular nuclei — they both project to laminar nucleus which is the first to receive inputs from both nuclei

One keeps track of time & another of intensity.

How does auditory nerve represent information?



At a given freq, activity increases with increasing intensity.

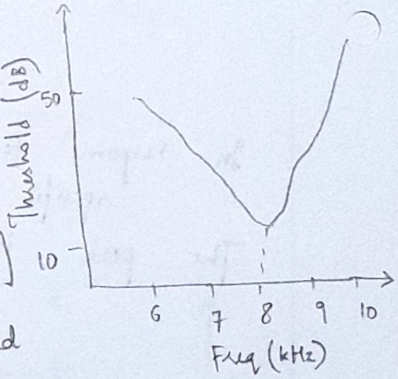
Threshold intensity at which nerve starts responding differs for different frequencies

Auditory nerve tuning curves cover a space, so certain dB and freq will activate various neurons at various rate.

This allows it to keep track of intensity

Minimum intensity that makes neuron fire faster than background firing rate. [Tuning curve] for a single neuron

This neuron is tuned to ~8 kHz



At higher intensities, neurons will respond to varied frequencies

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Lecture 15

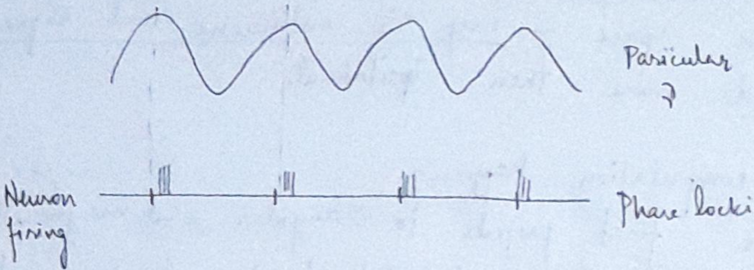
23/2/22

Prey capture in Barn Owl - Computation of ITD in nucleus laminaris

Refer to Owl auditory pathway.

Auditary nerves projects to magnocellular nucleus and later from there to the laminar nucleus, which recieves bilateral input.

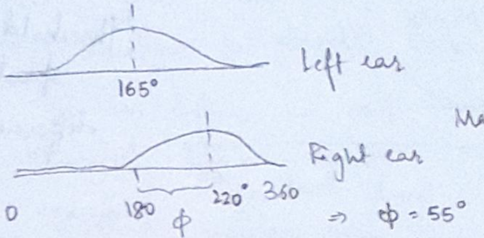
Pure tone is like this :



Neuron that responds to a particular tone (of certain freq) show phenomenon called phase locking - they fire at a particular phase of every sinusoidal wave.
Similarly, other nerves lock other phases.

How does laminar nucleus compute ITD from phase locking?

Phase histogram

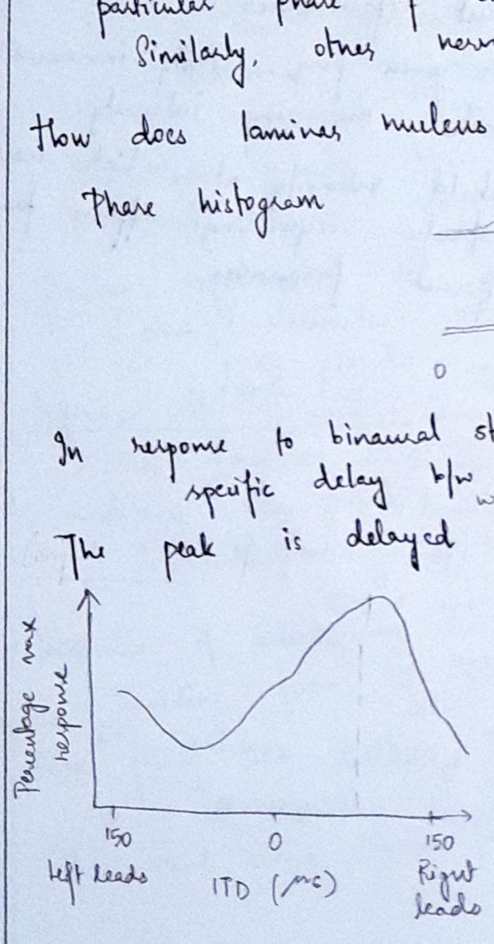


Monaural stimuli
Max phase is shifted a bit

⇒ ϕ = 55°

In response to binaural stimuli, neuron responds best for specific delay b/w left & right ear (when phase difference is ϕ)

The peak is delayed ~~in~~ when input is from the right ear



Neuron responds maximally when sound arrives in right ear ~40 μs before left ear.

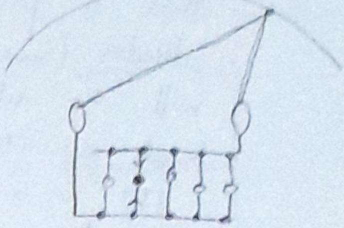
360° = 1 period of sin wave = $\frac{1}{3920}$ = 255 μs

50° corresponds to - $\frac{50}{360} \times 255 \simeq \underline{\underline{40 \mu s}}$

If right ear neuron fired 40 μs sooner, then the peaks would overlap and the neuron would fire maximally

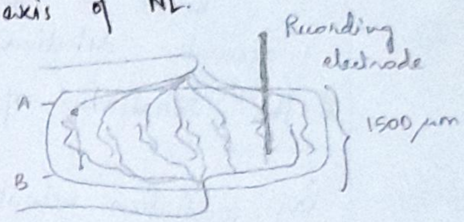
How is ITD computed in Nuclear Laminaris ? - Jeffres model

- By using a combination of delay lines & coincidence detectors. - Neurons that fire maximally when they recieve simullaneously input from left & right
- Delay lines : Axonal length based delay in arrival of action potential

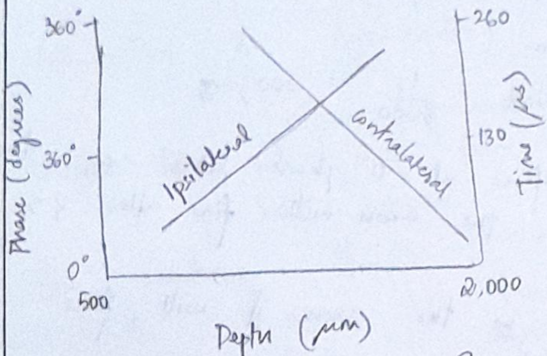


NL neurons are good candidates for coincidence detectors and the architecture of neuronal network shows delay lines.

Axons from NM enter NL through the dorsal side when they're from ipcilateral side So there are junctions or cell bodies along dorso-ventral axis of NL.



They did intracellular recording along the dorso-ventral axis.



AB = 1500 µm

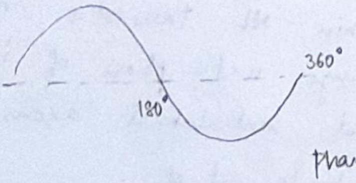
Conduction speed = 3m/s

Time difference between point A and point B - 500 µs

So, along the axis, the phase at which the axon fires will differ

Say, $f = 7.5$ kHz

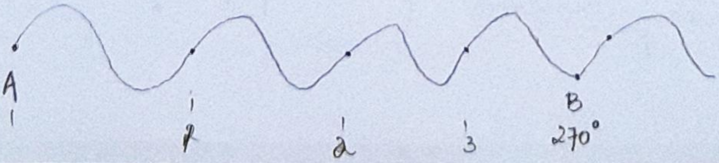
time period $= \frac{1}{7500} = 133\ \mu s$



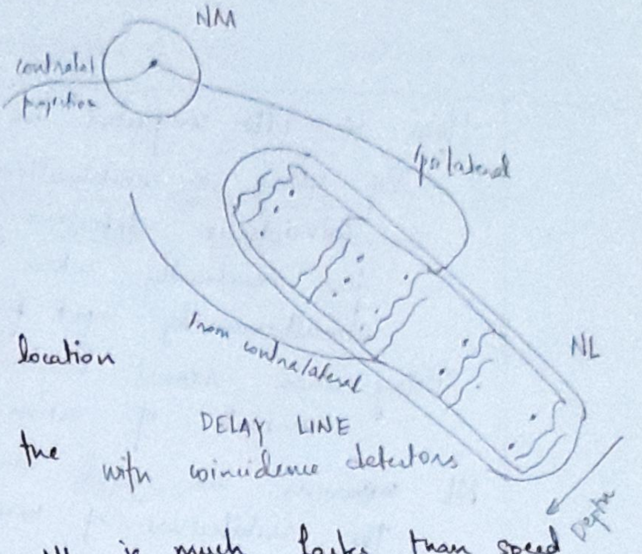
~~No.~~ Phase at A = 0°

phase at B $= \frac{500}{133} = 3.75$ cycles

∴ Phase angle changes systematically over the depth of nucleus laminaris (for all frequencies) $= 0° + 3(0) + 0.75(360) = 270°$



Lecture 16



When sound source is equidistant from both ears, then a particular coincidence detector (somewhere near middle) will be activated. Similarly, based on CD activated indicated ITD — a representation of location of the sound

The width of NL determines the resolution of detection.

The speed of conduction outside NL is much faster than speed inside — its an adaptation that helps with more accurate detection.

The reliability of phase locking also important

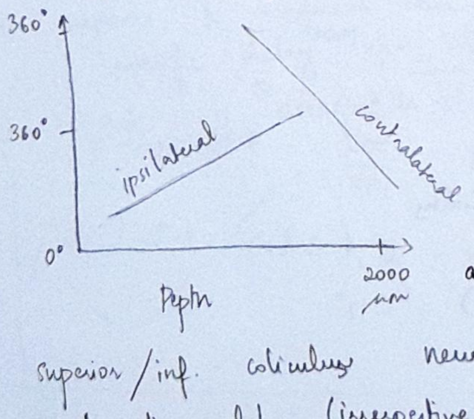
Say conduction velocity = 1 m/s = 1mm/ms

Width of NL = 1500 μm

5 kHz frequency ⇒ Period = $\frac{1}{5000}$ = 200 μs

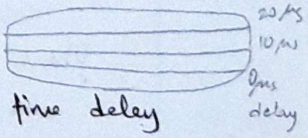
1st point in the axon fires at 0° phase, let's say, then the last point in the axon will fire after 7.5 periods at the phase of 180°.

So, at any given point in the axon, it will fire at a particular phase



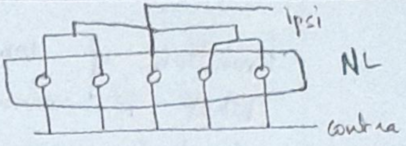
Within NL, there's a smooth change wrt. phase of ipsilateral and contralateral axons.

So particular set of cells in NL are attuned to a particular time delay



In superior/inf. colliculus neurons that are attuned to a particular ~~to~~ time delay (irrespective of the frequency)

~46-48 mins
③
Read the paper.

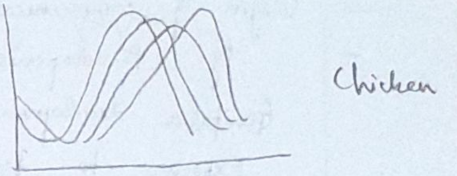


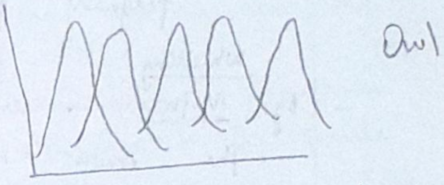
In chicken, the delay line is do. along the longitudinal axis of the nucleus laminaris.

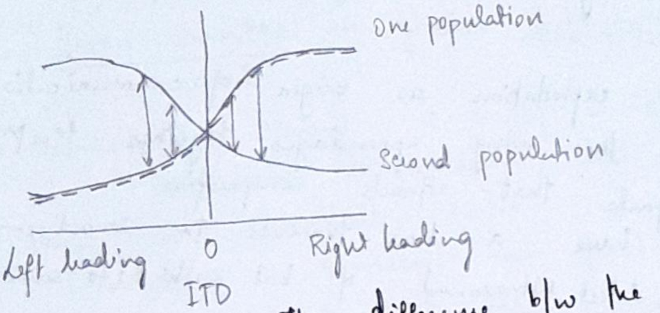
So, the resolution of detection is not as ~~rough~~ fine.

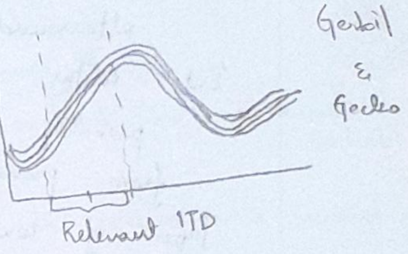
In mammals, sound processing happens in a different way. the Jeffres model can't explain it.

But they do use ITD for sound localisation. They could be using a population level code to compute ITD



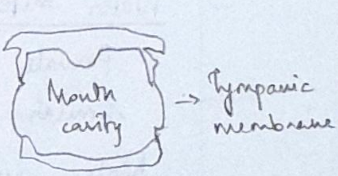






~~Lecture 17~~ The difference b/w the activity of these ~~codes~~ populations help compute LTD.

The anatomy of the brain circuit is the same, but there's an extra inhibitory connection which is important for shaping the tuning curve and computing ITD.



Geckos – They recieve input to right & left tympanic membrane through a common mouth cavity. So distinguishing ITD is harder.

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Lecture 17 — 28/2/21

Clarifications

Evolution of communication

What is communication?

A display is considered an evolved form of communication if BOTH signaler and reciever, benefit.

If costs > benefit, then display would have evolved

Origin of communication signals

- Eg: Pseudopenis in female spotted hyenas

Genitalia development in mammals is governed by hormones.

Exposure to testosterone could be a cause -

pregnant female hyenas have high level of testosterone.

but pregnant with male/female pup?

- Eg: Moths — sensory exploitation as origin of communication

Whistling

The moth rubs the wing appendages together to produce ultrasound signals that attracts conspecifics.

But moths must have a bias towards the sound — ancestors probably could detect ultrasound of bat calls (to save themselves from predation)

Tapes of courtship signals & simulated bat calls triggers female receptivity

↓ why?

- Water mites — sensory bias

Female is in prey catching position. Male makes movements similar to prey, so if it is grabbed but released

Male deposits spermatophores which is picked up by female if she's receptive

- Sensory exploitation or retention of ancestral trait?

Sceloporus virgatus : doesn't have blue patch on abdomen, but the ancestor had them

Lizard

When blue was painted blue, then lizards of this species would respond submissively.

2/3/22

lecture 18

If sensory bias exists, then we should be able to create artificial modifications to elicit preferences.

Eg: Attaching crests to different places in male auklets
How do the females respond?

Large crest > small crest > Breast crest = Control
↳ Decreasing order of sexual display frequency by female auklets.

Sensory bias or retention of ancestral traits?

- Green swordtail - genus Xiphophorus. They have an elongated caudal tail
- Having long 'sword' is costly - slows swimming & it's more conspicuous to predators, but its attractive to the female
- How did swordtail evolve?
  - Coevolution of swordtail and female preference for it.
  - Pre-existing female bias for swordtail (evolved under different context)
  - 3 criteria for establishing pre-existing -
    1) Female preference for sword is present in species with sword
    2) Preference present in species without sword *
    3) Ancestor was swordless.

Testing preference for a sword

- Males with yellow or transparent swords were placed on opposite sides of 3 compartments

We're controlling for surgical suturing ig.

- They quantified the time spent by female next to the male

More time with yellow ⇒ preference for sword

- Other controls - no tail attached, sight preferences, switching yellow & transparent tails

In fish with swordtail and sister genus without swords, females do show a preference for presence of long yellow swords.

Initial study constructed a phylogeny based on morphology and concluded that ancestor was swordless. So pre-existing bias exists in females.

Later, another phylogeny based on DNA sequencing was constructed. Based on this, they argued that ancestor had a sword, so preference is an ancestral trait.

Why have sensory bias – swordtail represents a sperm-depositing organ and that's why females prefer it.

Lecture 19

Pseudopenis in hyena

- Mother's social status is correlated with cub's status & reproductio

  By product of excess testosterone during pregnancy?

- Adaptation?
  - Display of pseudopenis could indicate subordinate status
  - Its a display in males that's co-opted by females (?)

Threat displays

Why have elaborate threat displays evolved?

Elaborate displays are used to resolve conflicts. Benefit? Cost?

Eg. Toad threat display during courtship

Toads cling to females back & wait till she lays eggs to fertilize them

Considerable comp. among males for mating – fighting b/w males to displace each other.

→ Bigger toads win more fights

Its hard to displace males & toads seem to use size to decide whether to attack. Bigger toads are less likely to be displaced or attacked.

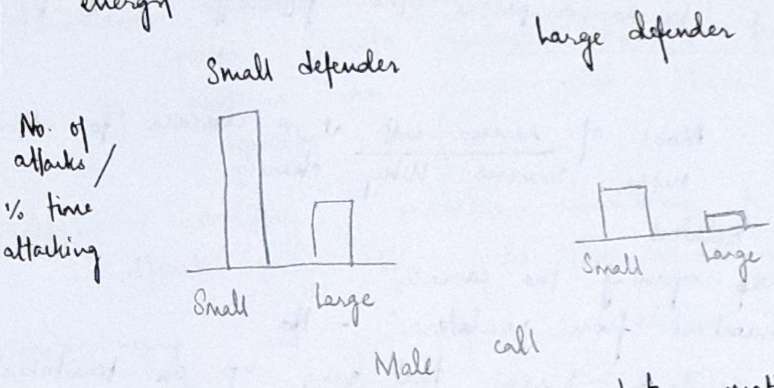
Threat display – vocalization

When male on the female's back is touched, it croaks, and attacking toad often leaves after hearing the croak.

The croak frequency is correlated with size of the toad

Larger male – lower fundamental frequency.

This behaviour is adaptive because based on the information in the threat, males wouldn't have to expend energy or risk injury by actually fighting.



- Defenders are silenced with rubber band, and playbacks are played.

Visual and audio cues are both matter.

Even if its a small defender, when playback is that of a large male, they decrease the no. of attacks.

	Signaler	Receiver
Benefit	Avoid costly fight that could be injurious	Avoid energy expenditure & risk of injury
Cost	Energy used to produce croaks	Potentially loses an opportunity to breed

Display evolves when benefits outweigh cost.

- They are beneficial when they provide an honest indication of fighting abilities – Honest signals.
- They're not prone to deception
- Individuals with poorer fighting ability cannot produce signals of higher quality

In other animals too, specific features of signals are correlated with the strength. Eg: Barking gecko – frequency of vocalization

Paper wasps – face markings

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- Cheaters are caught out : weak wasps with false paints are attacked more than expected.
- Signal production require energy
  Lizards that have run on a treadmill cannot produce as many push-ups.
- Species that donot display have more intense fights - eg. crickets
- What if signal is easy to mimic ? - It would cease to be a proper signal. There could be dynamics.
- For a weak animal, why produce the display?
  - Could be an innate behaviour
  - It would be attacked anyway, visually it's gonna be obvious.
  - It doesn't know a priori the fighting ability of attacker.

Darwinian puzzle : Mobs of ravens call at a carcass to attract more ravens. Why share?

- They are not related
- Don't need help opening the carcass
- 'Safety in numbers from predators' - No
- They are non-resident ravens that gang up on territorial pair
  Predictions: • Resident owners don't call , only non-residents call
  - Calling increases chance of recruiting non-residents
  - Resident pairs can't repel large group of non-residents
  - Food should be eaten by -
    - Solitary / pair of ravens
    - Large groups (>10 - 15) , no in b/w nos.

21/3

Lecture

Dishonest signals of communication

Types of deception - dif

→ Camouflage : a) Crypsis : blending with background to avoid detection this is a genetic factor , it cannot adapt to new environments

b) Mimesis : resembles different structures (leaf, twig etc) altogether

c) Active camouflage - visual deception by changing the colour of the body.

→ Mimicry

Ability to reflect similarity in appearance, scent, display or behaviours

1) Defensive mimicry - weaker prey species to fend off predators

2) Baterian mimicry - harmless species mimicking certain cues used by dangerous / harmful species.

This is like a parasitic behaviour

Difference b/w defensive & Baterian ?

3) Mullerian mimicry - similar signals produced by two or more species, with mutual benefit to each other.

Eg. patterns on wasps and bees. but they're not equally harful.

4) Aggressive mimicry - predator mimicking to be harmless to attract prey. Eg: spider tail horned viper

5) Automimicry - one part of body mimics another part to confuse the receiver. Eg: eye spots on butterfly & tigers.

Niche partitioning

↳ local environment of a partical species.

Species break up resource pool ∵ theory of limiting similarity

Eg: firefly species flash lights in different patterns.

This is important to recognise individuals of the same species, leads to reproductive isolation.

Aggressive mimicry egs.

Female Photuris firefly mimics Photuris female to attract males and prey on them.

Katydid cicadas - make clicking sounds to attract different species.

Why not evolve the ability to distinguish or change the signal?

→ Novel environment theory: they haven't had enough time to evolve the ability. Also possibly due to disruptions

→ Net benefit theory: ignoring signals in fear of mimicry will cost the individual. No evolution to move away because there's net benefit.

Sexual deception by Orchid (Australian)

Male thynnine wasps are attracted by odor and appearance of female Australian orchids, shaped like females. The plant decieves the males to use it as a pollinating agent. This is similar to Batesian mimicry.

Sundews exude droplets that look like sugary fluids, but are instead sticky which traps the insect

→ Tactical deception

Use of signals or displays other than normal repertoires to confuse individuals or attract females while deceiving other males.

This is done through sensory trap hypothesis:

sexual signals can evolve in a way s.t. one sex uses deceptive mimicry to manipulate the other sex into mating

Eg. Lyrebirds

Males climb on a hillock & display for the female. If the female starts leaving, male mimics mob calls to confuse the female & mate with it.

This also attracts smaller birds to add to the commotion. Lyrebirds can mimic a whole range of birds and their mobbing calls.

Eg: Eavesdropping in Tungara frogs

Male frogs have courtship calls, which attracts predator bats. 'Chucks' in the calls / vocalisations increase when they are present in larger groups. Chucks attract bats, so they are dropped when frogs are present in smaller groups

→ Environment also dictates signal

Nestlings of ground birds have high frequency calls which doesn't travel far & reduces the risk of predation.

When tree nesting chicks (with low freq. calls) are placed on the ground, they experience higher predation rates.

23/3

Lecture

Interaction dictates signal properties

Great tits call differently when they see a flying hawk (7.5 - 8 Hz) vs a perching hawk (4.5 Hz)

They sound a harsh call to its offsprings when its a snake and softer sound for a crow.

(?) → High freq. when the hawk is far away and can't hear the call? — Not sure.

Softer call - burrow into the nest when there's crow

Acoustic niches — hawks can't hear ↑ frequencies very well, whereas the chicks can hear them.

Convergence of alarm call signal — different birds have evolved very similar successful alarm calls.

Other kinds of deceptive signals —

1. Feigning death — possums, humans - grizzly
2. Concealment — cephalopods using coconut shell as protection
3. Deimatic distractions to draw attention elsewhere.
   Horned lizard shoots/ squirts blood from its eyes, which distracts the predator.

→ (?) Combating novel environment theory —

Chorthippus grasshoppers — males from roadside produce signals with elevated frequencies as compared to their non-roadside conspecifics

⇒ Signals don't change fast enough? They change v. quickly?

Movements

We can classify movements based on different criteria -

- Innate / Hard-wired vs Learned
- Based on muscles involved - simple vs complex
- Neurons involved - Reflex movements vs Planned/complex.

We'll focus on 3 types of movements -

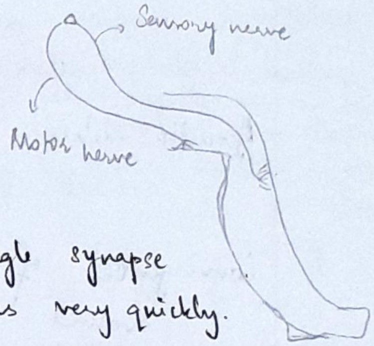
Reflexes Rhythmic movements Complex movements.

Reflex movements

- No "thinking" involved ; reflex circuits pass through the spine or brain stem, but not cerebral cortex
- Open loop - doesn't require continuous stimulus.
- Very fast

Examples

1. Knee-jerk reflex



It takes 100 - 100 ms to happen

The fibers are myelinated, there's a single synapse in the spine, so the reflex happens very quickly.

Removing-hand-from-hot-pan reflex also occurs in the spinal cord.

2. Pupillary reflex

Pupils widen / shrink based on ambient light available

Retinal nerve → Midrain → Ciliary muscles
(Ganglion cells)

Midrain → Pretectal nucleus
Midrain → Edinger-Westphal nucleus → Ciliary muscles
Pretectal nucleus → Edinger-Westphal nucleus: Right & Left

Evolutionary importance - reflexes are very important for survival

Eg: Circuitry for escape response is conserved across taxa.

Missing reflexes can be used to diagnose which parts of neurological system are damaged.

Reflexes can also be modular ; & then there's habituation.

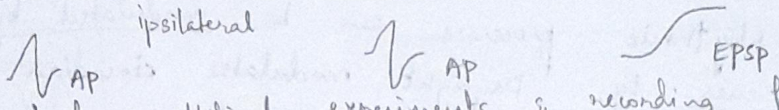
- Only 8 type of neurons; Small – not so easy so paralysed cell recording

---

Tadpole : Model system to study movement

Tadpoles have relatively smaller numbers of neurons. When tadpoles first emerge, they tend to stick around for a day or so. But when touched, they have a reflex to move away. – swimming response

Skin → RB sensory neurons on skin ⟶ dlc dorsolateral commisural interneurons ⟶ Motor neurons (contralateral) → Muscles (contralateral) ↱ swim response



Something about parallelised experiments & recording from neurons

dlc neurons produce excitatory post-synaptic potential in the motor neurons. The magnitude of EPSP depends on number of dlc neurons that are active

24|3|22

Lecture

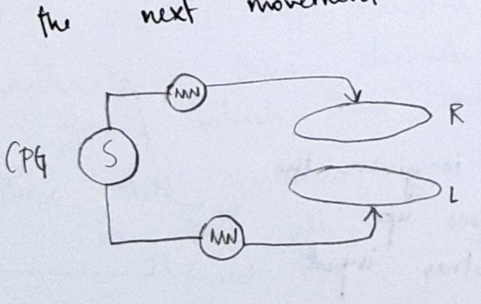
Rhythmic movements

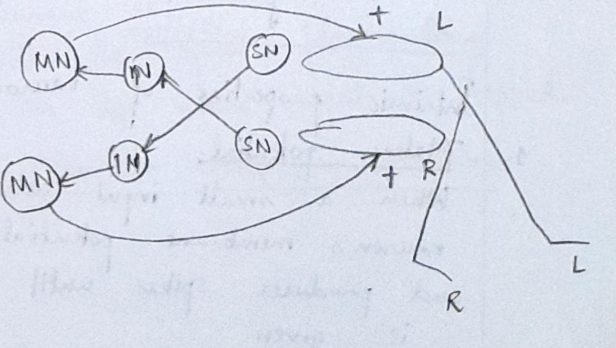
History

Early idea : 1) They are just a chain of reflexes
2) They're due to Central Pattern Generators (CPGs)

1) Chain of reflexes

Each movements acts as a stimulus, ~~to~~ which activates the next movement and so on.

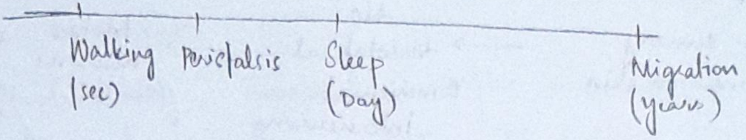




In the chain of reflexes model, sensory input is very important. In some bird & in a cray fish, even when sensory inputs were cut off, the rhythmic movement didn't stop, they were still produced

In CPGs, there's no oscillation in inputs –

Different timescales of rhythmic processes:



The rhythmic processes can be modulated by external cues. Eg: Daylight modulates circadian rhythm.
But these movements are produced even in the absence of any inputs.

Fictive motor patterns: even when neurons are isolated in vitro, they show the same rhythmic activity as the movement / behaviour.

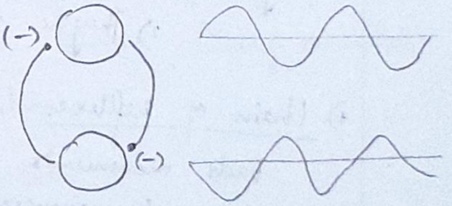
Mechanisms

1. Individual neurons can act as pacemakers – they produce oscillatory activity. Any neurons connected to this neuron follow its activity.

   Intrinsic oscillator → Follower

2. Half center oscillator

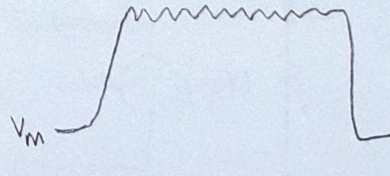
   There, two neurons inhibit each other one after the other.
   So, they oscillate in opposite phase



Reciprocal inhibition

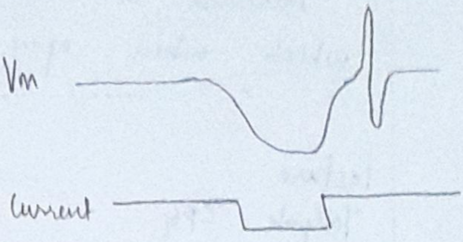
Intrinsic properties of neurons

1. Plateau potential.
When a small input current is given, the neuron's membrane potential goes up and produces spikes until another input is given.

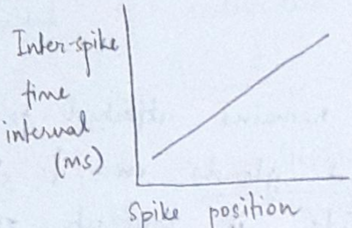


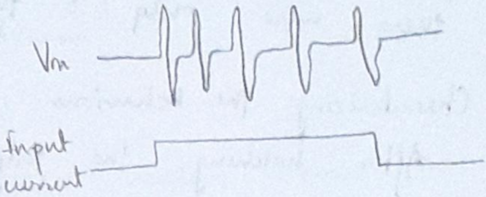
2. Post-inhibitory rebound potential

It's a feature where-in after a long inhibitory pulse, the receiving neuron fires a couple of APs. This is counter-intuitive, but observed in a lot of neurons, including CPGs.



3. Spike frequency adaptation





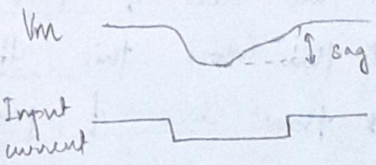
When there's continuous input or a neuron is firing continuously, the duration of 1st goes up. This gradually reduces inhibitory spikes, which allows the second neuron to produce a post-inhibitory rebound potential.

Ion channels

→ Ih - HCN channel

- Hyperpolarisation-activated ~~cation~~ ~~cu~~ cyclic nucleotide channel

When there's a long hyperpolarising input, these HCN channels open, allowing cations to come in, which creates a sag in the membrane potential, as the cell tries to drive it back to resting membrane potential.



If negative/hyperpolarising current is given for a long time, then these channels will be open for a long time, which can cause an AP when input is stopped.

These HCN channels are sensitive to cAMP concentrations in the cell.

Ca^{2+} activated K^+ channel (K_{Ca})

Permeability of this K^+ channel varies with Ca^{2+} conc. in the cell

Increased Ca^{2+} in cell increases the conductance of K_{Ca} channel, which when open hyperpolarises the cell.

28/3

Lecture

Tadpole CPG

People wanted to study vertebrate CPGs, and in tadpoles, the no. of neurons and connections were very less, and there were only 8 types of neurons.

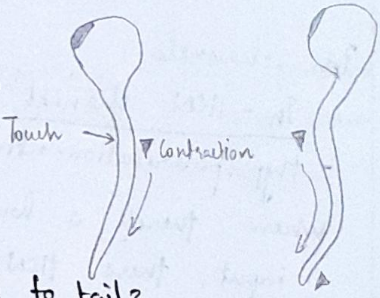
Characterizing the behaviours

After hatching, the tadpole remains attached to a surface for a day through cement glands on its head

But if touched on one side, it contracts on the other side and swims away. A small simulation (touching) elicits seconds to minutes of swimming (rhythmic behaviour).

The contraction progresses from head to tail. After initial contraction, the other side also contracts.

And it alternates b/w 2 sides & ultimately the tadpole swims away.

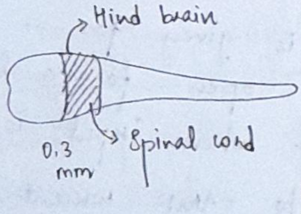


* How does it start?

* How does this alternate?

* How does it progress from head to tail?

\# α - bungaro toxin – Ach receptor blocker. This paralyses the animal, but neurons still generate APs.



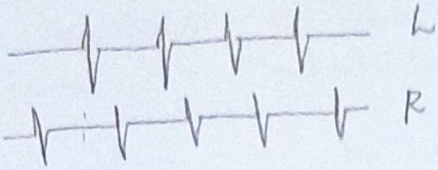
Stimulating the hind brain causes long minutes of swimming – fictive motor pattern.

Removing this segment will not produce behaviours.

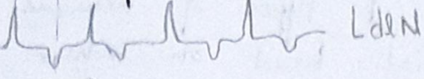
The CPG in this segment requires an external stimulus (touch) to start producing APs.

#Also, use neurotransmitter blockers to figure out which NTs are released.

Extracellular recording in spinal cord axon shows that the brain sends rhythmic APs to the muscles.



Intracellular recordings gives us information about membrane potential of individual neurons.



Recording from a particular LdlN neuron shows that its excitation is synchronised with motor neurons of Left side. Moreover, when the Right side motor neuron fires, there a hyperpolarisation of LdlN → there's an inhibitory input.

- After recording, a dye can be injected into the neuron, so in later histology study, this tagged neuron can be studied further.
- You can also record from 2 neurons simultaneously. Fire one neuron and see the effect on the second neuron – whether it provides EPSP or IPSP. It can be monosynaptic or disynaptic – which can be figure out based on delay & variability of EPSP shape. #

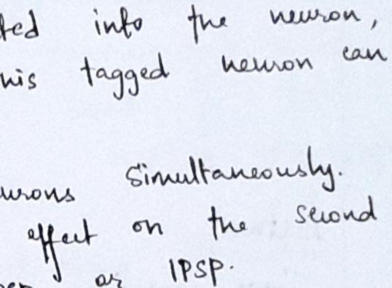
These methods can be used to figure out the circuitry of particular behaviours.

- Also, we can record individual neuron response to certain input current. This can tell us about the kind of ion channels expressed in the neuron.

Eg: descending interneuron (dIN)

This neuron fires only once when prolonged input current is given.

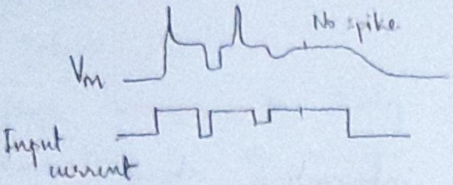
In this case, inactive Na^+ and slow-opening K^+ channels contribute



Also, this cell doesn't fire a post-inhibitory AP

What happens when hyperpolarising current, a strong one, is given when V_m is already slightly depolarised, then the dIN neuron fires. This post-inhibitory rebound is specific to hyperpolarisation in the midst of depolarising current.

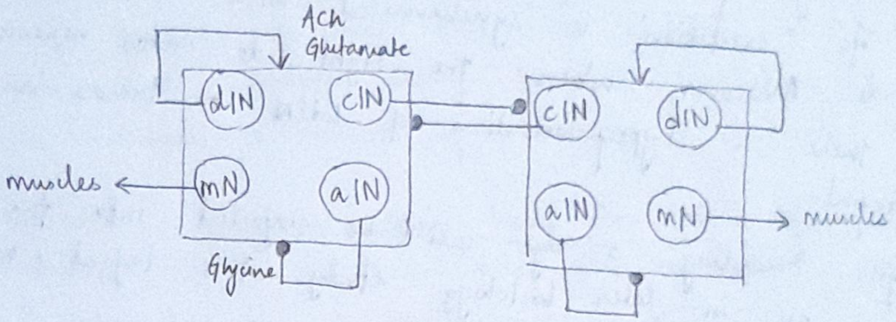
⇒ Hyperpolarising current closes the slow-opening K^+ channels.



This is to characterize intrinsic properties of the neuron.

The circuit is made of 4 types of neurons –

\# Interneurons are classified based on where they send their axons/ where they're present.



Lecture

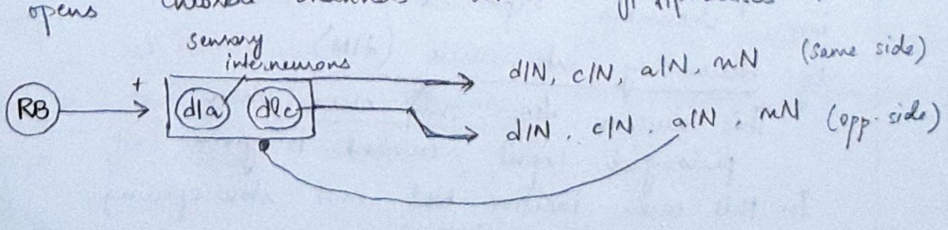
30/8/22

Three questions in tadpole movement –

1. What starts the swimming?
2. Mechanism of Left-Right alternation
3. How does it progress from head to tail?

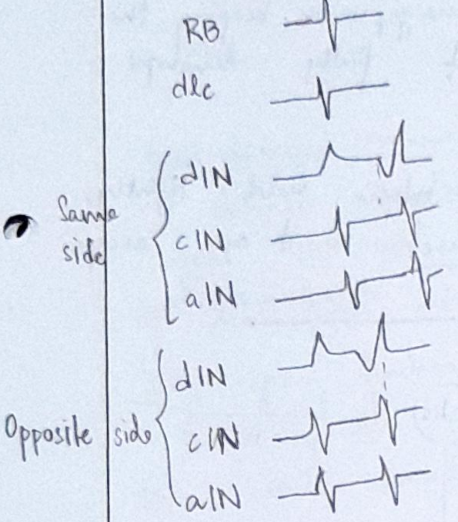
- dINs stimulate all ipsilateral group of neurons including itself
- aINs inhibit all ipsilateral groups
- cIN inhibit all the contralateral groups.

\# Glycine opens Chloride channels which hyperpolarises the neuron.



There are also gap junctions (resistive connections) among neuron group, which allows transmission of signal.

- dIN has a longer shape ie ~~de~~ remains slightly depolarised ⇒ when it receives inhibitory input, it produces a post-inhibitory rebound AP.



The opposite side from RB cells always fires first (triggered by dlc). As Op. dIN is depolarised, the signal from same cIN reaches and inhibits it – so there's a post-inhibitory rebound in the Op. dIN. This further inhibits sa. dIN, which also fires a post inhibitory rebound AP.

aIN provides inhibitory input to sensory interneurons, which shuts off any further input from them.

dIN spikes only once, then plateus – this is very important for generating rhythmicity.

This is what generates the left-right alternation.

aIN's role is not very clear yet, but even when spine is split in the middle, half of it can still produce some rhythmicity.

→ How does it propagate?

dINs send excitation to the next segment down the spine. The consecutive segments ~~do~~ receive lesser excitation, so the strength of the signal is reduced. So this progresses slowly down the body.

mhrs
medial
hindbrain
reticulo-
spinal
neuron

The whole thing stops when it receives strong inhibitory input from elsewhere. mhrs neurons project to spinal cord, where they inhibit the swimming neurons

This neuron has tonic activity on the first day of life. when the cement gland is stuck to a surface

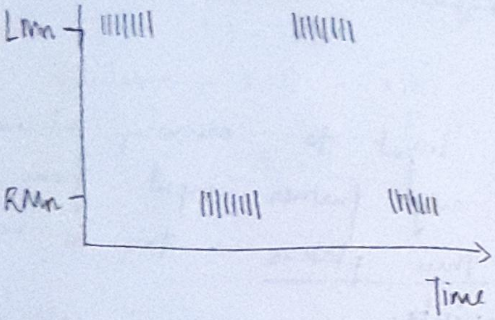
So it is activated when the tadpole bumps into another surface.

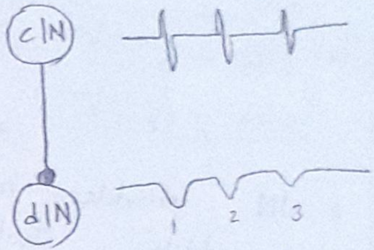
Disrupting mhrs neuron makes the tadpole more active in the first day which increases predation rate.

So tadpole invests considerable energy in keeping the mhrs neurons active till it fully develops.

Another rhythmicity in ~~neuron~~ tadpole: when held tightly, it has a struggling response so it can escape

Rhythm progresses due to short-term depression in a modified circuit





Short-term depression
2nd pulse is smaller than the first one

The neurons identified in this circuit are similar to swimming neurons. but include others as well.

The Left Mn fires, inhibits the Right Mn but there is short term depression, which releases the right side from inhibition, so RMn fires and inhibits LMn.

31|8|22

Lecture

Songbird

Model organism for complex movement sequences: Zebra finch

Their song constitutes of 4 notes that are characteristic and are produced in the same sequence

a b c d
100ms 40ms

The entire song is of duration of ~1 second
Notes are produced during exhalation, and the gaps are during inhalation.

Goal-directed movements: a set of movements that are chained together in a particular order to acheive a goal. Its not necessarily rhythmic.

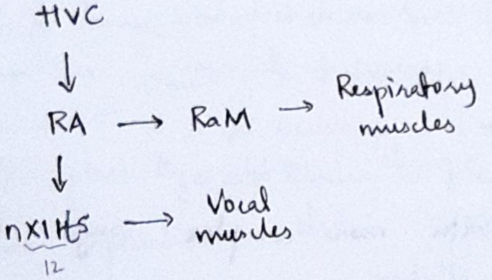
Eg: Zebra finch song, free-throw in basketball.

In Zebra finches, this is a learned complex movement.

The sounds are produced by the syrinx & respiratory organ

Here, each sound is a combination of small movements.

Brain regions involved - HVC ~ premotor cortex



HVC : controls the timing of song production, & the order of notes

If HVC is lesioned, there's no normal song production.

Effect of Temperature

With increased temperature, movement of molecules & metabolic processes' rate increases, so synaptic transmission should speed up. Cooling slows down synaptic transmission, axonal conduction

When HVC is warmed, all the notes become slightly shorter & conversely, when cooled, the song proportionately stretches by ~ 10 ms when ΔT ~ 4-5°C

The gaps don't stretch & compress by the same proportion

Cooling RA nucleus didn't affect the timing of the song.

HVC recording during singing : a particular neuron would fire a burst of action potentials for particular note, or particular time during the song.

This gave rise to the idea that there are <u>particular neurons</u> that <u>represent a particular time period</u> (~6 ms) during the song & activate the next set of neurons required.

This is called the <u>feedforward circuit/chain</u>

<table>
<tr><th></th><th>a</th><th>b</th><th>c</th><th>d</th></tr>
<tr><td>1</td><td>||||</td><td></td><td></td><td></td></tr>
<tr><td>2</td><td></td><td>|||</td><td></td><td></td></tr>
<tr><td>3.</td><td></td><td></td><td>||||</td><td></td></tr>
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</table>

1 → 2 → 3 → 4

Different sets of neurons fire during ab gap vs bc gap

The sequential firing is also observed in the hippocampus – it keeps track of the position of the rat.

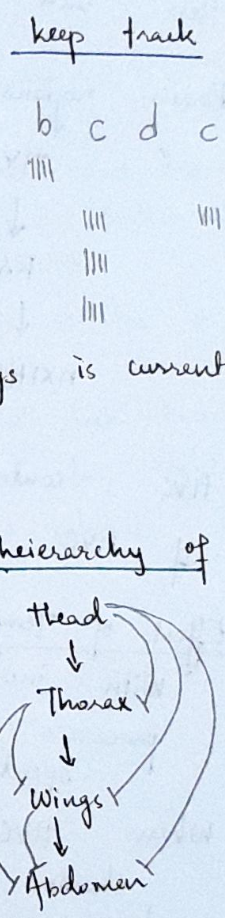
In Bengalese finch, neurons firing pattern <u>keep track</u> of the <u>order of sounds produced</u>.

<table>
<tr><th></th><th>a</th><th>b</th><th>c</th><th>d</th><th>c</th><th>b</th></tr>
<tr><td>When note b is produced 1.</td><td></td><td>||||</td><td></td><td></td><td></td><td>||||</td></tr>
<tr><td>When note c is produced 2.</td><td></td><td></td><td>||||</td><td></td><td>||||</td><td></td></tr>
<tr><td>When note c is produced b4 d 3.</td><td></td><td></td><td>||||</td><td></td><td></td><td></td></tr>
<tr><td>When note c is produced after b 4.</td><td></td><td></td><td>||||</td><td></td><td></td><td></td></tr>
</table>

Recording in birds with more complex songs is currently deficient.

Another eg. Grooming order in fruitfly
there, the <u>order</u> is maintained by <u>heierarchy of inhibition</u>.

Head is the most important segment, so it is groomed first, & it inhibits other segments.



1/4/22

Lecture

Neuromodulation of behaviour

In a reflex arc, the responses to stimuli are identical

Motivational systems: Responses vary based on the internal states which affect the perception of stimuli.

Motivation: physiological state of the organism that can modulate sensory perception and processing

Neural plasticity: ability of NS to adapt its response to stimuli by reorganizing its structure, functions or connections.

Two mechanisms :-

Structural reorganisation of networks

- Generation of new neurons & glial cells
- Elimination of older cells
- Changes in dendritic ~~cells~~ structure of neurons
- Retraction & outgrowth of axon
- Dramatic change in behavioural response, common in seasonal breeders

Chemical modulation of networks

- Through peptides biochemical switch
- Changes are fast but short-lived

Eg: Dendritic plasticity: Seasonal changes in weakly electric knife fish

They have specialised electric discharge organs. There's a pacemaker neuron in medulla oblongata which generate APs, but its not solely responsible for electric discharge, which only occurs in breeding season.

There was another prepacemaker nucleus in dorsal thalamus which projected to pacemaker neucleus.

Multipolar neurons in pre-pacemaker had 3-4 dendrites branching in 3 different territories - medial (>50%), ventral and dorsolateral.

Nucleus electrosensorius : sensory processing area

(48) 'Chirp' response in knifefish

- l-glutamate injection to pre-pacemaker leads to chirping behaviour, irrespective of maturity.
- Experiment :

One group provided with artificial rain - medial branching exists.

Another group kept in dry season - medial branching greatly retracted.

→ Structural reorganization in white-footed mice

Spinal nucleus of bulbocavernosus - innervates muscles responsible for ejaculation etc

- Avg length of dendritic arbor reduced in castrated mice
- This could be rescued by testosterone implants
- Shorter day length causes regression of testes → reduction in testosterone level which affects androgen sensitive areas.

→ Structural reorganisation mediated by glial cells.

hypothalamic neurosecretory system - Vasopressin regulates osmolality

During prolonged dehydration, glial cells shrink and the juxtaposed neurons* extend their processes in the free space which increases production & release of neuropeptide

* paraventricular neurons

Lecture 6/4/22

Neuromodulation

Neuromodulators are chemical agents that can change the functioning of neurons and networks of multiple synapses.

Unlike neurotransmitters, neuromodulators are not always released in the synaptic cleft, ~~to transmit information from~~ and their activity is not restricted to the post-synaptic neuron - they can diffuse & bind to other neurons.

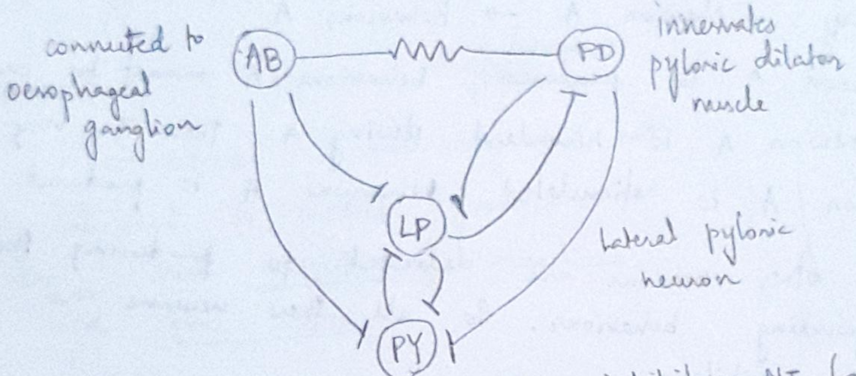
Neuromodulators bind to GPCRs (metabotropic receptors) ⇒ they act on longer timescales than NTs.

Stomatogastric ganglion in crustaceans -

- controls feeding activity and digestive system of animal
- It has 3 ~~pa~~ teeth-like structures (together called gastric mill) that move in concert to . There's also a pylorus.
- The ganglion innervates midgut and hindgut of the animal.
- Direct recording is possible
- Ganglia of the SNS -
  - OG - oesophagal ganglion
  - CoG - commisural ganglion
  - STG - controls muscles of gastric mill and pylorus

The neurons are self-oscillatory

Pyloric activity filters food. Gastric activity is stimulated only in presence of food



Here, glutamate - inhibitory NT (activates Cl^- channels)

Researchers recorded from various neurons of ST Ns when bathed in saline vs when exposed to different neuromodulatory compounds.

Eg: Adding serotonin to haemolymph of crayfish modulates its behaviours when faced with much larger opponents, the usual withdrawal is abolished

Conclusion: Neuromodulation increases the range of possible responses from the same network

7/4/22

Lecture

Neuromodulation

Same stimulus can produce different movement based on structural changes and biochemical context.

How are decisions made?

Nixon's lab :	Odour A	Odour B
	Lick	No lick

The mouse has to distinguish between two odours and change its action. Sensory neurons detect the differente odors & motor neurons convey behavioural response

Sensory neurons → Decision neurons → Motor neurons

1. Command neuron

There are distinct, particular ~~behaviour~~ neuron(s) that produces a particular behaviour.

Say : Neuron A → Behaviour A

Important criteria

- If neuron A is removed ~~produced~~, behaviour A won't be produced
- If neuron A is recorded during A, then it's very active
- If neuron A is stimulated, behaviour A is produced

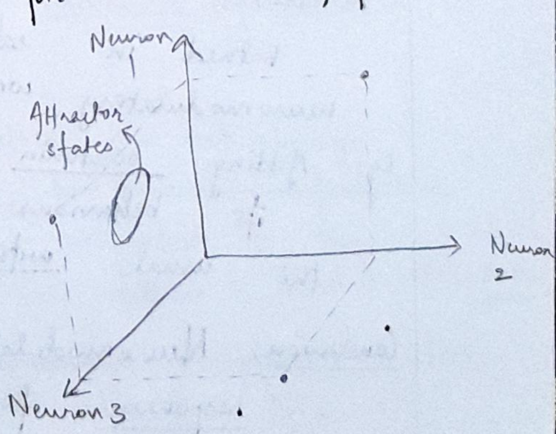
Similarly, other neurons are dedicated to producing their corresponding behaviour. So all these neurons are mutually inhibitory.

This idea comes from initial studies in invertebrates. But this mednot be true for all individuals / specie.

2. Dynamic system

Same set of neurons produce ~~the~~ different levels of activity

These neurons fire differently during different behaviours.



24/4

Eve Marder lectures

Part I : CPGs

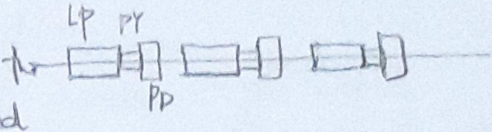
Crustacean stomatogastric ganglion

When recording from lobster pyloric rhythm in vivo, they found a triphasic rhythm of 3 neurons – LP . PY . PD.

This rhythm changed with the behaviours of the organism.

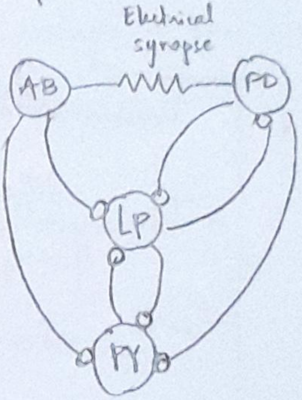
Usually, the nervous system is fixed in vitro and kept is a physiological saline solutions. Neurons of SGG are recorded through microelectrodes, and also nerves are recorded extracellularly

The circuit (in isolation) produces the same fictive motor pattern observed in the live animal, without any input from muscles.

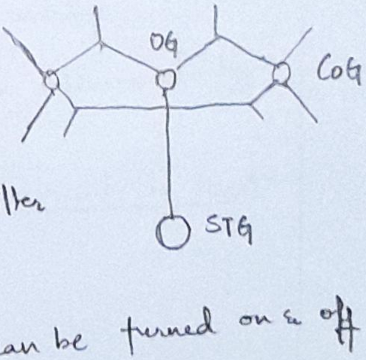


Connectivity of pyloric rhythm

The connectome is necessary, but not sufficient to predict dynamics – we also need weights of connections and time scales.



Commissural & Oesophageal ganglion project onto the STG via the stomatogastric nerve



When recording from all neurons – 2 rhythms emerge –

1. Pyloric rhythm - always on. moves the filter at the back of the stomach
2. Gastric mill rhythm - episodic - moves the teeth inside the stomach - can be turned on & off

Full connectome – involves pyloric rhythm neurons. which are also connected to gastric mill rhythm

Questions about CPG :-

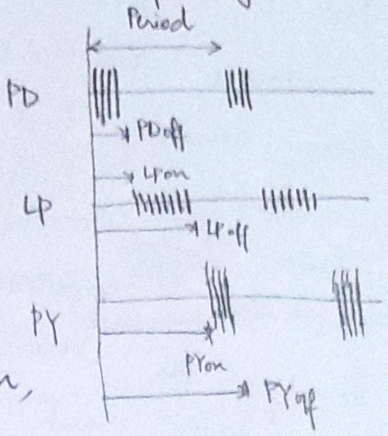
→ ½ center oscillator

1 What generates the rhythm? a) Pacemaker neurons b) circuit interactions

In pyloric rhythm, AB - pacemaker neuron, connected to PD neuron

2. What determines the phase relationships of rhythm?

The pyloric period can vary quite a bit (0.6 - 1.6 s), but phase relationships (eg. $\frac{\text{PD on}}{\text{period}}$) of relative timing are invariant



<u>Phase constancy</u> is <u>not</u> an automatic property - the firing of neurons change to maintain the same pattern, same phase constancy.

Neurons can <u>switch between functional circuits</u>

Eg: LG neuron fires with gastric mill rhythm when it's on, and with the pyloric rhythm when gastric rhythm is off.

Part II Neuromodulation

How different modulators (neurotransmitters) affect the firing patterns of particular neurons.

Distinct activity patterns that represent stable states of neural network

Attractor states : These are stable states of 3 neurons corresponding to certain behaviour.

Eg: Leech - touch can result in the leech swimming or crawling away.

They measured a population of neurons, which showed different patterns of activity for swimming & crawling.

Optical imaging - recording electrical activity neuron through light using
1) voltage sensitive dyes
2) Ca^{2+} indicators.

Based on this, they found evidence for attractor-state model - relative activity of neurons is important (Look at the paper)

In dynamic behaviour, all neurons matter - you would need to make multiple measurements at the same time

Hyperpolarizing cell 208 during a stimulus biases a the leech to swim & depolarizing it biases leech to crawl & delay swimming.

Ind. Discriminator cells - showed activity just before expression of actual behaviour

Zupane Group discriminator cells - produced subtly differentiated activities, 300 ms before a specific response

Individual and group disc. cells don't overlap.

- Decision depends on rest state, which is influenced by past behaviour and motivation
- After each stimulation, decision-making circuit is reset

Lecture 11/4/22

Anti-predator behaviours

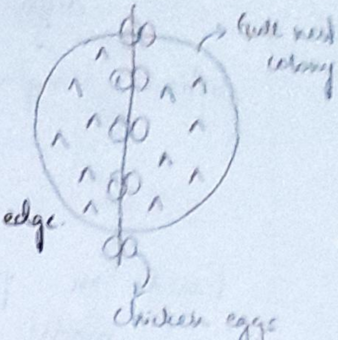
1. **Mobbing**

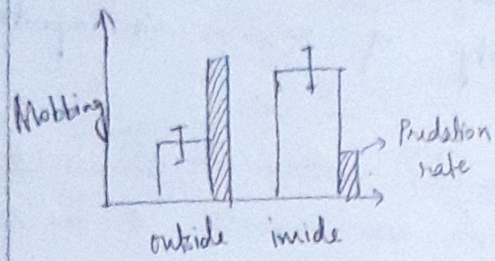
A large group of individuals attack the predator together to distract the predator (hypothesis).

This also involves making a lot of noise.

Is it useful? – Look at predation rates

* Eg: Looking at predation on eggs in different places in a nest colony, because mobbing levels are higher inside the colony & lower near the edge.





Levels of predation rate are inversely related to mobbing behaviour

* Comparative phylogeny in mobbing behaviours of gulls

Cliff-nesting gulls face lower predation pressure than ground nesting gulls.

Costs of mobbing: puts the birds at risk

Mobbing is common in ground-nesting and not prevalent in cliff-nesting.

Ancestral gull: cliff or ground nesting? – Use principle of parsimony

This is also found in the order of swallows – convergent pressure due to common selection pressure

But we've to be skeptical of our inferences, based on the evidence we have – correlational / observational

* Game Theory : Hawk vs Dove game

Opponent

Focal animal	Hawk	Dove
Hawk	$\frac{B-C}{2}$, $\frac{B-C}{2}$	B, 0
Dove	0, B	B/2, B/2

Pay-off matrix : represents costs & benefits of different strategies.

B - benefit

C - cost

This is for pairwise interaction b/w individuals of same species.

Hawk : always fights in an aggressive encounter, until injured or the other one backs away.

Dove : this individual backs away in an aggressive encounter.

Based on the pay-off matrix, we can ask who has better fitness? What is the stable strategy?

Fitness of hawk : $w(H)$

Proportion of hawk : p Proportion of dove : $1-p$

$$w(H) = w_0 + \underbrace{p}_{\text{chances of meeting another hawk}} \cdot E(H,H) + \underbrace{(1-p)}_{\text{meets a dove}} E(H,D)$$

E(H, D) → expected value of interaction.

Similarly for $w(D)$.

The fitness leads to better reproduction - ↑ $w(H)$ means more hawks in the next generation. We can see how the system evolves over time. Does one of them take over the other?

Based on values of B and C -

If B > C, the dove strategy will be lost

C > B - hawk won't exist

What would be the stable state? Evolutionarily Stable Strategy (ESS).

A strategy is called an ESS, when other strategy can't take over this strategy.

Say, prop of I = p   prop of J = 1-p

I is ESS if p >> 1-p.

W(I) > W(J)

Important derivation

$$W(I) = W_0 + \underline{p \cdot E(I,I)} + (1-p) \cdot E(I,J)$$

$$W(J) = W_0 + \underline{p E(J,I)} + (1-p) E(J,J)$$

Given that p >> 1-p, 2nd term will dominate the equations. I would remain as ESS if —

* 1) $E(I,I) > E(J,I)$

2) When $E(I,I) = E(J,I)$, $E(I,J) > E(J,J)$ *

This will keep $W(I) > W(J)$.

Coming back to the hawk-dove scenario —

1. $E(H,H) = \frac{B-C}{2}$ $E(H,D) = B/2$ 0 → benefit to the dove.

⇒ Hawk is an ESS when $\frac{B-C}{2} > 0$

2. $E(D,D) = B/2$ $E(D,H) = B/2$ → benefit to the hawk

So when a hawk invades a population of doves, its fitness is greater. So it will take over the population.

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Lecture

Focal animal	H	D
H	$\frac{B-C}{2}$ ↑	B ↑
D	0	B/2

If B > C, then it's better off if you're a hawk rather than a dove

If B < J, say there's a population of doves and Hawk invades, then it's also not an ESS. No ESS in this scenario

Cost associated with display is less than that of fighting

Say I has mixed strategy I — pH + (1-p) D

Prob of playing hawk/dove is passed on

For these probabilities to be fixed over time -

$$E(H, I) = E(D, I)$$

$$E(H, I) = p\,E(H, H) + (1-p)\,E(H, D)$$

$$E(D, I) = p\,E(D, H) + (1-p)\,E(D, D)$$

$$\left.\begin{aligned} & p\frac{(B-c)}{2} + (1-p)B \\ & = 0 + (1-p)\,B/2 \end{aligned}\right\} \quad p\frac{\cancel{B}}{\cancel{2}} - \frac{pC}{2} + B - \cancel{pB} = \frac{B}{2} - \cancel{pB/2}$$

$$\Rightarrow p = \frac{B}{C}$$

If prob of being ... is B/c,

Even in pure strategies, the proportion of hawks at equilibrium would be B/C

There are many variants of this 2-strategy game.

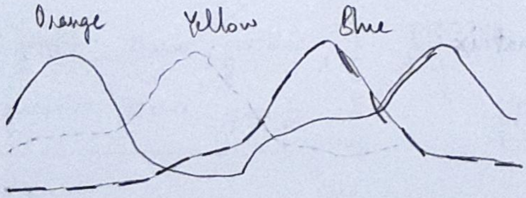
3 ~~varian~~ strategy game : Rock - paper - scissor

Eg: Lizard with 3 throat colours

Orange	Blue	Yellow striped
Dominant w/ big territories	Medium size territories	Sneaky

The population of these variants cycle over time - with one population peaking at a time

Orange defeats blue → Yellow sneaks around orange → Blue defends better than yellow → ...



Game theory can successfully explain the dynamics of this population. There's no ESS, but it seems like there are stable dynamics

Prisoner's dilemma

Payoff for prisoner 1 –

$$\begin{array}{cc|c|c} & & \multicolumn{2}{c}{P2} \\ & & \text{Defect} & \text{Silent} \\ \hline P1 & \text{Def.} & 5 & 1 \\ & & \uparrow & \uparrow \\ & \text{Silent} & 10 & 2 \end{array}$$

If P2 defect, P1 should defect
P2 is silent, P1 should still defect
⇒ Animals should never cooperate

Tit-for-tat is a stable strategy in long term, reciprocal interactions.

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Lecture

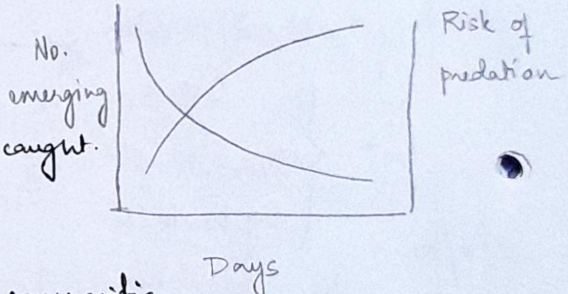
Predator avoidance and foraging behaviour
↳ Mobbing

→ Dilution effect

Social anti-predator behaviour. For example, in many insects, pupae eclose at the same time, together, and mammals move around in herds.

Dilution effect : If no. of predator is very less than prey, then the probability of getting caught reduces per individual.

This assumes that all of them emerging have equal probability of getting caught.



→ Selfish herd

Where one animal uses another conspecific animal to avoid predation. So, when would the benefits of group living ~~arise~~ be more than cost?

Cost : groups are more ~~susce~~ visible than solitary animals.

Game theory payoff matrix

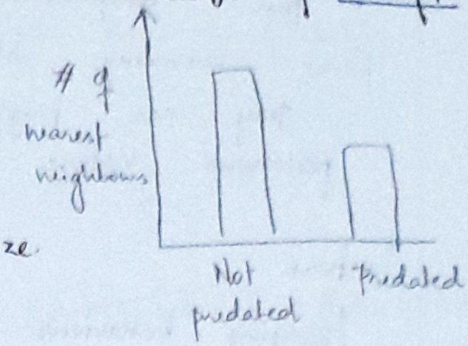
$$\begin{array}{c|c|c} & \text{Sol} & \text{Group} \\ \hline \text{Sol} & 1)\ P & 3)\ P - B \\ & \uparrow & \uparrow \\ \hline \text{Group} & 2)\ P + B - C & 4)\ P - C \end{array}$$

1. Solitary meets solitary : P - payoff
2. Group meets solitary : P + Benefit (predator avoidance) - Cost (energy)
3. Solitary meets group. Group animal takes advantage of sol – So, solitary loses '-B'
4. Group meets group : 'P – C' : it wins half the time

4. When group meets another group, $P + \underbrace{\frac{1}{2}B - \frac{1}{2}C}$ loses half the time, gains half the time

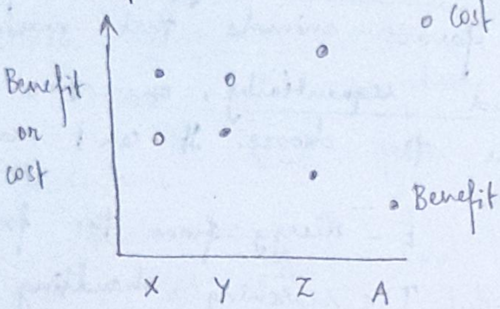
'Group' is an evolutionary stable strategy if benefits are greater than cost.

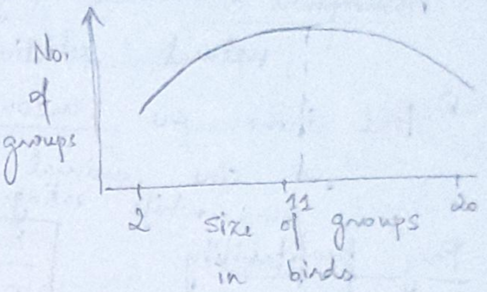
There have been several empirical studies to show that group living can be beneficial based on group size.



Optimality

If costs and benefits can be measured using the same units (say, no. of offspring produced) for different variants, then you can ask where (benefit - cost) is greatest / most optimal and see if that variant is most abundant.

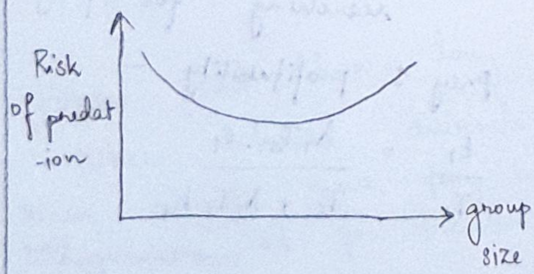


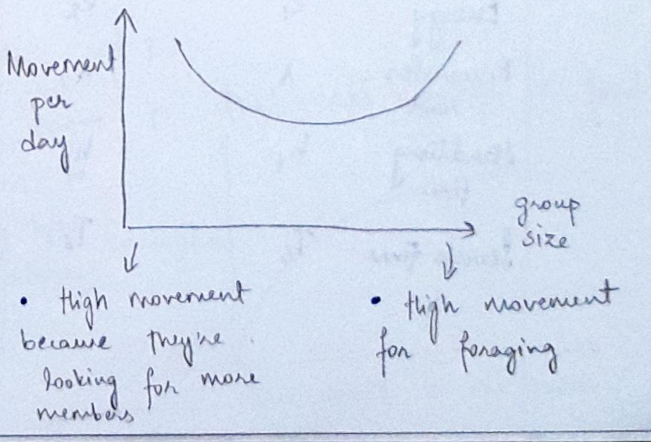


In some group living birds, the size ranges from 2 - 20, but most common is around 11.

Benefit : reduced risk of predation

Cost : movement per day - because they consume lots of resources





Another example : a fly with striped wings moves its wings to mimic a jumping spider to avoid predation.

Caterpillar produces a hissing sound when it notices predator — this conspicuousness startles the predator away.

Same reasoning with conspicuously colored animals — they are brightly colored to advertise their poisonous nature.

27/4

Lecture

Foraging behaviour

Optimal foraging theory — it talks about what animals eat, how long they eat for and where they eat (particular location), and risks involved.

1. What to eat?

Assumption : a) animals try to maximise energy consumption, and natural selection favors animals that maximise this.

b) Food items are encountered sequentially, one at a time, so the animal has to choose. It can't search while eating.

Prey profitability : $\boxed{\dfrac{E}{T}}$

E - energy from the food/prey

T - searching & handling time.

Say there are 2 preys, and Prey 1 gives enough energy. When should predator include Prey 2 in the diet?

	Prey 1	Prey 2
Energy :	e_1	e_2
Encounter rate :	λ_1	λ_2
Handling time :	h_1	h_2
Search time :	T_S	T_S

Say $e_1 > e_2$, when should it consume prey 2 over searching for prey 1?

Prey 1 profitability —

$$\frac{E_1}{T_1} = \frac{\lambda_1 T_S \cdot e_1}{T_S + \underbrace{\lambda_1 T_S \cdot h_1}_{\text{total handling time}}}$$

$\lambda_1 T_S$: no. of prey consum

$$\frac{E_{1,2}}{T_{1,2}} = \frac{\lambda_1 T_S e_1 + \lambda_2 T_S e_2}{T_S + T_S \lambda_1 h_1 + T_S \lambda_2 h_2}$$

The animal will also include prey 2 when –

$$\frac{E_{1,2}}{T_{1,2}} > \frac{E_1}{T_1}$$ i.e. it gets more profitability.

$$\Rightarrow \frac{\lambda_1 e_1}{1 + \lambda_1 h_1} < \frac{\lambda_1 e_1 + \lambda_2 e_2}{1 + \lambda_1 h_1 + \lambda_2 h_2}$$

$$\cancel{\lambda_1 e_1 (1 + \lambda_1 h_1)} + \lambda_1 e_1 . \cancel{\lambda_2} h_2 < \cancel{(1 + \lambda_1 h_1)(\lambda_1 e_1)} + \cancel{\lambda_2} e_2 (1 + \lambda_1 h_1)$$

$$\lambda_1 e_1 . h_2 < e_2 (1 + \lambda_1 h_1)$$

: λ_2 gets cancelled entirely it doesn't influence whether prey 2 gets included or not!

$$\lambda_1 (e_1 h_2 - e_2 h_1) < e_2$$

$$\lambda_1 < \frac{e_2}{e_1 h_2 - e_2 h_1}$$

When encounter rate of prey 1 falls below this, then it's profitable to include prey 2.

Researchers have tested this by presenting different mealworms on a conveyer belt to a bird in a cage. The bird chooses the prey based on the formulation derived above.

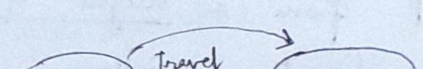
This also explains generalist and specialist strategy.

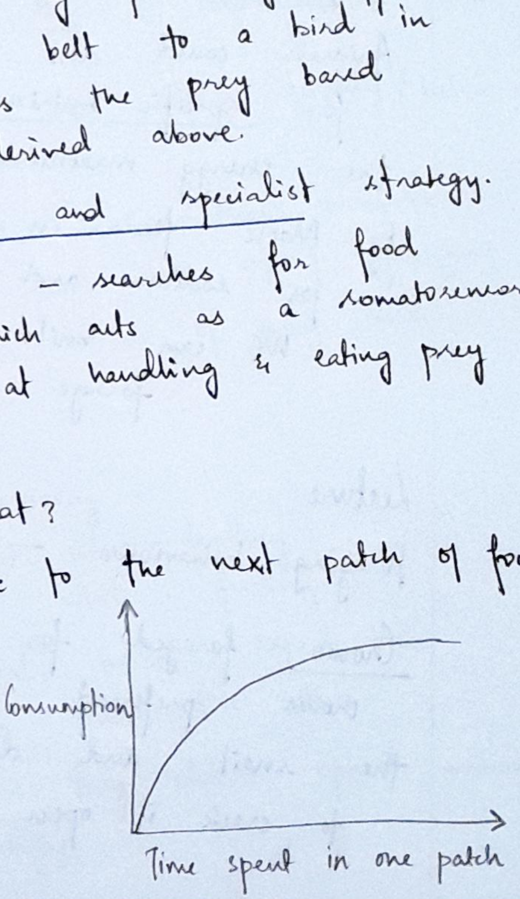
Another example: starnosed mole – searches for food though its snout which acts as a somatosensory organ. Its very efficient at handling & eating prey

2: Where and how long to eat?

When should animals move to the next patch of food?

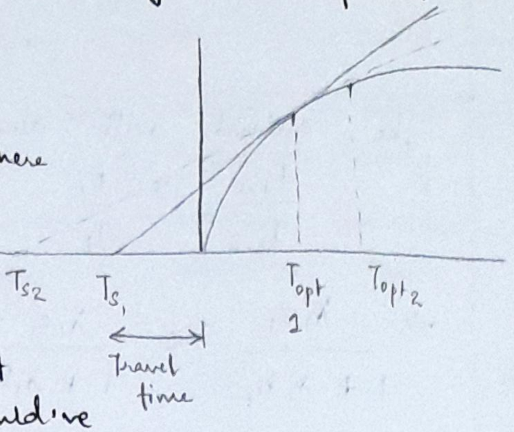
When animals move, they have to pay some cost for travelling b/w patches.





How long should an animal stay in a patch?

Animals should maximise energy intake per unit time. It is maximised (T_{opt}) at the time where the tanget from travel time on -ve x-axis touches the curve.



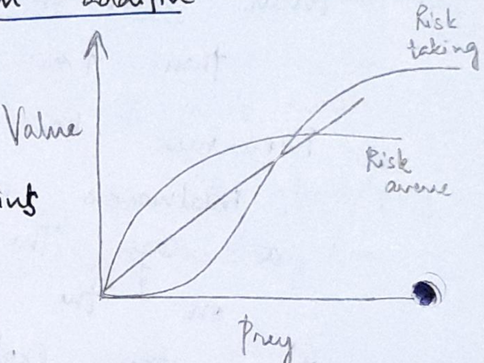
If ~~you~~ it spends lesser time, it loses out on energy it could've gotten. If it stays longer, it's losing time which it could spend on another patch.

This was again tested in birds.

3. Risk and constraints

What if we add variance to the quality of patches

Based on the tendency of the predator (risk averse vs risk taking), the value of each additive prey would change



Animals could also be looking for specific nutrients, which constraints the energy maximisation of animals.

Eg: Moose feeds on acquatic plants for sodium, and terrestrial for energy. We can build models for how the moose should forage.

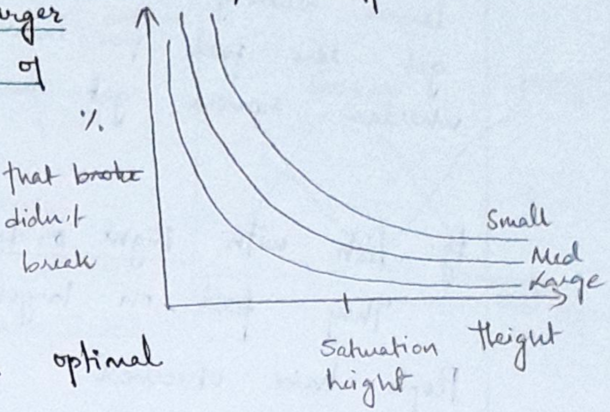
28/4/22

Lecture

Foraging behaviour - Adaptive behaviour

Crows foraged for sea snails. They observed that crows preferred larger snails, and they would take the snail and drop it from a height of ~5m, to crack it open and eat the insides.

They dropped snails of various sizes from different heights and saw that larger shells have greater probability of breaking, and the content would also be more



After a certain height, the % that didn't break doesn't decrease, so about ~5m of dropping height is optimal

These crows keep picking up and dropping the same shell till it breaks because -

a) prob. of the shell breaking in subsequent trials is higher
b) Search time to look for a new shell would be greater

For these behaviours to be passed on -

- there should be a heritability & reproductive fitness to it
- learned behaviours - animals that learn quickly / behaviours will be selected for

Same model might not work in another environment.

Factors other than just food can affect foraging pattern - presence of predator, nature of prey and social hierarchies.

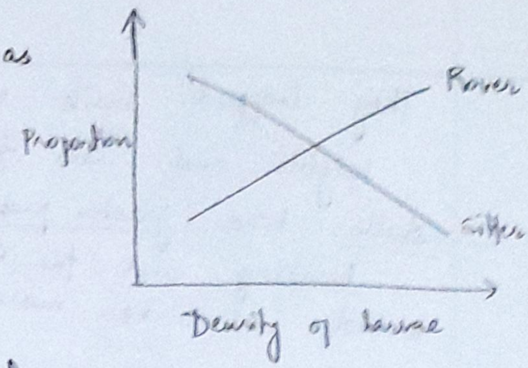
Drosophila mutants related to foraging -

Rovers : move around a lot while feeding
Sitters : stay in one place while feeding.

If one behaviour is beneficial, we'd expect one allele / mutation to dominate over the other.

Say, sitters do better because they don't spend ~~enough~~ ~~ever~~ too much energy.

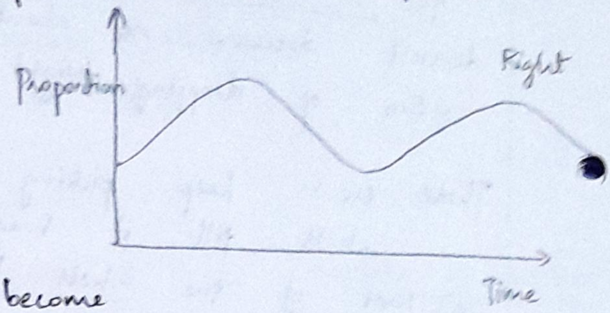
But, when these larvae are mixed, there is density dependent selection. At low density, sitters do better, but as larval density increases, sitters get less food per individual, whereas rovers get more.



Eg: fish with Right or left mouth

They feed on larger fish by biting out flesh/scales.

People have observed an oscillating dynamics of phenotype (R/L) proportion



This is possibly because the larger prey fish become more vigilant and keep a lookout on one side which disadvantages the more common phenotype

This is another example for condition-dependent selection.

Lecture 2/5/22

Development of Behaviour

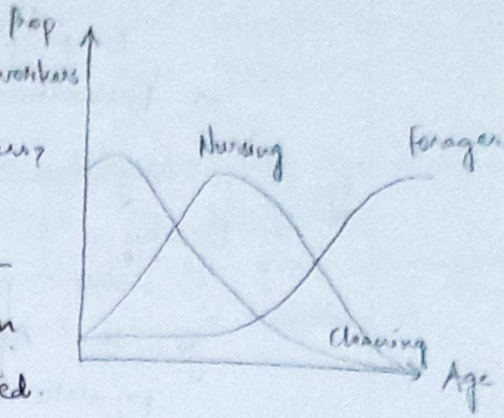
There's always been a nature vs nurture debate. But for any behaviour, both of them are important.

Song learning in birds - interesting model to study

When chicks were transferred from one region to another, chicks produced songs characteristic to the particular location.

But, songs are produced due to neural circuits of the birds. Sub-ossine birds don't learn the song - it's innate. Whereas, ossine birds learn their song

Age polyethism in bees



What determines the trans~~mission~~ition from nurses to foragers?

The transcription network is different b/w nurses & foragers — the expression pattern of certain genes are upregulated / downregulated

Other factors potentially explaining this pattern —

- male parentage
- sunlight / external environment
- diet
- age - remove foragers, & you see that oldest nurses become the foragers & so on.

They also found out that juvenile hormone is important for the transition from nurse to forages.

Foragers bring back pollen, and along with pollen, ~~and~~ ethyl oleate which blocks the transfer juvenile hormone in nurses and stops them from transitioning.

Another factor that increases JH secretion in foragers is flight and flight distance.

So, both environment & genes contribute to behaviour

Another example: Imprinting by geese on Konrad Lorenz

Eg. 3 : 2 species of birds were cross-fostered and their mate choice was observed.

B_A (B raised by A) looked for mates of B

A_B though looked for mates of B

So, the effects of cross-fostering can be different

Eg 4 : Squirrels react to littermates by comparing their odours with the other's odour, and based on the difference in scent, they recognise relatives, conspecifics and other animals.

⇒ Environment plays a role.

Eg. 5 : Migration in birds

Usually, a species migrates together and follow the same path. In Blackcap warblers, some populations go to Africa for the winter, whereas other populations from Europe go to Great Britain and spend winter there along with some local population there.

Migration can be studied in the lab using the migratory restlessness of the bird to study the direction in which they want to go.

They saw that the direction in which they want to go is dependent on the location where they were collected from, and the choice in migration has a genetic correlation.

Eg 6 : Garter snakes in California

Inland population won't eat the banana slug, but coastal population like to eat the banana slug. They showed that this difference is genetic. Cross hybridised snakes show intermediate preferance for sea slugs.

4/5/22

Lecture

Recall : flies feeding behaviour phenotype : Rover vs Sitter

Rover is the dominant genotype, these flies have more c-GMP dependent kinase - called 'for' gene

This is one of the few behaviour that's controlled by a single gene

Another example: Mutation in Fosb gene results in no pup retreival behaviours in mice mothers.

Monogamy vs polygamy in prairie vole ~~vs~~ and mountain vole is through some change in vasopressin gene. In other animals, there's no correlatⁿ b/w gene & monogamy.

But most behaviours are determined by a number of genes. and vice versa.

'for' gene in Honey bees also affects the transition from Nurse to forager.

Hox genes are conserved to produce body plans in various organisms; but in drosophila, they produce wings. whereas in other animals they produce limbs.

Transcription factors and regulation of genes are important nodes through which genes determine behaviours.

- Developmental homeostasis

  The development of system/behaviours is conserved - it has to happen, no matter what. So, if perturbed, the system will ensure that things are developed.

\# Waddington

Rhesus monkeys with even minimal socialisation showed 'normal' social behaviours as compared to completely isolated monkeys.

- Adaptive switches

  Development can be variable for individuals, based on the environment.

Eg. Tiger salamanders - they can either become small insect-eating salamander or they can become large, cannibalistic salamander. This is density-dependent, sort of.

(66) These switches are adaptive, because there are certain conditions when benefits outweigh costs

Eg: Learning can also be adaptive
Some birds store seeds so they can use these stores over the winter. In these birds, size of hippocampus correlates with life history or maybe gender.
This is also true for female cowbirds which need to remember which nests they parasitized

Skinner box & behaviourist paradigm - animals can learn any relation

But, any combination is not learnable. For instance, animals can associate certain food with indigestion, but not a sound with it. Because, it's not ecologically important to be able to make that connection

⇒ Learning is adaptive ∵ it has certain costs, so learning develops only when there are benefits as well.

Summary