Lectures 1/2: Development

January 4, 2011

<u>Introduction To Development</u>

- Development refers to the changes and continuities that occur within the individual between conception and death
- Developmental psychologists are interested in understanding how you change over time and also how you stay the same

Maturation

- The biologically-timed unfolding of changes within the individual according to that individual's genetic plan
 - How that plan unfolds is influenced by specific environmental conditions

- Learning

- The acquisition of neuronal representations of new information
- Relatively permanent changes in our thoughts, behaviours and feelings as a result of our experiences
- Through learning processes, we avoid touching a hot stove and look both ways before crossing the road
- Learned processes can be controlled, but can also become so practised as to become automatic
- Ex. As a child learning to cross the road, we learned to first look left and then right and cross when all is clear
- As an adult, we do so automatically
- o However, this "left then right" strategy is not always the optimal behaviour
- Many North American tourists are a little thrown off when they cross the road for the first time in a country where cars drive on the opposite side of the road
- In this case, you have to overcome your past learning to use the optimal strategy to first look right and then left before crossing the road

Interactionist Perspective

- Emphasizes that most of your developmental changes reflect the interaction of maturation and learning
- Maturation affects learning
 - Some essential systems must be in place before learning proceeds
 - Ex. You won't learn to walk until you've developed muscles in your torso and limbs and the ability to balance
- Learning affects maturation
 - Ex. Imagine a child who was given proper nutrition, but isolated in a dark room, never being allowed to play or interact with anyone
 - You would expect problems in developing normal vision, speech, motor and social skills compared to any other child exposed to normal environmental stimulation

 Without some minimal level of input to learn from the outside world, maturation will be absent or delayed

Studying Development

- Changes that occur earlier in life are much more dramatic than those occurring later in life
- Many researchers believe that the developmental changes that take place during these early years play an especially important role in shaping who you become
- Four ways to measure abilities in infants
 - Habituation procedure
 - To determine if an infant can detect the difference between two stimuli
 - Infants normally tend to show interest in novel objects in the environment
 - The habituation process begins by repeatedly presenting the infant with the same stimulus, such as a tone or a picture, while measuring changes in physiological responses, like heart rate and breathing or behavioural orienting responses like head and eye movements
 - When a novel stimulus is presented, an infant will initially show a burst of activity
 - As the same stimulus is repeatedly presented, the infant's responses will return to baseline levels
 - At this point, the infant has demonstrated habituation to the stimulus
 - At some level, the infant still recognizes the stimulus as the same, it is just no longer important
 - The stimulus can be changed and if the infant recognizes the change by distinguishing the new stimulus from the old one, she is said to dishabituate and shows another burst in physiological response
 - Habituation
 - A decrease in responsiveness to a stimulus following its repeated presentation
 - Dishabituation
 - An increase in responsiveness to a stimulus that is somehow different from the habituated stimulus
 - Event-related potentials
 - An measure of the brain electrical activity evoked by the presentation of stimuli
 - To measure ERP, a special cap with an array of electrodes is carefully placed on the scalp
 - These electrodes can detect changes in electric activity across a population of neurons in the brain
 - The particular behaviour being measured will evoke changes in various brain regions of interest

- If you were presenting the infant with a visual stimulus, you may expect changes in activity in the occipital lobe of the brain, an area devoted to visual processing
- If you were presenting an auditory stimulus, you may expect changes in activity in the temporal lobe region, an area devoted to auditory processes
- Together, habituation and ERP provide complementary behavioural and neural measures to understand an infant's sensory interactions with the environment
- High-amplitude sucking method
 - How do you ask an infant what she likes or dislikes
 - One method takes advantage of the fact that infants can control their sucking behaviour to some extent, which can be accurately measured by a special pacifier in HAS method
 - You first measure the baseline sucking rate for the infant in the absence of relevant stimuli
 - During the shaping procedure, the infant is given control over the presentation of a stimulus to be tested, such as a series of musical notes
 - If the infant sucks on the pacifier at a faster rate than the baseline, a switch is activated in the pacifier that causes the stimulus to be presented
 - If the infant can detect the musical notes and likes what she hears, she can keep the musical notes playing for longer by increasing her sucking rate
 - If the infant doesn't like the sounds, she can stop sucking sooner to end the presentation
- Preference method
 - Infant is put in a looking chamber to simultaneously look at two different stimuli
 - The researcher can accurately measure the direction that the infant is looking to tell if more attention is being directed to one stimulus over the other
 - Researchers have found that infants tend to prefer looking at big patterns with lots of black and white contrasts and prefer looking at faces
- Inferences and Assumptions of Procedures
 - Suppose you were measuring evoked fear by measuring the escape time of a person presented with a stimulus of a ghost in a haunted house
 - If the subject had a broken leg, it would obviously be a mistake to infer a lack of fear from a slow escape time
 - Such a test would lack validity of the intended measure
- Competence-Performance Distinction
 - Researchers testing infants and children must be particularly aware of the competence-performance distinction
 - If a child fails to perform a certain task, this may reflect a genuine lacking in competence in the cognitive ability of interest

- However, a child may have indeed developed the cognitive ability of interest, yet still be unable to perform the task
- Ex. A child who is preverbal will be unable to respond to your questions on her preferences between two different toys
 - If you were unaware that she was preverbal, you may wrongly assume that failure to respond to your questions indicates that she is unable to discriminate between the two toys
 - Given a better test, the child may be able to demonstrate her preference to you

<u>Introduction to Developmental Research Designs</u>

- Longitudinal design
 - Researchers examine the abilities and characteristics of the same individuals repeatedly over a subset of their lifespan
 - If you were interested in how memory for lists of numbers changes with age, you might test the same group of people every year on the same type of test from 5-75 years old
 - o Can uncover age differences and find patterns that are common to all people
 - o Allows researchers to assess developmental change
 - Drawbacks
 - Very expensive and time consuming
 - Problem of selective attrition
 - Some participants may quit, become unfit to continue or even die
 - Leaves a fundamentally different sample at different time points
 - Problem of practice effect
 - Subjects may improve performance based on prior exposure alone rather than on natural development over time of skills being studied due to same or similar tests being administered over years
- Cross-sectional design
 - Many different individuals from different age groups are tested at once without the need to be tracked over the span of many years
 - Allows researchers to assess developmental change
 - o Relatively less time consuming and expensive
 - Can uncover age differences
 - Drawbacks
 - Can't be sure if differences between age groups are due to developmental changes or due to generational effects
 - If 25 year olds perform better than 50 year olds, perhaps the generation of 50 year olds have had less early training with numbers compared to the generation of 25 year olds
 - Are not directly tracking changes with age

- Each person is only studied at a single timepoint, you are not really observing what happens as a person ages
- Instead, are making inferences on trends in group data
- Final alternative is to combine both designs
 - o Combines the strongest and weakest features of both design types in one

<u>Introduction to Hereditary Transmission</u>

- When a sperm penetrates an ovum, a new cell is formed, called a zygote
- This single cell contains 46 chromosomes, 23 chromosomes from each parent
- A chromosome is a threadlike structure that is made from DNA
- Segments of DNA comprise **genes**, which provides the chemical code for development
- Results from the Human Genome Project have estimated that our chromosomes contain between 30,000 to 40,000 genes
- The zygote doesn't remain a single cell for long, it quickly divides at an exponential rate until at birth, you end up with billions of different cells, each with the same 46 chromosomes inherited at conception
- Monozygotic twins are genetically identical because they come from the same sperm and ovum, which formed one zygote and then split into two separate zygotes
- Dizygotic twins are no more genetically similar than any two siblings because they come from two different sperm and ova and start off as two different zygotes from the moment of conception
 - Share around 50% of genes (same as any two siblings)
- From the 23 pairs of chromosomes, 22 are called autosomes and are similar in males and females
- The 23rd pair of chromosome determines a person's gender
 - A female carries two X chromosomes, while a male carries an X and a Y chromosome
 - The mother always passes on an X chromosome, while the father can pass down either
- The 46 identical genotypes in each of your cells translates into the genes that make up your genotype
- The expression of the genotype into observable traits and characteristics is called the phenotype
- Four main patterns of genetic expression
 - Simple dominant-recessive inheritance
 - Expression of trait is determined by a single pair of genes called alleles
 - One allele is inherited from each parent
 - Together, this pair of alleles determines the phenotypic expression for a particular trait
 - In a homozygous condition, the two alleles are the same and have the same effect on the phenotype
 - In a heterozygous condition, the two alleles are different and have different effects on the phenotype

- Only the dominant allele is expressed in the phenotype
- The carrier allele type, which is not expressed is recessive
- Polygenic inheritance
 - When multiple genes are involved in the expression of a trait
 - Ex. Height and weight are determined by the interaction of multiple genes that add complexity

Codominance

- Two dominant alleles are both fully and equally expressed to produce a phenotype that is a compromise between the two genes
- Ex. ABO blood type proteins in humans, in which there are two dominant alleles (A and B) and one recessive allele (O)
- When both dominant A and B alleles are present, the offspring expressed both equally leading to a blood type of AB
- Sex-linked inheritance
 - Involves genes expressed on the X chromosome
 - Some recessive genes expressed on the X chromosomes are responsible for disorders like colour blindness or haemophilia
 - Because females have two X chromosomes, the phenotypic expression of the recessive allele occurs less frequently in females relative to males, who only have one X chromosome
 - Thus, females rarely express sex-linked recessive gene disorders in their phenotype, although they are often genetic carriers

The Interactionist Perspective

- At one extreme, some scientists believed that nurture was important and that a person's development was largely independent of genetic factors
 - Strongly favoured by the behaviourist Watson
- At the other extreme, some scientists believe that who you become is largely predetermined by inherited genes and that the environment had a minimal effect
- Most scientists believe that genetic and environmental influences interact to produce complex traits such as intelligence
- According to the canalization principle, the genotype restricts the phenotype to a small number of possible developmental outcomes
 - Some developmental processes are protected from variability in the environment
 - Classic example is infant babbling
 - Despite the range of language cultures that a child may be born into, all infants babble in the same way, making similar sounds
 - This universal phonemic sensitivity is independent of the environment
 - It is only later that cultural influences shape the final phonemes that are selected to remain
- The range-of-reaction principle states that an individual genotype establishes a range of possible responses to different kinds of life experiences

- Height is a phenotypic trait that is influenced by the interaction of genes and the environment
- Your final height is determined by a number of factors including access to proper nutrition, sleep and exercise during development
- However, the potential range of your height across poor and optimal environmental conditions is determined by genetic factors
- Your genes determine the range of potentials for different traits and the input that you receive from your environment influences how your genotype is expressed as a phenotype
- Just as the environment influences expression of genes, genes can influence the type of environment you seek out
 - o Three different ways that genes influence your environmental experiences
 - Passive genotype/environment correlations
 - The environment that your parents chose to raise you in was influenced by their own genes and so this environment will likely complement your genes
 - Ex. Imagine a couple who are both athletic with good hand-eye coordination and reflexes
 - When designing the environment to raise their children, they might focus on an active playroom with many physical toys
 - The environment chosen by parents is likely to go well with the inherited genetic potential of the child
 - Evocative genotype/environment correlations
 - Traits that you have inherited affects how others react to and behave towards you
 - In this way, genes can affect social environment
 - Ex. A child with a difficult temperament may more likely evoke negative responses from caregivers, whereas a child with a sunny disposition may evoke more positive responses from the same caregivers
 - Active genotype/environment correlations
 - Your genotype influences the kinds of environments that you seek
 - Ex. A person with a sensation seeking temperament may actively choose environments that satisfies these thrill-seeking urges
 - The influence of each of these gene-environment interactions changes across life span
 - Early in life, passive genotype/environment correlations influence you the most when you cannot choose your own environment
 - Active genotype/environment correlations begin to play a larger role in your development in childhood and continues into adulthood as you have more opportunities to make decisions
 - The way that your inherited traits affects how others respond to you via evocative genotype/environment correlations can be influential throughout your entire life span

- To this end, a useful population to study is twins
 - Monozygotic twins have identical genotypes whereas dizygotic twins share only half their genes, like all other sibling pairs
 - Because both types of twins normally develop in the same environment at the same time, you can assume that if monozygotic twins are more similar for a trait than are dizygotic twins, the difference is presumably due more to genetic factors
 - In cases where twins are raised apart, psychologists have another opportunity to study the relative contributions of genes and environment
 - In both scenarios, monozygotic twins have a higher correlation for intelligence than dizygotic twins
 - This pattern suggests that genetic factors may play a larger role than environmental factors for this trait

Introduction to Critical Periods

- One question that researchers are curious about is how these passive environment-gene correlations can affect your development
- In some cases, parents are reading to their children in the womb and playing them classical music
- Then, when the child is born, they're being bombarded with flash cards and lessons
- Critical periods refer to specific times in development in which particular environmental stimulation is necessary in order to reach developmental and permanent changes in specific abilities
- After this critical period, the same environmental stimulation will not have the same benefit
- An example of research on critical periods comes from animal studies on the development of visual pathways
 - o In the first 4 to 6 weeks of life, one kitten is visually deprived
 - o He becomes permanently unable to discriminate visual patterns properly
 - No amount of visual stimulation following this critical period can help them to regain normal visual abilities
 - For another kitten, he is visually deprived for the same amount of time as the first kitten, but only after having reached 4 weeks of age
 - In this case, the kitten's visual abilities are unaffected by the period of deprivation and its discrimination of visual input is normal
 - Taken together, this suggests that there is a critical period in visual development in the first 4 to 6 weeks of life
 - During this period, visual input is necessary for normal visual pathways to become established
- Other research shows that rats raised in an "enriched" environment with lots of toys and social stimulation have more connections between neurons than rats raised in a deprived environment
- The implications of the Leap of Thinking

- Such studies suggest that without a normal level of environmental stimulation, the brain may not fully develop some of its functioning to its full potential
- Some have speculated that extra stimulation should happen as early as possible in development, to maximize the gains

Implications

- Can lead some parents to over-stimulate their children even before they are born
- Also has problems with adoptions
 - Would you adopt a child who was over 3 years old with a history of neglect?
- This type of thinking affects public policy on how and when we should intervene in a child's development if they are found to be off the normal course

Problems with critical period evidence

- o The environmental manipulations in the animal research were extreme
 - In the kitten study, subjects had normal visual experience or were completely deprived of visual input
 - In the rat study, subjects were raised in a rat-like vacation resort or a standard lab environment

Doesn't look at enriched environments

- Consider that in a natural environment, perhaps a minimal amount of input is all that is necessary to achieve normal development and that these extreme cases are not necessarily comparable
- Also possible that studies of "enriched" environments are perhaps more comparable to the stimulation that a rat would normally receive in its natural habitat
- For the rats in the lab cages, we are probably witnessing the effects of abnormally poor environments rather than the effects of enrichment over normal levels

Extra stimulation is not always better

- Quite an assumption to conclude that children who are given extra stimulation will be superior to their peers at a developmental level
- It is possible that these activities may help to build positive habits and attitudes
- Also possible that children exposed to extra stimulation before they are ready may actually withdraw and lose interest in learning

More synapses

- During early development, we start out with an excess number of synapse in the brain which are pruned as we develop
- Brain circuitry is not made permanent at 3 years of age or at any other age and remains malleable throughout the life span
- This means that you can continue to learn new skills later in life

- Experience-Expectant Brain Growth
 - o The brain has evolved to expect a certain amount of environmental input
 - Ordinary levels of visual, auditory and social input ensure that the brain develops properly
- Experience-Dependent Brain Growth
 - Refers to unique way in which your brain develops according to your own personal experiences
 - This type of brain growth is specific to each individual and reflects more subtle changes in brain structure across individuals based on their varied experiences
- Sensitive periods
 - Has replaced the term "critical period"
 - Sensitive periods captures the idea that the brain maintains at some residual capacity for change and growth into adulthood
 - There is a greater flexibility in the timing of when normal levels of stimulation are required and less specificity in the exact type of stimulation necessary for development to proceed normally

Development Live Lecture

- Sex, Gender and Sexual Orientation
 - Studies show that adults treat children differently if they think they are boys or girls
 - Only recently were boys and girls separated by blue and pink
 - Before that, babies all wore white dresses
 - Reimer Family
 - Twin boys born
 - One boy was accidentally castrated
 - The solution was to raise him as a girl
 - Boy was given hormone therapy as he went through puberty
 - However, he reported that he was never comfortable being a girl
 - When he found out, he got surgery to turn him back into a male
 - Kinsey
 - Came up with a scale to rate sexual orientation
 - Rodent birth
 - Behaviour of babies can be predicted based on their location in mom's uterus
 - Female surrounded by no males/1 male/2 males
- The First Three Years Movement
 - Biological exuberance
 - Lots of activity in baby's brain in the first three years
 - At 2 years of age, baby has more synaptic connections than adults
 - Critical periods
 - First three years of life are important for stimulation
 - The Mozart Effect

- The Orienting Reflex
 - Novel stimulation doesn't necessarily mean cognitive skills are being trained
- Headstart program
 - Gave poor kindergarten kids breakfast and their education improved

Lectures 3/4: Evolution

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<u>Introduction to Adaptations</u>

- Adaptations are biological traits or characteristics that help an individual survive and reproduce in its habitat
- Can be physical or psychological
- Adaptations perform specific functions that make an organism better suited to its environment
- Adaptations are always "for" something; they serve identifiable functions in the life of the individual
- Adaptations emerge in development as a result of the activation of relevant genes in interaction with relevant aspects of the environment
- Scientists categorized as "adaptationists" look for processes that are capable of accomplishing tasks of detecting stimuli
 - o In other words, they look for the relevant adaptations
 - Scientists describe how hypotheses about adaptive functions guide their investigations
- Cognitive psychologists study things like selective attention, memory encoding and retrieval and word recognition
 - The very names of these tasks refer to tasks that the mind needs to accomplish to do its job
 - They refer to the adaptive functions of mental activity
 - Therefore, cognitive psychologists are also adaptationists

Evolution By Natural Selection

- Natural selection is one of four basic mechanisms of evolution, the others being mutation, genetic drift and migration
- The process of natural selection can be described as the differential survival and reproduction of organisms as a result of the heritable differences between them
- Three essential components to Darwin and Wallace's insight
 - First is that there are significant **individual differences**
 - Within any population, there is variation among individuals for any given characteristic
 - Second, these differences affect individuals chances of surviving and reproducing, causing differential reproduction

- Some individuals will have more offspring than others
- Lastly, the traits that give rise to differential reproduction have a genetic basis, meaning they are heritable
 - The offspring of successful reproducers will resemble their parents with respect to these variable characteristics
- Ex. Imagine a population of fish that vary in colour
 - Some individuals are blue and others are red
 - The blue fish camouflage well in the blue ocean water and the red fish are much more visible to predators
 - Therefore, the red fish get eaten more often and so on average, the blue fish survive and reproduce better than the red fish
 - Blue fish tend to have blue coloured offspring because body colour is a heritable trait
 - Over successive generations, there will be selective transmission of heritable parental traits and the population will be mostly blue
 - This is because the specific characteristics that are best adapted for survival and reproduction are going to be reproduced at higher rates
 - o Eventually, if this process continues, the entire fish population will be blue

Natural Selection In the Wild

- What researchers usually observe in wild populations is stabilizing selection, selection against any sort of departure from the species-typical adaptive design
 - o This sort of selection tends to keep traits stable over generations
- Ex. Blue would remain the most common colour in the fish population because it is adaptive and minimizes the risk of predation
- However, in some cases, especially when there has been a significant change in the environment, selection favours traits that are not typical and evolutionary change can be observed
- A classic example of rapid evolutionary change comes from work on the evolution of beak shape and size in a particular species of Darwin's finches, the medium ground finch, which lives on Daphne Island in the Galapagos
- Peter and Rosemary Grant who studied these birds, were able to observe natural selection within only a generation
- In 1977, a drought hit the island and decimated the vegetation
 - Food was scarce and all of the small seeds were quickly eaten up, leaving only large, tough seeds that the finches usually didn't bother with
 - The birds that had unusually big, heavy beaks were able to eat the hard seeds that remained and so survived the drought, whereas the birds with small beaks died of starvation
 - Between 1976 and 1978, the average beak depth increased
 - The large-beaked survivors went on to reproduce when conditions were again favourable for breeding and because beak size is heritable, their offspring inherited large beaks as well

Reproductive Success – Fitness

- Natural selection favours those individuals who are not only best at surviving, but also those who are best at reproducing
- Fitness in biology refers to how good a particular genotype is at leaving copies of its gene in the next generation relative to other genotypes
- Therefore, the fittest individual is not always the smartest, biggest or fastest
- Darwinian fitness is the average reproductive success of a genotype relative to alternative genotypes
- Because fitness is ultimately about the competition between genotypes to leave copies
 of themselves in the next generation, some evolutionary biologists like to define
 evolution as a change in gene frequencies over generations

Sexual Selection

- In sexually reproducing organisms there is often competition for mates and natural selection acts on mate-finding and reproductive behaviours
 - Known as sexual selection
 - The component of natural selection that acts on traits that influence an organism's ability to obtain mates
- Peacock's tail
 - Energetically expensive to produce
 - Makes male more conspicuous to predators and it actually interferes with his ability to escape from a predator
 - A peacock's tail is no help at all with respect to physical survival
 - Increases the risk of dying and for that reason, he'll shed his tail at the end of the breeding season and grow a whole new one next year
 - However, the tail contributes to a male's fitness by increasing his chances of mating
- Traits like these that led Darwin to propose a second theory, the theory of sexual selection
- Some evolved traits like the tail elevate mortality and are actually being selected against, but they can still evolve and become more elaborate under the countervailing pressure of sexual selection
- Stag's antlers
 - Only males have antlers and carry them around to fight for females
 - o In some ways, the stags are more vulnerable than the females
 - Because of their bulk, males don't have as much stamina as females for running away from predatory wolves and a stag is more likely to get stuck in deep snow
 - o The total effect on survival for all his weaponry is negative
 - In fact, like the peacock's tail, stags shed their antlers at the end of the breeding season and grow new ones each year
- In both examples
 - The male trait has a negative effect on survival, but has evolved and persists anyways because it has a big positive effect on the male's chance of mating

- An important difference between these two examples of sexually selected traits
 - Peacock's don't use their tails to fight with
 - Antlers have evolved to be effective weapons in fights with other males, but the peacock's tail evolved solely to dazzle the females
- The selective force in the evolution of the peacock's tail was female choice, whereas the selective force in the case of the elk's weaponry was success in combat with other males
- Considering the definition of sexual selection, there are two distinct ways of getting more access to mates than your rivals
 - Being chosen by the opposite sex (female choice)
 - More attractive
 - Beat up your rivals (success in combat)
 - If you keep your rivals at bay, then your mate can only choose you
- It's been shown experimentally that peahens respond to peacock's tails
 - They make very find discriminations
 - Females discriminate between males based on the number of eyespots (the more the better) and they also prefer males with good left-right symmetry (same number of eyespots on each side)
 - o Female choice picks out male with best resistance to disease
 - Best genes for being healthy

Species-Typical Behaviour and The Comparative Approach

- The recognition that behaviour is an evolved characteristic of a given species was the starting point for the modern science of animal behaviour
- Ex. Sandpipers
 - Three different species
 - Sanderlings
 - Semipalmated
 - Dunlin
 - They all look very similar, but a birdwatcher is likely to recognize these birds at a glance, just by watching their behaviour
 - These birds can also be differentiated by their vocalizations, dietary and habitat preferences
 - Sanderlings like sandy beaches, whereas the other species like muddier shores
 - More obviously, is their signature way of foraging
 - Little flocks of sanderlings race out after receding waves and furiously peck at tiny insects on the wet sand, then race back towards shore in front of the next wave, with their little legs spinning like wind-up toys
 - An example of species-typical behaviour
 - Physical form (typography)
 - Habitat preference
 - Group size

- Social system
- One way we can confirm that behaviour evolves is by doing selection experiments, what are sometimes known as **behaviour genetic** experiments
- You can keep animals in captivity and selectively breed those who are most or least aggressive and you can change the animal's typical behaviour in a few generations
- The popular animal in behaviour genetics is the fruit fly, **Drosophilia**, because of its short generation times

Introduction to Social Behaviours

- Organisms evolve to maximize their fitness and reproductive success
- Yet, there are many examples in humans and social animals where individuals appear to behave altruistically
 - Ex. Virtually all honey bees in a colony don't ever reproduce, they don't even have functioning reproductive organs
 - Instead of reproducing themselves, they spend their lives in the service of the colony helping to raise eggs laid by the Queen and many bees often die defending their colony from predators
 - Ex. In Belding's ground squirrels, individuals frequently give alarm calls to warn others that there is a predator in the area, giving everyone a chance to flee and hide
 - By giving the alarm call, the "whistle blower" draws attention to itself, altering the predator to its exact location
 - Ex. Why do humans spend so much time cooperating and helping family, friends and strangers
- Evolution acts at the level of genes and those genes that contribute to an individual's fitness will consequently get replicated more often, increasing in frequency in successive generations
- People sometimes refer to this concept as the "selfish gene"
 - Means that natural selection will favour the genes and gene complexes that best serve their own interest, namely replication
- Table of social behaviours

	Effect on Actor's well-being		
Effect on		+	-
Recipient's well-	+	Cooperation	Altruism
being		Selfishness	Spite

- Sometimes cooperation can contribute more to your own success than being selfish
- Ex. Imagine you're on a hockey team with only six players
 - One of the players isn't quite as skilled as the rest of the team and when other teams score, it's usually because he made a mistake
 - You'd rather not have him on the team, but to be able to play, you need all six people on the ice, so you can't send him off

- One thing you can do is invest in the time and resources required to teach him to play better
- On the surface it looks like you're unselfishly doing extra work, but it may pay off as you may win more games
- Assuming that the cost of teaching him to be a better player is less than the benefit you get from simply joining a better team, it would be in your own interest to help him
- What looks like a cost in the short run may in fact be a benefit in the long run because your team performs better, which means that you do better than players on other teams
- In the language of evolution, increasing the fitness of others can sometimes improve your own fitness prospects

Group Selection

- Adaptations aren't for the good of the group or the species, they are for the good of the gene
- In the previous example, helping out the worst player on your team do better may help the group, but in evolutionary terms, that's not a good enough reason to help someone out
- What matters is that the increase in group success translates into better success for the metaphorical helping gene
- Ex. Geese foraging for food in groups
 - Doesn't seem to make sense, doesn't having more hungry mouths nearby make foraging more competitive?
 - Not always, when food is hard to find, it can be useful to have more individuals looking around for it
 - o If you happen to discover some food, then yes, others may come and take some
 - However, you'll also have opportunities to take food from others when they find it first
 - Another advantage to foraging in groups is when animals are busy searching for food, their heads are down and their attention is diverted, giving predators the advantage of a surprise attack
 - o To remain vigilant, foragers need to keep their heads raised, to look around
 - Called a "trade-off" because you can't be vigilant and forage at the same time
 - The trade-off is reduced when animals forage in groups because while some forage, a few can scan for predators
- If every individual spends less time scanning and more time eating, group foraging works to everyone's advantage so long as there is enough food to go around and every individual benefits from the vigilance of others
- This example illustrates the point that selection favours the "good of the group" only as a side-effect of favouring the good of the individual
- But couldn't selection be for the good of the group, even if the helpful genes involved suffer?

- The answer is no, due to the "problem" of altruism
- Altruism is a type of social behaviour in which the actor pays a cost to provide a benefit to a recipient (involves a decrease in the actor's fitness)
- The example above isn't really altruism because in such cases the actor gains from performing the behaviour
- Problem of altruism
 - A group full of altruists will thrive because individuals in that group are regularly helping one another
 - o But how will the individuals that make up that group do?
 - An individual that behaves altruistically decreases its own direct fitness by definition, whereas an individual that behaves selfishly won't

Lemmings

- The myth is that lemmings commit suicide when their populations become too large
- This behaviour is altruistic because the remaining lemmings now have enough food to survive
- Unfortunately, the story is not true
- In terms of genes, one gene is for altruistic suicide and another for selfish restraint
- The gene that leads to altruism will die along with the suicidal lemmings, whereas the gene that leads to selfish behaviour will live to compete with the rest of the survivors
- The chances of any particular selfish survivor may not be very good, but each is still doing better than the ones that drowned themselves
- So unless the genes involved in the altruistic behaviour produce more copies of themselves than other genes that don't lead to altruism, the good of the group cannot explain the evolution of altruism

Inclusive Fitness

- Like honey bees, individuals that give up their own reproductive opportunities to help other individuals survive and reproduce seem to be altruistic
- A behaviour called eusocial hymenoptera, where tens of thousands of individuals work to let a single Queen be the sole reproducer
- It doesn't make sense that natural selection will allow this altruistic behaviour to continue
- The explanation was that genes for altruism could be successful if they helped identical copies of themselves
- Inclusive fitness
 - Keeping in mind that an individual's fitness is measured by the number of copies of its genes left in the next generation, Hamilton (researcher) broke the traditional view of fitness into 2 parts
 - Direct fitness is an individual's genetic contribution through its personal reproduction

- Indirect fitness is an individual's genetic contribution through the reproduction of close genetic relatives
- Direct fitness + Indirect fitness = Inclusive fitness
- This means that you can increase your fitness by helping kin to successfully raise their offspring, sometimes even when doing so has negative effects on your own direct fitness
- Because of inclusive fitness, natural selection can favour not only behaviours that increase an individual's own reproductive success, but also behaviours that increase the reproductive success of close genetic kin
- Shared genes between relatives can drive the evolution of altruism

Hamilton's rule

- Predicts that an altruistic act will be favoured when br > c, where "c" is the reproductive cost to the actor, "b" is the reproductive benefit to the recipient and "r" is the degree of relatedness between the two individuals
- Relatedness is the probability that the actor and recipient share the gene in question, in this case the gene that leads its bearer to be helpful
- o This probability will depend on the way individuals inherit their genes
- o Ex. In humans, we get two copies of each gene, one from mom and one from dad
- However, these copies are not always identical
- Moreover, the one you pass on to your offspring and the ones mom and dad passed on to your siblings will also not necessarily be the same two you received
- Probability of identical genes
 - Let's say a person has a copy of gene A
 - If mom has the gene, she has a 50/50 chance that she passed it on to you and so does dad
 - We say then that you have a relatedness of 0.5 to your mother and a relatedness of 0.5 to your father
 - If your sibling has both the same mother and father as you do, then you are full siblings
 - There's a 0.5 probability that you inherited the gene from your mom and a 0.5 probability that she passed it on to your sibling, which equals a 0.25 chance that you share identical copies of the same gene through your mother
 - However, there's also a 0.5 chance that your dad passed on the gene to either you or your sibling
 - In total, that makes a 0.5 chance of sharing an identical copy of the same gene with your full siblings, so for both parents and full siblings, relatedness if 0.5
 - For half-siblings, relatedness is half of what it would be if both parents are shared, so 0.25
 - Using the same logic, relatedness to grandparents, aunts and uncles is also 0.25 and relatedness to first cousins is 0.125

Hymenoptera

Some do not reproduce, but choose to help the colony due to relatedness

- Colonies are often founded by a small number of individuals so they are made up of very close relatives
- This means that it pays to help your colony, especially when you're competing with neighbouring colonies who are not very closely related to you
- Also explains the level of aggression between colonies
 - The level of aggression and the percentage of alleles shared is indirectly proportional
- Violence and relatedness in humans
 - Stepchildren are more often the victim of abuse than genetic offspring
 - In Detroit, only 6% of homicides committed were by genetic-relatives

Kin Recognition

- How do you know who is your kin
- In organisms with limited migration following maturity, neighbours are most likely to be close kin
- One simple rule then is to be altruistic towards individuals that are spatially close to you
- In this way, individuals don't need to recognize kin at all, they can help neighbours who happen to likely be relatives
- Returning to example of Belding's ground squirrels, who is most likely to behave in the altruist manner
 - Female ground squirrels stay in their natal territory for life, while males disperse to establish their own territories
 - Thus, females give alarm calls more often than males, who almost never gave the calls
 - Because females live near kin
- Humans use several methods to discriminate kin from non-relatives
 - Babies notice that mother's reared them from infancy and breastfed them
 - Can also distinguish their own mom by smell
 - Older children can watch their mothers rear and feed their younger siblings from birth, so they know who their siblings are
 - Younger siblings notice that siblings usually live together for a number of years
 - Also the obvious characteristic that you tend to resemble your family members, known as **Phenotype Matching**
 - The evaluation of relatedness between individuals based on an assessment of phenotypic similarity, either between yourself and another individual (self-referential phenotypic matching) or between another individual and a known family member
 - Isn't necessarily a conscious comparison
 - The unconscious process of kin recognition can affect your social behaviours
 - If phenotype matching in humans influences your actions, you might expect that individuals would exhibit more pro-social behaviours such as trusting and sharing when interacting with others who resemble them

- Dr. DeBruine's Investment Game
 - A two player trust game
 - P1 and P2 are playing a game over the internet
 - P1 is given \$4 and she can make one of two choices
 - If she is untrusting of P2, she can simply choose to divide the money equally between them
 - But P1 has the possibility of earning more money if she chooses to trust P2
 - In this case, P2 is given control of a larger pot of money, \$5
 - P2 can now choose to share the larger pot however he wants, either equally with P1 or selfishly and give only \$1 to P1
 - The dilemma is that P1 has the chance to earn the most money by trusting P2 to share the money equally
 - P2 on the other hand, can earn the most money by betraying P1's trust and keeping the money for himself
 - DeBruine predicted that individuals would exhibit more pro-social behaviours, when interacting with people who resemble kin
 - In other words, P1 will be more trusting of a P2 that looks like him
 - In the experiment, P2 was a computer generated strategy
 - Subjects played a total of 6 rounds as P1 and in each round they saw a picture of their so-called partner that they thought they were interacting with
 - P2 could be a picture of a complete stranger or one that looked more like kin
 - To create cues of kinship, DeBruine photographed each subject and digitally morphed their picture with others, to create a novel face that looked a bit like them
 - As predicted, subjects were more trusting of P2 when P2 resembled them
 - These results demonstrate that facial resemblance, a form of phenotype matching, can modulate behaviour in ways predicted by Hamilton's Inclusive Fitness theory
- However, there are many examples of people behaving altruistically to unrelated friends, acquaintances or even total strangers
- Therefore Inclusive Fitness does not entirely explain the suite of altruistic behaviours seen in humans and other animals

Direct reciprocity

- Refers to situations in which individuals help each other and both benefit
- In some circumstances, individuals who reciprocate acts of generosity can have a selective advantage over others who do not

Indirect reciprocity

- Occurs when individuals help those who have helped others
- By helping others, you establish a good reputation for yourself and overall will get more help from neighbours
- o People who are known to be selfish are often punished by others

- Research suggests that people are more generous and less likely to break rules when they are observed by others
- Behaviours that appear altruistic from the perspective of the individual, are actually selfish from the gene's perspective

Evolution Live Lecture

- Ex. Humans like sweet, salty and fatty foods
 - From an evolutionary perspective, the calories available in these foods were rare and helped in survival
- Aggression
 - Most extreme form is homicide
 - Homicide rates as an index of aggression
 - Men kill unrelated people a lot more than women do
 - Most murders happen around 20-24 years of age
 - City of Chicago has more homicides than Canada and England and Wales combined
 - Risky behaviour and outcome variance
 - Risky behaviour happens more often when there is a great degree of outcome variance, meaning there are many possibilities of what can happen
 - Outcome variance
 - Low variance
 - Everyone comes out with same result
 - High variance
 - A wider distribution in individual performance, some people will have a high quality of outcome, others will have low
 - Berg-Rietz gamble
 - Usually, women prefer less risky behaviours than men
 - As outcome variance increases, men take more risks
 - Men have a greater variance in leaving behind children (different rates of reproductive success)
 - Risky competition
 - Homicide is typically found in conjunction with some sort of social competition
 - Ex. Social status lowered (honour, place in society)
 - Nothing to lose
 - Most homicides are due to young, unemployed males (20-24 years)
 - No social status, nothing to lose, everything to gain
 - Makes them riskier
 - Males who are older and are employed are more risk adverse due to factors such as children, wealth, status
 - Marriage and divorce

- Single males are more likely to commit homicide than married males (less resources committed)
- Widowed and divorced males are also more likely to commit homicide
- Income inequality
 - As income variance increases, rates of homicide increase
 - As income variance decreases, rates of homicide decrease
- Homicide rates vs. Life expectancy
 - Lower life expectancy → less chance to plan for future → increased rate of homicide (nothing to lose)

Attraction

- Peacock tail
 - Even with a big, bright tail, if a peacock is able to survive, there must be something special about his genes
- What types of voices are we attracted to
 - Deep voice pitch is heritable
 - Testosterone almost exclusively determines voice pitch
 - Deep voice pitch comes at a cost
 - Testosterone actually weakens the immune system
 - If a male has a deep voice and is also able to survive, he must be biologically fit
 - Women also report that they like males with masculine features
 - However, preferences fluctuate due to menstrual cycle
 - During ovulation, they prefer masculine men
 - During menstruation, they prefer high-pitched voices on males
 - When they are ready to mate, women want a masculine male, but when they are pregnant, they want a male who will stay
- o The Hadza
 - Data from this group corresponds with hypothesis

Lecture 5: Neuroscience I

January 22, 2011

Introduction to Neuroscience

Descartes

- Tried to understand the mental processes that allow a person to learn, feel and act and relate it all to the brain
- His approach was to separate the mental processes of the mind from the physical processes of the brain
- In his dualist framework, the mind was seen as a separate entity existing outside of our biology, yet in control of our actions and thoughts
- The physical brain was thought to serve as a connection between the mind and body

o In modern times, the challenge for neuroscience is to understand how the biological brain produces the mental processes of the mind

The Neuron

- Neurons are cells that are specialized for communication
- Each of your 100 billion neurons are organized into signalling pathways to communicate via synaptic transmission
- What makes neurons good at communicating is their unique structure
 - A typical neuron contains two distinct zones
 - A receptive zone designed to receive signals from other neurons
 - Made up of dendrites branching out from the cell body
 - A transmission zone designed to pass on signals to other cells
 - Made up of the axon and terminal boutons
- The receptive zone
 - Begins with the cell body
 - The cell body contains most of the vital organelles, which keep the cell functioning
 - o Branching from the cell body are a number of projections called dendrites
 - These dendrites reach out to other neurons and receive signals to be relayed through the dendritic branch to the cell body, where some signals will go on to be conveyed down the axon
- The axon
 - Once a neuron receives a signal in the receptive zone, it is passed down a long fiber called the axon, which can vary in length
 - Some neurons have very short axons, while others have axons that can be 1m in length as they extend from your spine to the bottom of your feet
 - At the end of the axon, approaching the transmission zone of the neuron, is another cluster of branches
 - These branches at the end of the neuron are called end-feet or terminal boutons or terminal ends
 - The terminal ends reach out and make connections with receptive zones of nearby neurons to transmit a signal further
- A neural network
 - Each neuron can receive inputs from thousands of other neurons through their dendrites and terminal boutons to form a complex network of information transfer
 - The glial cells are the hardworking, co-stars of the nervous system
 - They provide structural support, nourishment and insulation needed by the high profile neurons
 - The glial cells and neurons that work together, resting in a bath of ion chemicals and blood vasculature make up the entirety of your brain

The Action Potential

- A neuron's cell membrane separates the intracellular fluid, which fills the neuron and the extracellular fluid, which surrounds it
- Each contains different concentrations of important ions, including sodium, potassium and chloride
- The cell membrane is selectively permeable, preferentially allowing different ions to pass through it with various levels of ease
- The cell membrane also contains a number of protein channels, which acts as passageways for ions to pass through
- Important channels to consider include the potassium channel and the sodium channel
- The selective movement of ions across the cell membrane into and out of the neuron is critical for neural communication

The resting potential

- The inside of a typical neuron starts of at -70mv relative to the outside of the cell
- This baseline imbalance is called the resting potential of the neuron
- The resting potential of a neuron is controlled by two forces, diffusion and electrostatic force
- Diffusion is the force that distributes molecules evenly throughout a medium
- The diffusion force interacts with the electrostatic force between charged ions
 - When two similarly charged ions meet, they repel each other and when two oppositely charged ions meet, they attract
- The net result of the diffusion and electrostatic forces leads to an overall resting potential of -70mv inside the cell compared to the outside
- At the start of the resting potential, the negatively charged large protein molecules within the neuron are so large that they cannot pass through the cell membrane and so they remain trapped inside
- o On the other hand, potassium, sodium and chloride ions are mobile
- Two different types of potassium channels
 - The leaky potassium channel is like a tap that's always open
 - It allows positively charged potassium to pass through the cell membrane out of the neuron
 - However, most of the potassium remains inside the cell at rest
 - Overall the leaky potassium channel is a major contributor to maintaining the resting potential of the neuron
 - Voltage gated channel
 - Important for the action potential
- The negatively charged chloride ions are also mobile and the electrostatic force of the negatively charged protein molecules keep them primarily on the outside of the cell
- Voltage gated sodium channels are closed in the resting state of the neuron and so the positively charged sodium ions flow in only very low concentrations into the cell
- Despite this subtle inward flow, most of the sodium ions remain resting on the outside of the cell and the flow of sodium is far less important to the resting state of the neuron than potassium

The threshold

- The forces governing the distribution of ions are not rigidly stuck in place and in reality, the resting voltage of the neuron is constantly fluctuating somewhere around -70mv
- Under the influence of nearby neurons and random ion flow, a large enough change in the resting charge will occur to reach an important threshold level
- When the threshold of -50mv is reached, the action potential is triggered

The action potential

- The fundamental unit of communication for neurons
- When the -50mv threshold is reached, a cascade of events is triggered
 - It starts with the sodium channels along the cell membrane beginning to open
 - Up to this point, most of the sodium ions are on the outside of the cell
 - With the sodium channels now open, the force of diffusion causes the positively charged sodium ions to being rushing into the neuron, causing the charge on the inside of the cell to rapidly become more positive relative to the outside
 - As the positively charged sodium rushes into the cell, the electrostatic force begins to push some of the positively charged potassium ions out of the cell through the leaky potassium channels
 - Overall, the net effect is to still increase the positive charge building up inside the cell to the point (0mv) where the voltage gated potassium channels open, which allows more positively charged potassium ions to rush out of the cell
 - After reaching a peak charge of about +40mv on the inside of the cell, the sodium channels close
 - This means that sodium stops entering the cell, but potassium continues to rush outward through the still-open voltage gated potassium channel
 - The inside of the cell begins to lose positive charge and continues to fall and actually overshoots the baseline -70mv resting potential (reaching -100mv)
 - At this point, the voltage gated potassium channels have completely closed
 - With the rush of ions complete, the cell slowly returns to -70mv and a short refractory period occurs, where the neuron cannot fire another action potential until it settles and recovers from the previous cascade
- Throughout the action potential and after it is complete, another active player along the cell membrane is the sodium-potassium pump
- This pump has the role of removing sodium from the cell and replacing potassium
 - To do so, it expels three sodium ions from the intracellular fluid and replaces them with two potassium ions
 - The sodium-potassium pump moves slowly and utilizes extensive energy, therefore playing little role in the action potential itself

- It is however, an important part of maintaining the ion balance of the neuron and recovering from action potential cascades
- The action potential begins in the receptive zone of the neuron, where the cell body connects to the axon
- The rapid change that occurs here causes changes in ion concentrations surrounding nearby channels, leading to an action potential in the adjacent location
- o And thus, action potentials cascade along the axon toward the terminal boutons
- This process of cascading action potentials along the axon maintains the signal, but it can be too slow for efficient communication
 - There's a clever solution
 - Special glial cells coat many axons with a type of fatty, insulating tissue called myelin
 - These special cells are the Oligodendrocytes in the Central Nervous System and Schwann cells in the Peripheral Nervous System
 - The insulating layer of myelin allows the action potential to travel down the axon much faster
 - When an action potential reaches a myelin sheath, it jumps across it through a process called saltatory conduction
 - Between the segments of myelin are open regions on the axon called the Nodes of Ranvier
 - These nodes are very important because as the electrical signals jump through the myelin sheath, it weakens
 - At the nodes, the signal can be strengthened again through ion channel cascades before continuing along and jumping through the next myelin sheath
 - Through this process, a signal can travel through a long axon very rapidly without any loss of strength

Sending a signal

- All action potentials produced by a given neuron are roughly identical in strength and duration and proceed in an all or none fashion
- Once the threshold is reached, the action proceeds to completion without fail, there is no such thing as a half action potential
- How then are different types of messages encoded
 - Instead of encoding messages by relative strength of an action potential, messages are encoded by frequency, how often an action potential fires
- Immediately following an action potential is the refractory period during which another action potential cannot begin
- However, shortly after, the neuron can potentially fire again, triggering another action potential cascade
- In this way, a strong signal will lead to many sequential action potentials, while a weak signal will lead to fewer action potentials in the same period of time
- The frequency and pattern encodes the message to be passed on to the neighbouring cell

- Once an action potential travels along an axon, it reaches a terminal bouton, where it can connect to nearby neurons
- This area of connection between the terminal bouton of neuron A and the receptive zone of neuron B, is called the synapse

The Synapse

- The synapse is not a direct physical connection and instead, special mechanisms exist to transmit a signal from the presynaptic neuron to the receiving postsynaptic neuron
- Neurotransmitters
 - Within the terminal bouton of the presynaptic neuron are a variety of chemicals collectively known as neurotransmitters
 - These neurotransmitters are found within small intracellular containers called vesicles
 - As the action potential reaches the terminal bouton, some of the vesicles move toward the cell membrane of the presynaptic neuron
 - The vesicle fuses with the membrane of the presynaptic neuron and opens, spilling neurotransmitter molecules into the extracellular fluid
 - There are a variety of different neurotransmitters that may be released, depending on the location of type of neuron and include
 - Glutamate, GABA, serotonin, dopamine
 - Each perform a different function
 - A single neurotransmitter can also have multiple functions, depending on the receptor on the postsynaptic neuron that it binds to
- The synaptic cleft
 - Once neurotransmitter molecules are released, they enter the space between two neurons, called the synaptic cleft
 - The neurotransmitter molecules float freely in the cleft along with a number of other molecules, which can have direct effects on the neurotransmitter
 - o Ex. Some may remove particular neurotransmitters from the cleft
- The postsynaptic neuron
 - Along the membrane of the receiving postsynaptic neuron are a number of receptors designed to receive specific types of neurotransmitter molecules
 - The free neurotransmitter molecules in the cleft can bind to their specific receptors to continue the process of signal transmission by a number of possible actions
 - One of the most common actions is to modify the ion channels nearby
 - During an excitatory post-synaptic potential (EPSP), Na⁺ channels open, allowing some positively charged sodium ions to flow into the cell
 - This depolarizes the cell, moving it away from the -70mv resting potential and bringing it closer to the -50mv threshold to fire
 - However, a single EPSP has a very small effect on changing the overall potential of the postsynaptic neuron

- To reach the -50mv threshold for an action potential to fire, a number of EPSPs must occur
- These can occur one after the other from the same presynaptic connection causing a slow climb towards threshold
 - Process called Temporal Summation
- On the other hand, multiple EPSPs can occur simultaneously from several different presynaptic connections with the receptive zone of the postsynaptic neuron
 - Process called Spatial Summation
- Naturally, not every receptor binding event leads to an EPSP
 - If it did, neurons would fire uncontrollably with far more noise than signal, leading to little relevant information being communicated
- The system becomes more refined with the addition of a second mechanism that inhibits the transmission of a signal through an **inhibitory post-synaptic potential (IPSP)**
 - When an IPSP occurs, chloride channels on the cell membrane open, allowing some negatively charged chloride ions to enter the cell
 - This neuron is said to be hyperpolarized as the action brings the resting potential of neuron to be even more negative and further away from its threshold to fire
- The balance between excitatory and inhibitory actions control the extent to which the presynaptic signal affects activity in the postsynaptic cell
- Fundamentally, this is the method your brain uses to communicate through complex patterns and networks to control everything from your thoughts, emotions and behaviours

Neural Development

- The developing brain
 - During the peak period of your developing brain, roughly 250,000 neurons were made every minute through the process of neurogenesis (birth of neurons)
 - As each new cell is born, it had to travel to the right final destination in your brain in a process called migration
 - Once there, each cell had to be physically modified to the right function, through a process called differentiation
 - The transformation of unspecified cells into specialized cells that differ in structure and function
 - Finally, each neuron mature and established connections with other neurons (maturation)
- Neurogenesis
 - The development of the nervous system begins as early as 18 days after conception, when the outer layer at the back of the embryo begins to thicken, forming a plate

- The edges of this thick plate then curl upwards and begin to fuse together by day
 21, forming the neural tube
- The neural tube is completely closed by day 28 and will eventually become the CNS, with the brain at the top of the tube and spinal cord making up the bottom
- o By week 20, this mass of cells starts to look like the brain
- How neurons form in the neural tube
 - Inside the tube is the ventricular zone, which is lined with founder cells, that begin dividing as soon as the tube is closed at day 28
 - From day 28 to around day 42, cell division is said to be symmetrical as the division of each founder cell leads to two identical founder cells
 - However, from around day 42 to day 125, cell division is now asymmetrical, as the dividing founder cell now produces one founder cell that stays put, along with a cell that will become a neuron or glial cell, which migrates outward from the ventricular zone

Migration

- Neuronal migration begins almost immediately after the first neurons are born at day 42 and continues for about 6 weeks after the last neuron is born
- Neurons are almost always produced before glial cells, which support the neurons
- There is one exception to that rule, radial glial cells are produced before neurons
- The radial glial cells are fibers that extend outward from the ventricular zone like a form of scaffolding and they end at the outer layer of the cortex
- The neurons use the radial glial cells to migrate from the ventricular zone to the surface of the cortex
- So the brain grows from the inside out, with the deepest layers of the brain being formed before the outer most layers
- As the brain increases in thickness with the addition of more neurons, the radial glial cells grow as well so that they always end at the outermost surface
- Neurons that are born later have to travel a lot farther and push their way through other neurons to reach their final resting place

Differentiation

- After a neuron reaches its final destination, the neuron differentiates and takes on a specific function, which is partly determined by genetics
- Ex. Some founder cells may be pre-wired to become part of the visual cortex because of where these cells came from in the ventricular zone, whereas others may be set to become part of the frontal cortex
- However, it would be a disadvantage for the brain to be completely pre-wired because it wouldn't allow the brain to change with experience
- Neuronal differentiation is sensitive to the input a neuron receives from its connection with other neurons
- o If an emerging neuron is connected with a neuron from the visual cortex, then that neuron will end up doing something related to processing vision

- o Environmental input also plays an important role in cell differentiation
- Suppose that you have a group of neurons that were meant to process binocular information from both eyes, but the child was born with a cataract in one eye
- In that case, those neurons that were "reserved" for binocular vision would not develop correctly because they lacked the essential neural inputs that are needed to differentiate properly
- o This group of neurons would likely be recruited to perform another task
- In this way the neuron's role is determined by both genetic factors and environmental factors

Maturation

- After neurons have differentiated, they need to mature by growing dendrites, axons and synapses
- This last phase of neural development begins as soon as the neurons reach their final destination after migration and continues into adulthood
- Making connections with other neurons is a matter of survival because the ventricular zone produces many more neurons than are needed
- Neurons that fail to make connections are pruned away
- All neurons receive neurotrophic factors from other neurons, which is like food for the neuron
 - If these factors are taken away a neuron will die
 - However, there is only a limited amount of neurotrophic factors in the brain and all the neurons are competing with each other for it
 - In this way, only the neurons that make connections will survive and thus 20-80% of available neurons are eventually trimmed away
- Neural connections are also pruned
 - Many more synaptic connections are formed during this stage than are present later on in development
 - Ex. In the visual cortex, the number of synapses double between 2 and 4 months of age and then continues to increase until it reaches its peak at around 1 year of age
 - After that, the number of synapses begins to decline for the rest of the lifespan
 - This increases the processing efficiency of the brain and retains only the most useful connections

Cast Study: Depression

- Depression is characterized by a number of symptoms, including feelings of intense sadness, loss of motivation and trouble sleeping
- In recent years, two neurotransmitters in particular have become implicated in our understanding of depression, serotonin and norepinephrine
- These two neurotransmitters gained prominence with the advent of tricyclic antidepressants

- These drugs inhibit the reuptake of serotonin and norepinephrine back to the presynaptic neuron
- Reuptake is a normal process of recovering neurotransmitter
- Inhibiting this process increases the availability of serotonin and norepinephrine in the brain and in some cases, can alleviate the symptoms of depression
- Tricyclic antidepressants were the most popular treatment for depression until the arrival of monoamine oxidase inhibitors or MAO-Is
- Monoamine oxidase is normally found in the synapse to break down serotonin
- So MAO-Is inhibits the action of monoamine oxidase, preventing the breakdown of serotonin and making it more available
- The newest and currently most popular category of antidepressant drugs are selective serotonin reuptake inhibitors or SSRIs, which are more specific to the reuptake of serotonin and seem to have less side effects
- Although neurogenesis is usually considered as a process that occurs only early in development, in some select areas of the brain, new neurons continue to grow throughout your lifetime
- However, in severely depressed individuals, this neurogenesis seems to be stunted and the organization of neurons in some of these areas is disrupted
- This may be due to a compound known as brain-derived neurotrophic factor or BDNF, which are vital for the growth and survival of neurons

Neuroscience Live Lecture

- Receptor Trafficking
 - Knockout
 - Removing a gene that codes for a receptor
 - Ex. Removing opiate receptors from mice
 - Disruption of MOR gene disrupts effects of morphine
 - Morphine has a close structure to endorphin, a natural substance in our bodies
 - As a result, morphine can bind to the receptors in our bodies that normally bind to endorphins (morphine acts like natural endorphins)
 - Fate of MOP receptor depends on what it binds to
 - No treatment
 - Receptors are not internalized
 - Endorphin
 - Receptor-neurotransmitter complex are internalized inside the cell surface
 - Heroin
 - Receptor-opiate complex are not internalized
 - · Leads to addictive behaviour
 - Prolonged activation of ligand-binding is associated with addiction
 - Mice with designer genes (knock-ins)

- Knock-ins show reduced tolerance over several days
- Wild-type animals show large tolerance over several days
- Receptor expression
 - Neurons injected with amphetamine appear more spread than those injected with saline
 - Dopamine and reward
 - Dopamine is the primary neurotransmitter for reward feelings
 - People with lower dopamine levels would find other ways to get those feelings (opiates)
 - Addicted brain has fewer receptors than a healthy brain so wants to stimulate those receptors more often to achieve that feeling of pleasure
- Mirror neurons
 - Collection of neurons that are activated when we perform an action as well as when we watch someone perform an action
 - Motor neurons
 - Allow us to predict behaviour
 - Monkey watching a person eat fruit
 - Neurons in the monkey's brain appear as if the monkey is eating the fruit itself
 - Child development
 - By 18 months old, children can predict emotions
 - By 4-5 years old, children can predict states of mind of other people
 - Theory of mind
 - o The understanding of someone else's circumstance
 - If a child has not developed Theory of Mind, they expect that what they know is what everyone else knows
 - If a child has developed Theory of Mind, they understand that their own thoughts are not necessarily the thoughts of others
 - Development as a species
 - One organism sees another performing an action, another learns from it

Lecture 6: Neuroscience II

January 29, 2011

The Structure of the Brain

- In humans, the nervous system axis or "neuraxis" curves
- Dorsal always refers to the back of the axis and ventral means to the front of the axis or "to the belly"
- Because of the curve in the neuraxis, at the level of the head, dorsal is up, but at the level of the spinal cord, dorsal is to the back

- Rostral means towards the top of the axis and caudal means towards the bottom of the axis
- Locations in the brain that are more central or towards the midline of the brain are medial and regions towards the outside of the brain are lateral
- These terms can be combined to locate a very specific brain region
- Ex. The medulla is a region in the hindbrain, which can be further divided into several subregions
 - o One subregion is called the **rostral ventral medial** medulla
 - This means that it is towards the top, in front of the neuraxis and towards the midline of the brain

Studying the Brain

- Lesion studies
 - o In 1848, Phineas Gage was a foreman of a railway construction crew, in charge of using explosives to remove large sections of rock from the path of the railroad
 - o He was athletic, intelligent and full of life, by all means respected by his crew
 - One day, Gage was a victim of an accident, resulting in the blasting of a 3 foot iron rod completely though his left cheekbone and through the top of his skull
 - Remarkably, he survived and except for some loss of vision and facial disfigurement, he recovered completely
 - However, his friends barely recognized him as they Gage they once knew
 - o He now become prone to selfish behaviour and bursts of profanity
 - He became erratic and unreliable and had trouble forming and following through on plans
 - Gage's case provided support for the view that the brain has specialized structures for complex behaviours
 - An advantage of case studies such as Gage's is that it gives scientists a direct measure of a brain's structure and function
 - A disadvantage is that it is hard to selectively target particular regions and draw conclusions
 - This problem can be overcome by studying specific brain lesions induced in animal models
 - In such scenarios, a researcher destroys, removes or inactivates a defined brain region and observes the result on behaviour
 - The accuracy of this emerging understanding of structure and function can depend on the precision of the lesion
- An alternative approach to lesioning is to electrically stimulate an area of the brain and observe the result on behaviour to build an anatomical map related to function
 - This technique was used extensively by neurologist Penfield as he performed brain surgery to treat patients with severe epileptic seizures
 - Penfield revolutionized techniques in brain surgery as he perfected his "Montreal Procedure" to treat patients experiencing severe seizures
 - In doing so, he had to be sure that critical areas of the brain were left intact

- Because the brain itself does not have pain receptors, a patient undergoing surgery could be under local anaesthetic and fully conscious, working with Penfield to probe the exposed brain to locate and removed scarred tissue that caused the seizures
- o Penfield used a thin wire carrying a small electric charge to stimulate the cortex
- This stimulation leads individual neurons to fire and thus Penfield could accurately map perceptual processes and behaviours to specific brain regions
- Ex. If an area of the visual cortex was stimulated, a patient reported seeing flashes of light and if an area of the motor cortex was stimulated, a patient would experience a muscle twitch

Single cell recording

- Electrodes can also be used to record ongoing electrical activity in the brain through single cell recording techniques
- A small electrode is inserted into the nervous tissue of a live animal model with its tip held just outside the cell body of an individual neuron
- o From this electrode, neural activity is recorded while the animal performs a task or a stimulus is presented
- The pattern of firing reveals a particular neuron's functional role
- In a typical experiment, cats were presented with specific visual stimuli while recording from single cells in the visual cortex
- In this way, individual cell types were identified that responded to specific categories of visual stimuli

Structural neuroimaging

- To study large-scale structure and function of brain regions, neuroscientists use structural and functioning neuroimaging techniques
- The first structural neuroimaging technique developed was computed tomography (CT)
 - During a CT scan, a series of X-ray slices of the brain are taken and pieced together to produce a relatively quick and inexpensive picture of the brain
 - These scans are often helpful to diagnose brain injuries
 - A major limitation with the CT scan by today's standards is its relatively low resolution
 - It is very difficult to examine fine brain anatomy with a CT scan and as such it is not often used in neuroscience research
- For a more detailed structural image of the brain, neuroscientists use MRI (magnetic resonance imaging)
 - In an MRI machine, powerful magnetic fields are generated, which align the hydrogen atoms found throughout the brain
 - While these atoms are aligned, an MRI can be used to localize tissue very precisely throughout the brain

Functional neuroimaging

- Cognitive neuroscientists can use a functional imaging technique such as the positron emission tomography (PET scan) to learn how brain function relates to cognitive tasks such as language and memory
- In a PET scan, a radioactive tracer of glucose or oxygen is injected into the bloodstream
 - The radioactive molecules make their way to the brain and are used in metabolic processes, which are detected by the PET scan
 - The logic is that more active brain areas will use more metabolic resources and so an image of the brain's relative pattern of activity can be constructed
 - A disadvantage of the PET scan is that it requires a radioactive tracer to be injected, a relatively invasive procedure
- Functional magnetic resonance image (fMRI) is often preferred because it can produce a relatively clear image of the brain's activity without the need for a radioactive tracer
 - fMRI works by measured the blood oxygen dependent signal and uses many of the same principles as the MRI
 - It is able to measure the relative use of oxygen throughout the brain and operates under the same basic assumption as the PET scan (more active areas of the brain require more metabolic resources)
 - A limitation of fMRI is that it provides a very rough image of brain activation
 - Oxygen use by the brain often spikes a few seconds later than the spikes of activity in the brain, which can be a very long time in terms of brain function
 - As such, fMRI is not the best method to use if a researcher is interested in precise timing of brain activation and function
- A final neuroimaging method is the electroencephalogram or EEG
 - The electrical activity of the brain can be recorded through the scalp by wearing a cap of very sensitive electrodes
 - The EEG provides only a very rough image of the brain's overall activity, from populations of neurons
 - However, with a few modifications, the EEG can become more informative
 - In an event related potential (ERP) experiment, a specific stimulus is presented to the subject repeatedly, while the EEG is recording
 - Although the EEG will generally produce very noisy waves, the specific stimulus presented can have a small and consistent effect on the readout
 - By averaging the EEG signal across many trials, the noise can be balanced out and what remains is a characteristic signal
 - These ERP signals can still be difficult to interpret, but there are a number of reliable signs reported throughout the literature that serves as markers for different types of neural processes

- Ex. One marker is called the N170 wave, which is thought to correspond to face processing
 - When combined with a behavioural measure, EEG and ERP signals can be highly informative markers, with precise temporal resolution, on the order of milliseconds

The Brain Regions – Hindbrain

- All information into and out of the brain travels through cranial nerves or through the spinal cord, which connects to the hindbrain at the base of the brain
- The hindbrain consists of the medulla, pons, reticular formation and the cerebellum
- These structures are evolutionarily the oldest parts of the brain and found in some form in nearly every vertebrate species
- Primarily involved in the regulation of vital bodily functions
- Medulla
 - Most caudal part of hindbrain and lies directly above spinal cord
 - Structurally, looks like an extension of the spinal cord and plays an important role in vital functions such as breathing, digestion and regulation of heart rate

Pons

- The pons is a small structure that is rostral to the medulla
- Relays information about movement from the cerebral hemispheres to the cerebellum
- The pons also contains a number of nuclei that are generally part of the reticular formation
- Pons also processes some auditory information and is thought to be involved in some aspects of emotional processing
- Reticular formation
 - A set of interconnected nuclei found throughout the hindbrain (excluding cerebellum)
 - Two main components
 - The ascending reticular formation (also called reticular activating system or RAS) is primarily involved in arousal and motivation and may be a part of the network responsible for conscious experience
 - The RAS plays an important role in circadian rhythms
 - Damage to the RAS leads to devastating losses in brain function and in extreme cases, permanent coma
 - The descending reticular formation is involved in posture and equilibrium and plays a role in motor movement

Cerebellum

- o Resembles a miniature version of the entire brain
- Motor commands pass through the cerebellum as they signal muscles to contract and during the production of movement, sensory signals return to the cerebellum for immediate error correction

 Patients with damage to the cerebellum display exaggerated jerky movements, overshooting or missing targets completely

<u>The Brain Region – Midbrain</u>

- A relatively small region that lies between the hindbrain and the forebrain
- Generally the midbrain contains two major subdivisions, the tectum and the tegmentum
- Within these regions are a number of structures involved in a variety of functions, including perception, arousal and motor control
- The tectum
 - Located in the dorsal portion of the midbrain and contains two primary structures, the superior and inferior colliculi
 - These two structures are involved in functions related to perception and action
 - The superior colliculus is thought to be involved in eye movements and visual reflexes
 - The inferior colliculus is thought to be involved in auditory integration
- The tegmentum
 - Contains important structures, including nuclei of the reticular formation, the red nucleus and the substantia nigra
 - The red nucleus is an important structure involved in the production of movement
 - In vertebrates with less complex brains, the red nucleus is one of the most important structures for the regulation and production of movement, as it projects directly to the cerebellum and spinal cord
 - In humans, with their relatively advanced forebrain structures, the red nucleus plays a lesser role in the production of movement and instead serves primarily as a relay station for information from higher motor areas to and from the cerebellum and spinal cord
 - However, in the still developing brain of young infants, many motor behaviours may still be controlled by the red nucleus
 - The substantia nigra is another important and interconnected region of the midbrain, with projections into a variety of forebrain regions
 - The substantia nigra is involved in tasks such as motor planning and learning and reward seeking
 - The substantia nigra contains neurons that produce the neurotransmitter dopamine, which is released in high concentrations during a variety of rewarding behaviours
 - Artificial rewards such as drugs of abuse act to increase the amount of dopamine in the synaptic cleft to unnatural levels, which may contribute to the addictive properties of these drugs
 - At the other extreme, damage to dopaminergic neurons in the substantia nigra leads to reduced levels of dopamine
 - This has been directly implicated in motor tremors that are characteristic of Parkinson's Disease

The Brain Region – Forebrain

- Contains structures involved in complex functions such as emotion, memory, perception and thought
- Is the largest region of the brain
- Subcortical structures of the limbic system
 - Hypothalamus
 - Controls several integrative functions including directing stress responses, regulating energy metabolism by influencing feeding, digestion and metabolic rate and regulating reproduction through hormonal control of mating, pregnancy and lactation (Fight, Flight, Feeding, Reproduction)
 - Hypothalamus exhibits these regulatory roles through neurons that are capable of producing a variety of regulatory hormones and via connections with the pituitary gland and key subcortical structures that lie below the surface of the cortex

Pituitary

- The pituitary gland lies inferior to the hypothalamus
- Because of the variety of vital hormones it regulates and releases, it is often called the master gland of the endocrine system
- Contains two subregions, the anterior and the posterior
- The anterior pituitary receives signals from the brain, usually via the hypothalamus and releases stimulating hormones to regulate other important endocrine glands such as the thyroid, testes, ovaries and adrenals
- The posterior pituitary is an extension of the hypothalamus and releases two hormones called oxytocin and vasopressin
 - Oxytocin is involved in basic physiological functions such as lactation and uterine contractions in women and may also play a role in bonding, love and trust
 - Vasopressin is a vital blood hormone that regulates your levels of thirst by interacting with your kidneys to regulate glucose levels

Thalamus

- A large structure near the centre of the brain
- Axons from every sensory modality synapse in the thalamus, which processes and relays the information selectively to areas of the cerebral cortex
- Output from the cerebellum and limbic system also first relay through the thalamus on its way to the cortex

Amygdala

 The amygdala are two symmetrical almond shaped structures located below the surface of each temporal lobe

- Receives sensory information from the thalamus and contains nuclei, which among other things, play a role in decoding emotions, particularly stimuli that may be threatening
- During intense emotions such as fear, the amygdala becomes very active
- When nuclei of amygdala are damaged, animals often show deficits in classical conditioning of fear responses and amygdala functions have been implicated in disorders such as PTSD

Hippocampus

- Horseshoe-shaped structure in the temporal lobe
- Seems to be involved in the process of memory formation
- Activity in the hippocampus is related to your ability to hold short-term memories and may be involved in the process of transferring short-term memories to long-term memory
- Connected to the amygdala, which may be one reason why strong emotions may be triggered by particular memories
- Plays a vital role in your ability to navigate through the world and may contain a "spatial map" of the world around us
- One of the few regions of the brain in which neurogenesis continues throughout adulthood
- Production of new neurons in the hippocampus is thought to be related to memories
- Damage to the hippocampus has been implicated in Alzheimer's Disease and extreme trauma to the hippocampus can lead to severe amnesia

The Brain Region – Cortex

- Lies on the outside of the brain and is evolutionarily the newest part of the brain
- Most of the actual information processing, complex behaviours and cognitive functions that make you human take place in the cortex
- One of the signature features of the cortex is its ridged structure
- The cortex folds over itself and forms gyri and sulci
- A gyrus is a ridge on the cortex, or a bulge outward, while a sulcus is the indent or gap between them
- These folds increase the surface area of the cortex within the confines of being encased in the skull
- Very deep sulci are known as fissures, which often divide major areas of the cortex
- The four lobes
 - Occipital lobe
 - Lies at the very back of the brain
 - Exclusively responsible for visual processing and contains the primary visual cortex (called V1) and other visual areas
 - Where more complex processing of visual information begins
 - An individual with healthy eyes, but damage to the occipital lobe may become functionally blind

Temporal lobe

- Wraps around both sides of the brain, near your temples
- Lies at the sides of the brain below the sylvian fissure
- Through projections from the occipital lobe, the temporal lobe contains a number of areas responsible for processing the form and identity of visual stimuli
- Temporal lobe is the location of the primary auditory cortex (A1)
- It is here that auditory processing begins
- Partially responsible for processing of memory and language
- Individuals with severe temporal lobe damage may show deficits in the production of speech, amnesia and auditory processing

Parietal lobe

- Between the frontal and occipital lobe
- Lies anterior to the occipital lobe, above the sylvian fissure and terminates rostrally at the central sulcus
- Directly along the central sulcus, at the connection point with the frontal lobe, lies the primary somatosensory cortex, where the processing of touch begins
- Also involved in a number of complex visual and spatial functions
- For example, through projections from the occipital lobe, the parietal lobe processes the location and movement of visual objects
- Beyond that, the parietal lobe contains a spatial representation of the world that may be involved in visual attention and guiding eye and body movements
- Damage to the parietal lobe can result in deficits in somatosensory processing or even a loss of sensation completely
- Parietal damage can also lead to deficits in orienting, attention, coordination of targeted movements and in extreme cases, complete loss of attention to particular spatial regions

Frontal lobe

- Lies at the front of your brain
- Along the central sulcus, where the frontal lobe meets the parietal lobe, lies the primary motor cortex, where motor commands originate
- It is here where your most complex decision making processes occur
- Frontal lobe contains a variety of areas responsible for complex functions important to goals such as language, strategy formation, inhibition and manipulation of items in short-term memory
- Individuals with damage to frontal lobe can suffer a variety of dysfunctions depending on the specific area of the lesion
- These deficits can include spontaneous inappropriate behaviour, motor deficits, loss of motivation, deficits in decision making and learning and difficulty understanding language

Brain Lateralization

- Although many brain structures are found on both sides of the brain, neuroscientists have found cases of function specialized to one side of the brain
- This property is called asymmetry or brain lateralization
- Best evidence comes from lesion studies that can demonstrate a double dissociation (damage to a specific cortical region on one side of the brain, produces a specific behavioural deficit, whereas damage to other areas surrounding the region or on the other side of the brain, do not lead to the behavioural deficit)
- Early case study from Paul Broca
 - His research involved a patient nicknamed Tan who suffered a speech deficit known as aphasia
 - o Tan was one of the few words he could properly articulate
 - In Tan's autopsy, Broca noted a lesion in the left frontal lobe now known as Broca's Area
 - This area is vital for the motor production of speech
- The neurologist Wernicke noted that some language deficits were not motor production problems, but rather deficits in language comprehension
 - Wernicke found that damage to the left temporal gyrus, an area now known as Wernicke's Area, is important for language comprehension
- In both cases, language deficits seem to be caused by damage restricted to specific areas in the left hemisphere
- It seems that the right hemisphere contains a number of specialized regions involved in the processing of spatial representations of the world
 - Right hemisphere is responsible for non-verbal functions and processes involving spatial relations (non-verbal memory, non-language sounds (music), mental rotation of shapes, geometric patterns, faces, emotional expressions)
- In normal individuals, this lateralization of function across the hemispheres is not noticeable because the two hemispheres of the brain communicate through a thick bundle of axons called the corpus callosum
- The corpus callosum passes through the centre of the brain and carries information from one side of the brain to the other very rapidly
- In early 1960's, Sperry and Gazzaniga conducted research on patients in which the corpus callosum had been severed
 - These patients experienced the Split Brain Syndrome, effectively having two independently operating hemispheres
 - o In normal patients, sensory and motor information crosses over from one side of the body to the contralateral or opposite side of the brain through the thalamus
 - Normally, this information would also be available to the same side or ipsilateral hemisphere by travelling through the corpus callosum
 - However, in split-brain patients, once the information arrives on the contralateral side of the brain, it is trapped there and unable to travel to the other hemisphere because the corpus callosum is severed
- Split Brain Syndrome
 - It's as if the left side of the brain is a separate entity, unaware of what the right brain has received

- For most of the everyday activities performed by split brain patients, the disorder has little influence on their lives because most stimuli arrive on both sides of the body simultaneously
- However, Sperry and Gazzaniga conducted a set of experiments where this was not the case
- o Ex. A split brain patient stares straight ahead at a fixation point
 - Suppose you then present a picture of a cup to the left visual field of a split brain patient
 - Because visual stimuli are organized into visual fields and not by eyeballs, the image of the cup travels to the right hemisphere of the brain
 - If you ask the subject to name the object she just saw, she will be unable
 to do so because language is preferentially processed by the left side of
 the brain, which at this point has no knowledge of the cup
 - However, if you ask the split brain patient to close her eyes and feel through a set of objects to pick out the object she was presented, she will have no problem identifying the presented cup as this is a distinctly spatial task
 - If you presented the image of the cup to the right visual field, the image is processed in the left hemisphere so the patient will be able to name it, but will not be able to pick it out using the distinctly spatial task
- Although there is some variability between patients, almost all the tasks preferentially processed by the left hemisphere will be better performed when the information is presented to the right side of the body and conversely for the right hemisphere
- Interestingly, these patients do not realize they are behaving strangely as their conscious perception is based on whatever task they are being asked to perform at the time
- One case tells the story of a split brain patient reading a book that he is holding with his left hand
 - Although he consciously found the book fascinating, he found himself repeatedly putting the book down
 - It seemed that although the left side of his brain was reading the book and enjoying it, the right side of his brain was getting quite bored with the verbal activity

Neuroscience II Live Lecture

- Human brain is underdeveloped at birth because head has to fit through birth canal
- Rapid growth after birth
- Contrast with other species where some animals are born with an adult brain
 - o Ex. Deer
 - Hours after birth, can move around, follow their mothers
 - o Possibly because there is a lot of parental investment in human babies after birth

- Functional Organization of Nervous System
 - Nervous system can be divided into two parts
 - Central nervous system
 - Brain + Spinal cord
 - Peripheral nervous system
 - Nerve extensions from CNS
 - How brain and spinal cord communicates with outside world
 - Nerves
 - Bundles of many types of neurons
 - Typically are axons of many neurons
 - Connect CNS to outside world by connecting with muscles, sensory organs and glands
 - Pinched nerve
 - Restricts communication from CNS to body
 - Ex. Knot in garden hose
 - Feeling numb, tingly
 - 3 Classes of Neurons
 - Sensory neuron
 - Carry information from sensory organs through nerves to sensory neurons
 - Affront neurons
 - Motor neuron
 - Carry messages from CNS to control muscles and glands
 - Effront neurons
 - Interneuron
 - Carries messages between sets of neurons
 - Ex. Between sensory and motor neurons
 - Can modify signal or make it more efficient
 - Knee-jerk reflex
 - Stimulus acts on sensory neuron, which goes directly to motor neuron, causing quadricep muscle to flex
 - Some sensory neuron goes to inhibitory interneurons, which causes the opposite muscle (hamstring) to relax
 - Result is a kick
 - An automatic response
 - Response helps us to keep posture, balance and walk
 - Information does not have to travel all the way to your brain
- Case Studies
 - Sleep paralysis
 - Helps us understand the connection between hindbrain and pons
 - Pons receives information from visual areas to control eye and body movements (balance)
 - Controls patterns of sleep and arousal

- During REM sleep, pons inhibits signals to motor neurons and paralyzes muscles by blocking communication
- From evolutionary context, safer to be quiet during the night because there are predators
- Sleep paralysis occurs when certain brain events are out of sync
 - Brain awakens from REM sleep before paralysing effects of pons wear off
 - Can last for 15 minutes

o Capgras' Delusion

- Young male in a car accident, in a coma for three weeks, begins rehab and everything appears fine
- Observation, recognizes his parents, but thinks they are imposters
 - "Looks like my father, but he's an imposter, he isn't my father"
- Otherwise, appears completely lucid
- Delusion very specific to visual information
 - Can call his parents and will believe they are his parents
- Specific symptom
 - Believes whoever is acting like his parents are imposters
- Amygdala
 - Assess the emotional significance of a stimulus
- FFG
 - Neurons in the FFG respond to faces
 - Information from FFG travels to amygdala
 - When FFG is functioning normally, helps you to recognize
 - When damage to FFG, hard to recognize people's faces, even your own
- Visual stimuli of faces goes to FFG so you can recognize the face, but information then goes to the amygdala for emotional arousal of that face
- In the delusion (observations)
 - Recognition without emotion
 - Connection between FFG and amygdala is damaged (both regions are intact)
 - Delusion does not occur with auditory stimuli
 - Brain creates a running narrative to explain stimuli and events
 - o Patients make up a story for facts in front of them
- Galvanic skin response (objective way to measure response)

Hemispatial neglect

- Imagine you meet a 60 year old woman who has a stroke
- Appears to have recovered after, but has gained some odd behaviours
- She used to be strict with hair and makeup, but now only styles the right side of her hair and only puts makeup on right side of her face
- Also only eats food on right side of plate unless pointed out to her to eat food on left side

- Patients in this situation typically are unaware of contralateral stimuli
- Damage to inferior parietal lobe
- Patients aren't blind to left side of the world, they just don't pay attention to left side
- Patients also have troubles with mirrors
 - Person behind patient holding a ball to the right
 - When asked to reach and touch the ball to the right, will try to reach into the mirror
- Hemispatial neglect more often observed when ignoring left side of the world
 - Means right parietal lobe is damaged
- Clinical observations show that left hemisphere's intentional spotlight helps you focus only on right side of world
 - However, right hemisphere controls a much broader intentional spotlight than left hemisphere
- When left parietal lobe is damaged, do not typically see hemispatial neglect to right side of the world
 - Because right parietal lobe can make up for the lost spotlight
- People recover by memorizing and relearning sequences

Lecture 7: Behavioural Neuroscience

February 6, 2011

The Structure of the Brain

- Cognitive neuroscientists try to understand abstract mental processes in a neural framework
- And so, traditional paradigms used to study cognitive functions such as learning, memory, language and problem solving are complemented by techniques such as neuroimaging to trace the routes of neural processing
- Behavioural neuroscientists seek to understand the neural processes underlying behaviours such as reward, sexual motivation and feeding mechanisms
- Typically, these complex behaviours are simplified into component behaviours that are modeled in simple animal systems to use the full range of techniques available in neuroscience such as electrophysiology, pharmacology and behavioural genetics
 - Ex. Research of feeding can be divided into hunger and satiety mechanisms

Neural Plasticity

- Although recovery from brain injury is a particularly dramatic demonstration of its flexibility, your brain is changing in every interaction with the environment
- This "everyday neural plasticity" allows your brain to adapt incoming stimuli and rewire itself to optimize interactions with the outside world

- In 1950, researchers were well area that environmental influences can lead to enduring changes in complex behaviour that can be observed
- Ex. Classic studies by Bingham and colleagues demonstrated that exposure to complex environments made animal subjects into better problem solvers
- However, it was not until about a decade later that researchers realized the important of environmental experience on **enduring** changes in the physical structure and functional organization of the brain
- In 1964, Bennett and colleagues compared the brains of rats raised in enriched or impoverished environments
 - The enriched environments was like a little piece of rat heaven, where the rats lived in social groups in a complex environment filled with toys, ladders, tunnels and running wheels to explore
 - In the impoverished environment, rats lived alone in small cages with access to food and water only
 - Researchers found that brains from the two groups were wired very differently
 - The brains of rats exposed to the enriched environment had a much richer network of neurons with more dendrites and synaptic connections compared with brains of rats raised in the impoverished environment
- Another example of role of environmental input on enduring changes in neural structures comes from studies on maternal care in rat pups
 - Meany and colleagues have found that rats raised by mothers that engaged extensively in maternal care behaviours (licking and grooming) later grow to become less fearful and less responsive to stress than do those raised by mothers that do not engages as frequently in these maternal care behaviours
 - These stress and fear behavioural traits observed in adulthood were matched by measurable stress and fear changes in brain including increased expression of glucocorticoids receptors in adult rat's hippocampus
- Although research on role of environmental enrichment has been in animal models, many neuroscientists believe that similar effects may also be observed in humans
 - Important implications for education, parental care and treating neurological disorders of aging
- Coincidence Detection
 - The first practical theory based on neuroscience for understanding the connection between the mind and the brain came from a Canadian neuroscientists named Donald Hebb
 - Hebb's theory described how connections between individual neurons can be changed and how combinations of connected neurons can be grouped together as processing units
 - Hebb called these flexible units "cell-assemblies", which could adapt to the constant adjustments necessary to direct the brain's response to stimuli
 - o And so, complex thoughts can be built from sequential activation of neurons
 - Hebb himself summarized, "When an axon of cell A is near enough to excite cell
 B and repeatedly or persistently takes part in firing it, some growth process or

- metabolic change takes place in one or both cells such that A's efficiency, as one of those cells firing, is increased"
- Hebb's Law is often paraphrased as "neurons that fire together wire together"

Long-Term Potentiation

- A promising candidate mechanism for Hebbian learning is Long-term potentiation or LTP
- LTP is the strengthening of the connection between two neurons and this effect can last for an extended period of time, from minutes to a lifetime
- It is also sometimes referred to as an increase in synaptic efficiency, meaning a presynaptic neuron becomes more efficient at generating a large response in the postsynaptic neuron
- o In the lab, this LTP can be measured by the change in amplitude of the EPSP
- LTP first observed by student studying the functional circuitry of hippocampus, which plays an important role in memory
- Lomo observed that following activation by brief, repeated bursts of high frequency stimulation, a single test pulse could make it easier for adjacent cells to fire action potentials, an effect which could last for several hours over the duration of an experiment
- This LTP of signalling provided a cellular mechanism for the synaptic change described in Hebbian learning
- Several properties of LTP that make it a promising candidate for neural basis of learning and memory
 - LTP occurs rapidly and is long-lasting, giving it a dynamic flexibility to form new memories
 - Like memories, LTP is input specific, facilitating only the synapses activated during the original stimulation
 - The strong activity in Pathway 1 initiates LTP at the synapse, without initiating LTP at the inactive synapse of Pathway 2
 - LTP is associative, meaning that it can strengthen inputs from multiple pathways if they are active simultaneously, as might naturally occur when two related events are presented
 - The weak stimulation of Pathway 2 alone does not trigger LTP
 - However, when weak input from Pathway 2 occurs together with strong input from Pathway 1, both sets of synapses are strengthened

Mechanism of Classical Hippocampal LTP

- Lomo's original observations were made using an in vivo hippocampal preparation, which limited the techniques that could be used in an experiment
- However, with the development of an in vitro tissue preparation, a fresh hippocampal tissue slice could be kept alive in a dish, allowing many new experimental tools to be used

Mechanism of LTP

 When the neurotransmitter glutamate is released from the presynaptic neuron, it binds to AMPA receptor, which is both a receptor and an ion channel

- This binding causes the channel to open, allowing the flow of positively-charged ions
- This depolarizes the post-synaptic cell, moving it away from its -70 mv resting potential and closer to the -50 mv threshold for an action potential to occur
- And so, binding of glutamate at the AMPA receptor alone can be sufficient to cause a short-lived EPSP
- Classical LTP begins with the presynaptic release of glutamate, which can bind to AMPA receptor and another receptor called NMDA receptor
- Glutamate binding to AMPA receptor is associated with normal synaptic transmission
- Glutamate binding to both NMDA and AMPA receptor types is associated with induction or development of LTP
 - Concentration of positively charged calcium ions inside the postsynaptic cell must exceed a critical threshold
 - This process of calcium ion flow can only occur when glutamate binds to NMDA receptor
 - However, at the resting state, the NMDA receptor-channels are blocked by magnesium, preventing calcium from entering cell
- Fortunately, successive EPSPs via the binding of glutamate to AMPA receptor leads to sufficient depolarization that unblocks the Mg
- This allows calcium to enter postsynaptic cell and induce LTP
- LTP requires two events
 - Postsynaptic activity to remove magnesium block
 - Presynaptic activity to release glutamate
- Calcium entry requires both presynaptic and postsynaptic activity to occur
- Depolarization of postsynaptic neuron must be perfectly timed with firing of presynaptic neuron to allow calcium channel to fully open
- Calcium entry into postsynaptic neuron has a number of complex effects, but one important result of this activity is to promote the expression of more AMPA receptors in a specific region of the postsynaptic neuron
- And so, a specific synapse on the postsynaptic neuron becomes more sensitive to glutamate release from a specific presynaptic cell, strengthening the connection
- LTP and LTD
 - Increased expression of AMPA receptors in postsynaptic cell can last for a long time
 - Just as there are IPSPs to counter EPSPs, another mechanism, called long-term depression (LTD) exists to decrease the sensitivity of synaptic connections

Simple Circuits for Memory

 Eric Kandel has been responsible for linking behaviours associated with learning and memory with synaptic changes in the nervous system

- His research addressed the question, "what happens in a neural circuit when learning occurs?"
- Much of his research conducted on a slug called Aplysia
 - Nervous system of Aplysia has only about 20,000 neurons
 - This limited nervous system and its repertoire of simple behaviours makes the sea slug an ideal model to study neural basis of learning and memory
 - In his research, Kandel focused primarily on one particular behaviour, gill withdrawal reflex
 - At rest, Aplysia extends its gill outward to assist in collection of oxygen
 - o In response to danger, it rapidly retracts these organs for safety
 - This simple reflex is mediated by a relatively small circuit of neurons that can be used to study fundamental learning processes such as habituation and classical conditioning

Habituation

- Simple form of learning which involves decreased response to a repeated or constant stimulus
- In observing Aplysia, Kandel found that the strength of the gill withdrawal reflex became progressively smaller after repeated stimulation
- o It turns out that this behaviour is mediated by a relatively simple neural circuit
- At the surface of the skin, a set of sensory neurons receive signals from the outside world
- The sensory neurons synapse with motor neurons that return to the gill and control its withdrawal behaviours
- After mapping the neural circuit responsible for gill withdrawal reflex, the next step was to understand which part of the circuit was modified during habituation
- Kandel observed that across trials, presynaptic sensory neuron continued to fire just as many action potentials and receptors in the postsynaptic neuron remained just as sensitive
- o However, presynaptic neuron seemed to be releasing less neurotransmitter
- In fact, Kandel found that fewer vesicles were fusing with membrane, this releasing less neurotransmitters
- With repeated training, this change in efficacy of synapse would last for weeks, suggesting a mechanism, for long term memory

Classical Conditioning

- Involves the learning of a contingency between a CS and a US
- Prior to conditioning, US elicits a UR
- After conditioning trials in which the CS and US are paired, the CS alone can now elicit a response, called the CR
- Kandel demonstrated that classical conditioning could readily be demonstrated in Aplysia
- In these experiments, a separate area of the body called the mantle was stimulated before stimulating the gill withdrawal circuit itself
- The mantle stimulation served as a kind of CS which reliably predicted stimulation of the gill withdrawal reflex, which served as the US

- Eventually this mantle stimulation alone was sufficient to elicit the gill withdrawal reflex
- The sensory neuron of the Mantle synapses with the postsynaptic motor neuron of the reflex circuit
- The stimulation from the mantle causes a slight depolarization of the postsynaptic neuron, releasing the Mg blockage at the NMDA receptor
- Then, when the US stimulation arrives shortly after, the release of glutamate allows calcium to enter the cell and LTP to take place
- In this way, NMDA receptors can serve as a perfect contingency detectors in the learning circuit
- With these studies, Kandel was able to demonstrate a direct link between cellular mechanisms and behavioural output, strengthening the understanding of how learning and memory proceeds in the brain

Human Memory

- The first major breakthrough in understanding the neuroscience of memory in humans came in 1957, with what could become a famous case study by Scoville and Milner on a patient called H.M.
- The case of H.M.
 - When H.M. was 7 years old, he fell and hit his head, leaving him with seizures that continued to worsen throughout his life
 - By the time he was 21, the seizures worsened to the point where he could no longer function normally
 - After anticonvulsant drugs failed to relieve his symptoms, Dr. William Scoville proposed an experimental surgery to remove the medial temporal lobes from H.M.'s brain
 - The operation was successful in relieving the seizures, but it also had some distressing side effects
 - During the surgery, most of H.M.'s hippocampi were removed, leading him to experience some very interesting memory deficits
 - After his operation, HM returned home and lived a relatively normal life
 - Although his memory for the past was completely intact HM was completely unable to form new memories
 - o To HM, it was always 1953 and he was always 27 years old
 - Because he had a fully intact short-term memory, HM was able to carry on a normal conversation without difficulty, but once the conversation ended, his attention would break and he would forget everything that just happened
- Different forms of memory
 - The case study of HM revealed to researchers that distinct memory systems and functions exist in humans
 - One important distinction is between procedural memory and declarative memory
 - Procedural or implicit memory is your memory for actions, sequences and skills

- Often occurs outside of your awareness and can be difficult to explain to another
- Ex. Ability to ride a bike, play an instrument
- This "know-how" memory can be very durable
- Declarative memory is your memory for facts and knowledge and your personal experiences
 - Often prone to forgetting, but can be markedly improved by using elaborative rehearsal and active recall

Procedural Memory

- Because procedural memory encompasses such varied tasks as motor commands and spatial representations, its neural correlates are guite diverse
 - However, the processing mechanisms for procedural memory must be independent of those for declarative memory
 - This would explain why HM could have no difficulty learning new tasks, but never remember practicing them
- A key region involved in motor learning is the cerebellum
- Cerebellum is involved in conditioned motor responses ranging from simple eyeblink responses, balance and more complex motor tasks
- Another important region is called the striatum, a collection of nuclei in the forebrain
- The striatum is implicated in motor disorders such as Parkinson's and Huntington's Diseases and patients with damage to the striatum show marked deficits in learning new motor skills

Declarative Memory

- HM's case demonstrates that at least part of the declarative memory system must involved the hippocampus
- Declarative memory extends to include the cerebral cortex and parahippocampal region, the area of cortex immediately surrounding the hippocampus
- Process of forming declarative memories begin in the cortex, where information you are currently working with is processed
- From there, information travels to a sort of "intermediate-term memory storage" in the parahippocampal region
- Here, information is stored on the scale of minutes
- o Finally, the hippocampus begins the process of forming new long-term memories, which are later stored throughout the brain
- Once information reaches the hippocampus, it is represented in at least three levels
- At the lowest level, the hippocampus carries a representation of your current experience in the context of the entire event
- Next, the hippocampus links these episodes together based on common episodes and places you have experienced in the past
- Finally, the hippocampus creates a flexible declarative memory, which is organized according to the most salient or important information and stored permanently in the brain

- Place cells in hippocampus
 - In an early study of the cellular processes in the hippocampus, James Ranck Jr. attempted to understand how the hippocampus can accomplish the task of creating a new declarative memory
 - Ranck found that the firing of hippocampal cells correlated with specific behaviours, such as approach, withdrawal, eating and drinking
 - Later studies found that cells in the hippocampus can fire to even more specific events
 - o Ex. O'Keefe observed a very different sort of firing pattern in the hippocampus
 - He found that specific hippocampal cells fired in relation to specific location of the animal, independent of the behaviour being performed
 - o O'Keefe and colleagues would later call these hippocampal "place" cells
 - He proposed that hippocampus receives information about the outside world to create a cognitive map
 - Each hippocampal cell fires when the animal is in a particular region of this cognitive map
 - In later studies, researchers have identified a variety of hippocampal place cells that fire not only in response to location, but also to behaviours being performed in a particular location and perhaps even to rewards and implications associated with each

Behavioural Neuroscience Live Lecture

- Heuristics and Prior Knowledge
 - A bat and a ball together costs \$1.10 and the bat costs \$1 more than the ball
 - How much does each item cost?
 - Many people make the error that the bat costs \$1 and the ball costs \$0.10
 - Many people don't go through the problem, they make shortcuts
 - Are familiar with the \$1 so they make a quick conclusion
- Audio Top Down Processing
 - o "How to wreck a nice beach" vs. "How to recognize speech"
 - What makes the most sense given the top down processing of the context
 - o Interpretation of incoming stimuli is influenced by prior knowledge
- Visual Top Down Processing
 - Picture of mom "dancing around pole" when in fact mom was selling last snow shovel
- Learning and Memory in the Brain
 - o Donald O. Hebb
 - Argued that any explanation of mental phenomenon depends on how changes to memories can be mediated by changes to specific synapses
 - "Neurons that fire together wire together"
- Human Plasticity and Motor Memory
 - Homonculus

- A great deal of cortex in brain is for motor commands to hands than to feet
- Lips, tongue and face in general have a great deal of cortex specific to motor commands
- Sensory stimuli to face is connected to arms and hands
- Experience and Plasticity
 - Musician vs. Soccer player
 - Repeated practice shapes synapses in brain
 - Need 10,000 motor hours of practice
- Reduced Input and Plasticity
 - Phantom limb
 - Sensation that missing limb is still attached to body
 - Missing input into sensory cortex that corresponds to missing limb is taken over by adjacent areas
 - Ex. Taking a feather and stroking face, people will feel it on their missing hand
 - · Pain in missing hand
 - Hypotheses is that sensory neurons are still being fired
 - Solution was to shorten the limb even more
 - o Didn't work, more pain was felt in longer missing limb
 - Case of person clenching their fist very tight as their left hand was amputated
 - From that point on, left hand felt like it was still clenching
 - Could unclench right hand, but not left
 - Mirror box therapy
 - Took a box, put a mirror in the box and patient put both arms in front of him
 - When patient looked down, he saw right hand and mirror image of right hand, but looked like left hand
 - Was asked to clench both hands and then unclench.
 - Could then feel his left hand unclenching
- Multiple Memory Modules
 - Declarative memory
 - Memory for specific episodes and pure facts
 - Associated with hippocampal regions
 - Procedural memory
 - Memory for specific actions or tasks
 - Associated with striatum and cerebellum
 - Emotional memory
 - Memory related to attaching significance of memory to behavioural outcome
 - Associated with Amygdala (Capgras delusion)
 - Double Dissociations
 - o Radial Arm Maze

- Mouse placed in centre of radial arm maze
- Surrounding arms of maze contain different possibilities (food)
- Mouse at first were explore all possible arms, with time mouse will consistently and immediately go down to correct arm
- Example of using declarative memory
- Norman White did specific hippocampal lesion impairments and observed performance in standard maze
- Results show that mice with specific hippocampal regions were unable to use declarative memory and go to right maze
- Mice with lesions to amygdala or striatum did not have same problem
- Another experiment is that bright light is paired with food
- Mouse will follow specific rule, go to arm with bright light
- More specific to procedural memory task
- Mice with lesions specifically to striatum only had problems with procedural memory task
- Final manipulation of experiment was for quality, emotional memory
- Mice confined to one arm for thirty minutes, where they got as much food as they wanted
- In another arm, it was a low quality emotional experience, no food, just stuck there
- Mice with lesions to amygdala had a much more difficult time learning this emotional memory task as opposed to lesions to other parts of the brain
- Criticisms to studies
 - Problem with external validity
 - Whether or not these experiments are demonstrations of what happens in real situations
 - Human brain is more complex
- o HM
 - Surgery disrupted hippocampal regions
 - Could not form new declarative memories
 - Surgery caused minimal damage to striatum and cerebellum
 - We expect he can form new procedural memories and that was true
 - Can learn new motor tasks, but can't remember learning them
 - Part of amygdala was damaged
 - Seemed cheerful, little negative emotions
 - Everything seemed to be okay with him
 - Negative emotional memory and arousal was disrupted (speculation)
- Retrieving Memories
 - Free Recall
 - Activation of memory recall may start in frontal lobe and dissipate to other lobes
 - o Patient Dr. P

- Described by Oliver Sacks
- Has a condition called object agnosia, difficulty in categorizing and naming objects he sees
- Can describe what's before him, he can't name it and figure out what it's for
- Patient CK
 - Also has object agnosia
 - Can guess what he object is, but isn't exactly sure
 - He can draw a picture of a guitar, but when you show him the picture and ask him what it is, he can't identify it

Lecture 8/9: Vision

February 27, 2011

Introduction

- Nearly 1/3 of the brain is devoted to processing visual information
- In a showdown between our senses, if our visual sense is giving us information that is in conflict with information from another sense, we tend to bias our trust towards our sense of vision
- Ex. Watching a movie
 - The speaker could be mounted on the wall, but you will tend to perceive the sound as coming from the actors' mouths

The Stimulus: Light

- Three physical characteristics of light
 - Amplitude
 - Light waves can vary in two respects
 - The height of each wave, called the **amplitude**
 - The distance between the peaks of successive waves, called the wavelength
 - Variations in amplitude affect the perception of brightness
 - Generally, the greater the amplitude of the light wave, the more light is being reflected or emitted by that object and so that object appears brighter or more intense to us
 - Wavelength
 - Variations in wavelength affect the perception of colour
 - Wavelength is measured in nanometers
 - Smaller wavelengths refer to light waves with a higher frequency because there is less distance between successive peaks
 - Larger wavelengths refer to light waves with a lower frequency

- Humans are only sensitive to a tiny portion of the total range of wavelengths of electromagnetic radiation, the portion called the visible spectrum
- The shortest wavelength we can see is around 360 nanometres, which looks violet to us and the longest wavelength we can see is 750 nanometres, which is red

Purity

- Affects the perception of the saturation or richness of colours
- A light that is made up of a single wavelength is said to be pure light and the perceived colour would be described as completely saturated
- At the other extreme, we could have a light that is a combination of all the wavelengths
- This light would be perceived as white light and would be described as completely desaturated

The Eye

- Light first passes through the curved cornea, which begins the focusing process
- The cornea is a transparent window at the front of the eye
- The rest of the eye is covered by the white part of the eye called the sclera, a tougher membrane
- After the cornea, light passes through the **pupil** of the eye, which is the round window that you see as a black dot in the middle of your eye
- The **iris**, or the coloured part of your eye, controls the size of the pupil
- The iris is basically a band of muscles that is controlled by the brain so that if not enough light is reaching the retina, these muscles cause the pupil to dilate into a larger opening
- If too much light is entering the eye then these muscles cause the pupil to constrict into a tiny opening
- After going through the pupil, light passes through the lens, a transparent structure that does the final focusing of light on the retina
- The Lens
 - The curvature of the lens causes images to land on the retina upside down and reversed from left to right
 - However, the final perceived image is a product of brain activity
 - Thus, rather than seeing everything upside-down and reversed, there is a correction that allows us to see a properly oriented image
 - The lens is a flexible piece of tissue, the shape of which can be altered by surrounding muscles, allowing it to focus on objects that are close or far away
 - If the object is close, the lens of your eye gets fatter or rounder to produce a clearer image, but if the object is far away, the lens of your eye gets elongated to focus the image on the back of your eye
 - This change in shape of the lens to focus on objects that vary in distance is called accommodation
- The Retina

 After travelling through the lens, light passes through the vitreous humour, which is the clear, jelly-like substance that comprises the main chamber inside the eyeball, until it finally lands on the retina, which is the neural tissue that lines the back of the eye

The Retina

- Where the physical stimulus of light is first translated into neural impulses
- Retinal Layer 1: Photoreceptors
 - The retina is a paper-thin sheet that covers the back of the eye and is made up of a complex network of neural cells arranged in three different layers
 - The layer at the very back of the eye, farthest away from the light, is where the photoreceptors are located
 - Photoreceptors are cells in the retina that are responsible for translating the physical stimulus of light into a neural signal that the brain can understand
 - To reach the photoreceptors, light must pass through the other two layers of retinal tissue, which are transparent
 - The reason for this inside-out arrangement in the retina has to do with where the photoreceptors get their nutrients from, which is a layer of cells at the very back of the eye called the retinal pigment epithelium (RPE)
 - The photoreceptors would die without access to the RPE cells and if the photoreceptors were located at the front of the retina, facing the light, then they would not have access to the RPE that they need to live
- Photoreceptors: Rods and Cones
 - Humans have about 125 M rods, but only 6 M cones
 - Cones
 - Cones are designed to operate at high light intensities and are used for day vision
 - The cones provide us with the sensation of colour and provide good visual acuity, or sharpness of detail
 - Cones become more concentrated toward the fovea, a tiny spot in the middle of the retina that contains exclusively cones
 - When you want to see something in detail, we move our eyes so that the image falls directly onto the fovea

Rods

- Designed to operate at low light intensities and so are used for night vision
- Provide no information from which colour can be determined and offer poor visual acuity
- No rods in the fovea itself, with increasing concentration in the region just surrounding the fovea
- This arrangement makes rods useful for peripheral vision

- This explains why, when you're trying to see an object in an environment that is dimly lit, you're better off looking slightly to one side of the object as opposed to trying to stare right at it
- When you stare right at it, you're using your cones, which don't work in a dimly lit environment
- Photoreceptors: Response to Light
 - Photoreceptors contain a photo pigment, which is a complex molecule that is sensitive to light
 - The human eye has four different kinds of photo pigments, one for rods and three for cones, but they all work the same
 - When a photon of light is absorbed, it changes the chemical state of the photo pigment and splits into its two components of molecules, which sets off a biochemical chain reaction leading to an electrical current flowing across the membrane
 - The original light stimulus is now in a currency that can be understood and processed by the brain
 - Once light has caused a photopigment to split, high energy molecules within the photoreceptor cause the two molecules to recombine so that the photopigment is ready to react to light again
 - However, there is a brief period of time during which the photopigment will be unable to react to light
 - Each photoreceptor has thousands of photopigments and the number that are ready to react to light depend on the relative rate at which they are being split and recombined
- Photoreceptors: Dark Adaptations
 - When exposed to very bright light, the rate of splitting of photopigments exceeds the rate at which they are being recombined
 - This explains why it takes a few minutes for your eyes to get used to the dark, a phenomenon called dark adaptation
 - When you enter a dark place, most of your photopigments, particularly those in the rods, haven't had time to recombine yet, leaving few that are ready to react to light, causing you to see very little
 - But after a few minutes, most of your photopigments will have recombined and be ready to respond to light
 - That is the eye becomes adapted to the dark
- Bipolar and Ganglion Cells
 - After the first layer of the retina translates the physical stimulus of light into an electrochemical signal in the photoreceptors, the photoreceptors then send their information to the next layer of cells in the retina, called the **bipolar cells**, by means of a transmitter substance
 - o In turn, the bipolar cells send their information on to the next layer of cells in the retina, called the **ganglion cells**
- Retinal Layers 2 and 3

- The ganglion cells collect information from a larger segment of the retina and the axons of these cells all converge on one point in the eye, called the **optic disc** and then leave the eye to join the **optic nerve**, which travels all the way to the brain
- Because the optic disc is basically an exit hole in the eye for ganglion axons, this small area contains no photoreceptors at all and so it constitutes our blind spot
- We are not normally aware of our blind spot because our brains fill in the gap by blending the surrounding image most of the time
- To recap, light enters the eye and must pass through the ganglion cells, bipolar cells and strike the photoreceptors on the retina at the very back of the eye
- At that point the light is converted into a neural signal that is sent from the photoreceptors to the bipolar cells and then on to the ganglion cells, whose axons make up the optic nerve
- Processing in the Retina
 - There are also cells in the retina that allow areas within a retinal layer to communicate with each other, called horizontal cells and amacrine cells
 - These cells allow information from adjacent photoreceptors to combine
 - This means that some amount of visual processing is done in the retina, before the signal is sent on to the brain

Receptive Field in Retina

- Think of the photoreceptors in the retina has being divided up into specific groups and the information from each group getting assimilated into one signal that affects the ganglion cell down the line
- In the fovea, the photoreceptor group for a particular ganglion cell may only contain one cone, which means the ganglion cell is representing a very small area of the image
- Since each cone in the fovea has a direct link with the brain, a lot of the detail is preserved and more visual acuity occurs in the fovea
- But more often, the input from many rods and cones is combined into one neural signal for one retinal ganglion cell
- These groups get larger as we move toward the periphery of the eye, which is one reason why our visual acuity is so low for peripheral vision
- The collection of rods and cones in the retina that, when stimulated, affects the firing of a particular ganglion cell is called the **receptive field** of that retinal ganglion cell
- These receptive fields in the retina come in a variety of shapes and sizes, but most are basically doughnut shaped, such that the light falling in the centre of the doughnut will either excite or inhibit the cell ad light falling in the surrounding part of the doughnut will have the opposite effect on the cell
- Excitation and inhibition of the cell is determined by the rate at which that cell fires compared to baseline or the rate at which the cell would fire normally without any light signals

- A cell would be excited if the rate of firing of that cell increased compared to baseline and it would be inhibited if that rate of firing decreased compared to baseline
- Ex. A receptive field on the retinal surface that has a doughnut shape with the center being excitatory and the surrounding being inhibitory
 - This means that if light struck the center of the receptive field, this would cause an increase in the firing rate of the ganglion cell
 - If the light struck the surrounding of the receptive field, this would cause a decrease in the firing rate of the ganglion cell
 - If light covered both the center and surrounding of the receptive field, these two effects would basically cancel each other out and the cell would fire at the same rate that it does at baseline, when no light is available
 - Either way, when a receptive field of a ganglion cell is stimulated, that ganglion cell sends signals towards the brain

Lateral Inhibition

- Retinal cells can also affect signalling of adjacent retinal cells through lateral antagonism or lateral inhibition
- This is done through the horizontal cells, which are activated by the photoreceptors and also through the amacrine cells which are activated by the bipolar cells
- Whenever a retinal cell is stimulated by light falling on its receptive field, that cell sends signals onto the brain, but it also sends messages sideways to neighbouring cells that inhibit their activation
- The perceptual result of this kind of mechanism is that edges of objects are easier to detect
- Ex. Imagine we have 4 cells, A, B, C and D
 - Cell A, B and C are receiving intense stimulation from the same patch of bright light, whereas Cell D is receiving moderate stimulation from a dark grey patch of light
 - Thus, cell C is on the edge of the bright and grey light and with lateral inhibition, this cell ends up sending more stimulation to the brain than cell B, even though both cells receive the exact same input
 - So cells A, B and C are strongly stimulated and since they are also neighbours, they are inhibiting each other as well
 - Cell D is only moderately stimulated by the dark grey patch and it sends less inhibition to its neighbour cell C than cells A, B and C do to each other
 - As a result, cell B receives a lot of inhibition from the intense stimulation of both its neighbours, whereas cell C only receives strong inhibition from one of its neighbours
 - Because of this, cell C sends out a stronger signal to the brain than cell B does, even though cell C and B are receiving the same input from the world

The perceptual result for us is that edges look more distinct

Visual Pathways

- Visual Fields and Hemispheres
 - Recall that the right and left halves of our visual field are processed by the contralateral side of our brain
 - Visual input from our right visual field travels along the optic nerve to the left hemisphere and visual input from the left visual field travels along the optic nerve to the right hemisphere
 - A visual field receives information from both eyes and so each hemisphere receives information from both eyes
 - Before reaching their respective hemispheres, the axons from the inner region of each retina (region of retina closest to nose) have to cross over to the opposite hemisphere
 - The point at which the optic nerves from the inside half of each eye cross over to the opposite hemisphere is called the optic chiasm

Two Visual Pathways

- After the optic chiasm, the information from each visual field arrives in the opposite hemisphere, at which point the optic nerve fibres split and travel along two pathways
- Most of the retinal or ganglion cell axons travel along the main pathway and synapse in the lateral geniculate nucleus (LGN), which is part of the thalamus that receives visual information
- After being processed here, the visual signals are sent to areas in the occipital lobe that make up the primary visual cortex
- A smaller portion of the axons from the retinas takes a detour to an area in the midbrain called the **superior colliculus**, after which information is sent upwards to the thalamus and on to the occipital lobe or downward to structures in the brainstem
- This smaller, secondary pathway seems to deal with coordinating visual input with information coming in from other senses as well as localizing objects in space through head and eye movements and helping to guide those movements
- Main Pathway: Two Subdivisions
 - The **magnocellular pathway** is specialized to process movement information
 - The parvocellular pathway deals specifically with colour and form information
- Main Pathway: LGN
 - The first stop for information that is sent from retinal ganglion cells is the LGN
 - LGN cells also have receptive fields that are made up of a combination of many ganglion cells (like retinal ganglion cells)
 - o Smaller bits of information is getting combined into one overall neural signal
 - The LGN is made up of six layers
 - Information from each eye projects to different layers of the LGN

- Each layer receives input from a specific eye and also each layer of the LGN receives input from a specific subpathway
- Movement information that is processed along the magnocellular runs to two of the layers in the LGN, whereas information specific to the parvocellular goes to the other four layers
- From the LGN, the visual information is sent to the occipital lobe for further processing

Main Pathway: Occipital Lobe

- Over twenty cortical areas that process visual information, but most of the research done on visual processing has concentrated on area V1 of occipital lobe
- Collectively, the visual processing areas in the occipital lobe outside of the striate cortex are known as the extrastriate cortex

Primary Visual Cortex

- The receptive field of a single V1 cell is a combination of the receptive fields of many LGN cells
- Again, there is information from many sources being processed down into a single target
- Receptive field of many retinal ganglion cells → combine to form the receptive field of a single LGN cell → the receptive fields of many LGN cells combine to form the receptive field of one V1 cell
- The receptive fields from the retina are arranged in a topographical map in the primary visual cortex, such that neighbouring locations in the retina project to neighbouring locations in the visual cortex
- Primary visual cortex is made up of six layers and the LGN projects directly onto layer IV neurons, from which information is carried to neurons in the other five layers
- Layer four neurons connect information to the other five layers in the primary visual cortex
- The 6 layers of the primary visual cortex are organized into cortical columns, that are made up of about half mm squares of cortex that are perpendicular to the cortical surface
- Although the vast majority of neurons in the visual cortex can respond to visual stimuli presented to either eye, most have a stronger response to one eye than the other
- Therefore, information from each eye sent through the LGN projects more strongly to some cortical neurons and less strongly to others
- The eye preference is maintained within the individual cortical column so all neurons within a given cortical column respond more strongly to input from the same eye
- The cortical neuron is also the first site of binocular processing

Dorsal and Ventral Streams of Extrastriate Cortex

 From V1, processed visual information, whether it is colour, form, or movement, is sent on to the Extrastriate cortex and gets separated into the dorsal and ventral streams

- The dorsal stream is referred to as the "where pathway" because it processes where objects are, including their depth and motion in the field
- The dorsal stream progresses from the extrastriate cortex to the parietal lobe
- The ventral stream is referred to as the "what pathway" because it processes what the object is, including its colour and form
- The ventral stream runs from the Extrastriate cortex to the temporal lobe
- As information is processed, it is compressed

Evolution of the Eye

- Eyes may have started out as simple light-sensitive patches, like what jellyfish and worms have today
- Some individuals may have developed a light-sensitive patch that was formed into a slight depression, which would have allowed the direction of light to be sensed, incurring a survival advantage
 - Much like the cup eyes that today's clams have
- Some individuals may have later adapted a crude lens, allowing them to process visual input at different distances
 - From here, the lens could have successively improved to allow better focusing and accommodation, such as a more transparent lens or one with better curvature
- Cumulative Selection
 - Eye evolution is an example of cumulative selection, where small changes were made to the existing eye and then new small changes were made to the modified eye and so on, gradually increasing the sophistication of the eye
- One of the main driving forces for evolution of eyes is predation
 - o Animals in Precambrian period likely only had crude light sensors, if any at all
 - Their tracks tend to be small and slow moving
 - Thus, given the poor mobility, there was not much need for detailed vision
 - o In contrast, early Cambrian animals were larger and more mobile and eyes would have been useful for both hunting prey and escaping predators
 - This would have led to adaptive selection for better eyes

Different Eye Designs for Different Environments

- Importance of environment is clearly seen when comparing two closely related species with different ecological demands
 - Two species of crayfish
 - Cave Dwelling Crayfish and Open Water Crayfish
 - The cave dwelling crayfish lives in an environment where no light exists and has no need to form an image
 - For them, the biological costs of building and maintaining eyes would far outweigh the benefits of having eyes and so they do not have eyes
 - The open water crayfish would be expected to benefit from the ability to form an image and so have developed functioning eyes

- Image-forming eyes come in two different designs
 - Compound eyes
 - Found in anthropods such as insects and crabs
 - Eyes of these species are made up of an arrangement of individual tubular units called **ommatidia** that each point in a slightly different direction to gather the light that lays directly in front of it
 - These eyes manage to form a single image by putting together many separate signals from each ommatidium
 - Good for detecting movement, but only at close distances

Simple eyes

- Found in vertebrates as well as molluscs such as octopus and squid
- Have eyeball, lens and retina
- Can vary quite a bit in its design according to the environment that the species lives in

Pupil

- One aspect of the eye's architecture that varies across species is the shape of the pupil, some shapes allow more variation in size of pupil than others
- Primates have a circular pupil, which can't vary all that much in size compared to other shapes
- Ex. The pupil of a human can only increase the brightness of a retinal image by about ten times, which doesn't allow a human to see across a very wide range of illumination conditions
- A cat's pupil, called a slit pupil, can vary much more in size
- This allows the cat to capture more light in a dark environment and reduce the amount of light that enters in a very bright environment
- Slit pupils also vary in orientation, with some species having slits that are vertical (cats and climbing snakes), while other species have slits that are horizontal (horse, shark and land-dwelling snakes)
- If a species life is dominated by what is happening on the horizon, then its slits tend to be horizontal
- If what is important to them is what is happening above or below them, then their slits tend to be vertical

The Size of Eyes

- Two main function of eyes
 - Resolution (acuity) and sensitivity (ability to get enough light)
 - Larger eyes tend to be better at both of these functions
 - We see bigger eyes in species that need better eyesight, the benefit gained by having bigger eyes varies across species
 - Ex. Human and hawks have big eyes in order to get good resolution, white cats, horses and owls have big eyes in order to improve sensitivity
- Ex. Hawk

- How is it that humans have bigger eyes than hawks, but hawks can see so much better
- For one, they have a wider daylight pupil, which allows more light to enter the eye and improve sensitivity
- Hawks have narrower photoreceptors in the fovea, which means that they can have more densely packed receptors compared to us
- Their eyes have a built-in optical trick that functions as a crude telephoto system, magnifying the image they're looking at

Eye Placement

- Eye placement on the head leads to a trade-off between depth perception vs. the total view of the environment the animal can see
- Animals with eyes located on either side of their head have two laterally directed eyes
- This produces a large total view, with the animal being able to see almost all the way around their body without turning their head
- However, these animals have basically two separate fields of view, with very little binocular overlap and so depth perception is poor
- Prey animals have adapted eyes with placement like this to continually scan environment for predators
- Another design is to have both eyes directed toward the front, which is typical for predators, including humans
- This produces a very narrow field of view because both eyes are basically looking at the same scene
- However, there is a lot more binocular overlap, which results in a good depth perception, key for successful hunting

Photoreceptor Density Areas on the Retina

- Final example of variation in vertebrate eye designs has to do with the area of the retina where there is a greatest density of photoreceptors
- Called the fovea and for humans, is located in the middle of our eye
- Ex. Fish that live in tiny crevices of a coral reef need to focus directly in front of them and so, region of highest cell density corresponds to the part of retina that processes what is happening directly in front of them
- In species that need to pay attention to what is happening close to the horizontal plane, such as seabirds, their region of greatest cell density forms a horizontal streak across the eye
- In birds of prey like owls, their retina has the densest photoreceptors in the region that views the ground
 - An owl has to turn its head upside down to see something approaching from above
- Pigeon has two regions of concentrated cell density in the retina
 - One region is for looking at food directly in front to help guide pecking behaviour, while the other is for more peripheral and for locating distant objects

Development of Visual Architecture

- The eyes are formed during the second month of pregnancy and are capable of reacting to light in the sixth month of pregnancy
- Some random firing of retinal cells also occurs during the prenatal period that is critical for the organized wiring of retinal cells, determining how neighbouring cells will be connected to each other
- Newborn period
 - Lens muscles are weak, which limits how well the newborn can focus
 - Because the pupil doesn't react properly to changes in light, the clarity of the image is blurred
 - With environment interactions and continued exposure to light, by around 3 months, the infant's ability to focus has improved to almost adult-like
 - The newborn's retina has a much lower density of cells than an adult retina would have and even these cells are not yet fully developed
 - Especially true for the fovea, where retinal cells don't reach adulthood-like levels until after 4 years of age
 - The optic nerve and visual cortex also require several years to mature
 - By some estimates, the relevant brain development is not fully complete until around 11 years of age
- One technique used to study the behaviour and skills of infants is the preferential looking technique
 - Based on an infant's natural preference to look at a card that has sharp contrasts between light and dark, compared to a uniformly grey card
 - If the stripes were made progressively smaller and closer together, the baby will
 no longer prefer the striped card, since their visual acuity isn't sharp enough to
 tell the difference between the small striped card and the grey card
 - If you measure the point at which the infant shows no preference for either card, you have a good estimate of the infant's visual acuity
- Another way visual acuity is studied is by examining visual evoked potentials or by looking at the characteristic pattern of electrical brain activity that accompanies a new visual stimulus
 - o Different stimuli typically evoke different brain responses
 - Using these measures of brain activity, it is possible to tell when a baby can discriminate two visual images that differ in visual details
- Both techniques show similar patterns of development for visual acuity
- At birth, visual acuity is dismal, with the details that a newborn can see at 20 feet being about the same as what an adult can see at 600 feet
- By 6 months of age, the baby's visual acuity is already dramatically improved
- By one year of age, babies are close to adult-like levels for visual acuity, although they
 do not reach full adult acuity until around 4-6 years of age

Vision Live Lecture

Lateral Inhibition

- Mach Bands
- o As something is brighter, greater activation with photoreceptor cells
- From greater activation of photoreceptor cells, greater inhibition of cells around it
- Simultaneous Contrast
 - White and black box with same colour grey box in middle
 - White box causes greater stimulation, so greater inhibition in centre
 - Black box causes less stimulation, so less inhibition in centre
- Benary cross
- Primary Visual Cortex
 - Two Pathways
 - Main Pathway
 - Layer IV appears to receive the majority of sensory input
 - Ocular dominance columns
 - Alternates left and right eye
 - Orientation Columns
 - Can have cells specialized for input for right eye for light coming in horizontally
 - Specialized for lights in different orientations
 - Hyperacuity
 - **2**0/20
 - Means that from 20 feet you can see what an average person can see from 20 feet away
 - As denominator gets smaller, your acuity is greater
 - Vernier Acuity Task
 - Rapid Reorganization Charles Gilbert
 - Receptive field expansion following artificial scotoma (blockage in vision)
 - Perceptually relevant reorganization after one second
 - Neuron realizes in one second that it is useless so it alters its function to become more useful
 - Cortex is being reorganized quickly
 - Adaptable for environment
 - Functionally adaptable (adding function to cortex)
 - Rerouting V1
 - Went into thalamus of baby ferrets and rerouted the input of eyes from visual cortex to auditory cortex
 - Found that temporal lobe developed the layers similar to those found in occipital lobe
 - Implies that it's not occipital specific
- Secondary Pathway
 - Hypothalamus and Raphe Nuclei
 - For circadian rhythms (rhythms when we sleep)
 - Superior Colliculus

- For eye movement
- Blindsight
 - Occurs when we have damage to primary pathway of vision (ex. visual cortex)
 - Becomes functionally blind, but can still react to stimuli in environment
 - Can still reach for objects, can sense things that pass them by
 - Because of the two visual paths
 - If V1 pathway is damaged, other pathway is still preserved
- Three types of blindsight
 - Action blindsight
 - Can't see object, but can make physical response to it (reach out and touch it)
 - Retina → SC → Tectum → Parietal lobe
 - Ex. Taking a block and fitting it into a slot
 - Will accurately shaping their hands to grab block before even touching it
 - If we lesion visual cortex AND lesion parietal lobe, action blindsight goes away
 - TMS
 - Uses a magnetic to polarize and depolarize neurons in brain
 - Can temporarily shut down areas of brain
 - Attention blindsight
 - Riddoch phenomenon (sense that something has moved)
 - Agnopsia
 - Intact perceptual judgements (can say what colour an object is without ever seeing it)

Lecture 10: Colour Perception

March 5, 2011

<u>Introduction to Colour Perception</u>

 Objects don't inherently have a colour, the colour we see is due to wavelengths being reflected into our eyes

Evolution of Colour Perception: Why and Who

- Among mammals, only humans have colour vision, so how did primates evolve to get colour vision
- Primate colour vision is especially well suited to distinguish red and yellow against a green background
- This adaptation helps immensely with foraging for fruit in the bushes and trees

- In this way, one possible biological advantage of colour vision for primates is the ability to detect colourful objects in the wild
- Additionally, the ability to perceive colour is an important advantage for detecting predators or prey against a background, determining the ripeness of fruit, the richness of soil or even using the colour of sunsets as a means to predict weather
- Colour vision is also an important part of the lives of many non-mammalian species
- For birds, the colour of a potential mate's feathers provides signals to other birds about how healthy that bird is and can influence how likely that bird is chosen as a mate
- This type of colouration system would help the birds communicate with each other about how healthy they are, while still remaining inconspicuous in the forest to potential predators who are unable to see this bright colouration
- Colour vision can also be used for foraging
 - Bees might be attracted to flowers that look dull to human eyes because it is responding to specific patterns and colours on the flower that we are unaware of
 - Some flowers have adapted patterns on petals that are invisible to us, but serve as nectar maps to bees

Colour Mixing

- You don't need a million colour receptors to deal with every conceivable colour out there in the world
- Instead, you just need a few receptor types whose activity can be combined in various proportions to make every conceivable colour
- The three **primary colours** can be combined in various proportions to make every colour in the spectrum
- Primary colours are like a base colour, they cannot be reduced into other colours
- Two different types of colour mixing
 - Subtractive colour mixing is when coloured pigments selectively absorb some wavelengths and reflect others
 - Called subtractive because every reflective surface absorbs (or subtracts)
 the colours that it does not reflect
 - Adding other pigments to that surface alters the combination wavelengths subtracted
 - Ex. Mixing blue and yellow to get green
 - When we mix two pigments, what is happening is that all wavelengths are being absorbed except those that the two pigments jointly reflect
 - Ex. Shine a white light through both a yellow filter and a blue filter and look at the remaining light on the white screen
 - You would see green
 - This is because when the light hits the yellow filter, all the short waves (blues and purples) are being absorbed, or subtracted out and only the longer (green, yellow, orange and red) waves are allowed to pass through

- When these longer waves hit the blue filter, it absorbs the longest waves (yellow, orange, red) and what is left over is a middle band of wavelengths that is transmitted by both pigments
- This middle band that is left over is green
- Opposite each primary colour is its complementary colour
 - Red/green, yellow/purple, blue/orange
 - If you mixed a primary colour with its complementary colour, you always got brown
- Additive colour mixing is when coloured lights add their dominant colour to the mixture
 - Dealing with mixing of coloured lights
 - How our visual system processes colour, by adding the effects of different wavelengths together in our nervous system
 - With additive colour mixing, the primary colours are red, green and blue because these three colours can be added together in various proportions to make all the different colours we see
 - Complementary colours are also different
 - Blue/yellow, red/bluish-green, green/reddish-purple
 - When you mix a primary colour with its complementary colour, you get grey or white
 - Ex. Shine two white lights through the blue and yellow filter, but instead
 of passing the light through each filter successively, we overlap the
 coloured lights from each one onto the reflective surface
 - Because each coloured light adds its dominant wavelength to the mixture, you find that now blue and yellow do not make green when added together, but instead make grey
 - This is because grey light is the sum of complementary colours

Theories of Colour Vision

- The trichromatic theory of colour vision is based on the proposal that the retina contains three different kinds of receptors, that are each maximally sensitive to different wavelengths of light
- This theory follows from empirical observations about primary colours and colour mixing, namely that it is possible to match all of the colours of the visible spectrum by the appropriate mixing of three primary colours
- Thus, the theory postulated that you only need three different types of receptors to discriminate all the colours of the visible spectrum
- We now know that the human retina is equipped with three types of cones that contain spectrally selective photopigments that are maximally responsive to wavelengths of light that correspond to the primary colours red, green and blue

- "Maximally responsive" means that a given receptor will respond to other wavelengths, just not as much as it would to its peak wavelength
- When you perceive yellow, it is because the red and green cones are equally stimulated
- White is what you see when all three receptor types are stimulated
- Evidence for theory
 - Incorporated what we already knew about colour mixing
 - Subsequent physiological evidence led to the discovery of three types of cones, just as predicted
- Evidence against the theory
 - o Yellow seemed to be a primary colour and not a mixture of red and green
 - When people were asked to describe the most basic colours, yellow was usually included as one of them
 - Couldn't explain the law of complementarity, that certain pairs of wavelengths produce the experience of white
 - Phenomenon of complementarity of afterimages
 - Why do you see a yellow afterimage when you stare at a blue stimulus

Opponent-Process Theory

- Argues that there are three classes of receptors, but says that each of the receptors is made up of a pair of opponent processes
- Each receptor is capable of being in one of two opponent states and it can only be in one of those states at a time
- The ability to see blues and yellows is mediated by a blue-yellow opponent receptor, greens and reds is mediated by green-red opponent receptors and a third type of opponent receptors distinguished bright from dim light
 - The brightness detectors are excited by lights of any wavelength
- Evidence for theory
 - Successful at explaining how a mixture of wavelengths from complementary colours appear white
 - Also explained why the afterimage of a visual stimulus is the complementary colour
 - Also fit logically with the fact that most people can easily imagine a yellowish-red or a bluish-green colour, but it is more difficult to imagine a reddish-green or bluish-yellow colour
 - According to the theory, these colour pairs are opposite and occur from differential activation of the same receptor type
 - It would be impossible for a single red-green receptor to be active in both the red and green states simultaneously
- Turns out that both theories are needed to explain colour perception
 - There are three component receptors or cones in the retina that are each maximally responsive to light of a certain wavelength, just as the trichromatic theory suggested
 - The three cones are maximally responsive to red, green and blue

- The response of these receptors differentially affect what is happening in the brain, where things are organized as the opponent-process theory would have predicted
- The opponent pairs are red-green, blue-yellow and light-dark
- The combination of the two theories says that the output of the cones is input for the next layer of colour processing in the retina, which is organized in an opponent fashion
- Colour coding continues in this opponent agreement up to the brain's visual processing system
- Ex. A red light would stimulate a red cone in the retina, which would excite the red-green ganglion cells that are organized in an opponent fashion and this excitation of the red-green ganglion cell would signal the brain that the stimulus is red
- A green light, however, would stimulate a green cone, which would then inhibit the red-green ganglion cell
 - This inhibition of the red-green ganglion cell would signal to the brain that the stimulus is green
- A blue stimulus would activate the blue cone, which would send an inhibitory signal to the yellow-blue ganglion cell, signalling to the brain that the stimulus was blue
- With yellow it's a little bit more complicated
 - Since yellow is a mixture of red and green, yellow light would cause equal activation of the red and green cones
 - Activation of the red cone would send an excitatory signal to the redgreen ganglion cell as well as the yellow-blue ganglion cell
 - Activation of the green cone would send an inhibitory signal to the redgreen cell and an excitatory signal to the yellow-blue cell
 - The red-green cell, having received an excitatory message from the red cone and an inhibitory message from the green cone would send no change since the two effects cancel each other out
 - The yellow-blue cell would have received an excitatory message from the red and green cones, which would excite the yellow-blue cell
 - This excitation would then signal to the brain that the original stimulus was yellow

Colour Processing In the Brain

- So we have receptors that provide red-green information and others that provide blueyellow or black-white information
- The rate of firing of the colour receptor signals to the brain what colour is being seen so that a receptor that fires at a rate that is faster than baseline means one colour, but if that same receptor fires at a rate that is slower than the baseline, meaning it is inhibited, then this signals to the brain that you're looking at the complementary colour

- The reason afterimages occur is because when a colour receptor is excited or inhibited for a prolonged period of time, you get a rebound effect when you stare at a neutral colour like white
 - That same colour will go into the opposite state, causing you to perceive the complementary colour
- Ex. When you stare at a green square, all your green-red colour receptors are excited, firing at a rate that is much faster than baseline
- When you then stare at a neutral surface, all those cells that have been firing so fast for so long go into the opposite state and actually fire less than baseline, possibly because the pigments are partly bleached out by the prolonged exposure to the stimulus
- Firing below baseline levels in these receptors is perceived as red, so you see the
 afterimage of a red square after staring at a green square
- Colour Coding in the Retina
 - In high-resolution channels, one cone is transmitting information to one ganglion cell
 - With lower-resolution channels (away from the fovea), many cones are transmitting information to a single ganglion cell
 - In both cases, the ganglion cells are said to have a receptive field, or a region on the retina that, when stimulated, will cause the ganglion cell to increase or decrease its firing rate
 - In high-resolution cells, these fields are small, while in low-resolution fields, they are large
 - The receptive fields of the ganglion cells are donut-shaped and respond to colour in the center-surround fashion
 - There are colour-sensitive receptive fields that are responsive to yellow-blue and red-green, with one colour increasing the rate of firing of the ganglion cell if it strikes the middle portion of the donut and decreases the rate of firing if it strikes the outer ring of the donut
 - Ex. A ganglion cell is excited if the colour red strikes is middle region or if green strikes the surrounding portion, but that same cell is inhibited if the opposite were true, with red striking the surrounding region or green reaching the middle portion
 - The strongest response is seen when both conditions are true and you have red striking the middle and green on the surround
- Colour Processing in the LGN
 - From the retinal ganglion cells, colour information is sent to the lateral geniculate nucleus, LGN
 - Recall that the LGN has six layers, with two layers called the magnocellular layers, processing form, movement and depth
 - The remaining four layers, called the parvocellular layers, are where colour information from the red and green cones and information about fine detail is processed
 - In addition to these six layers, there is also a sublayer to each of the six layers, called the koniocellular sublayers

- These sublayers are especially important for transmitting information from the blue cones to the primary visual cortex
- Evidence from single-cell recordings in the LGN of monkeys show that cells here still respond in the same opponent fashion that the retinal ganglion cells do
- Ex. If a researcher presented the monkey with a spot of yellow light into a center of the receptive field or blue in the periphery, the LGN cell would fire more rapidly, but if the monkey was shown a blue light in the center or a yellow light in the surround, that same cell would not fire less than it did at baseline

CO Blobs and the Visual Cortex

- From the four parvocellular layers of the LGN, as well as the koniocellular sublayers, colour information is passed on to the primary visual cortex in the occipital lobe at the back of the brain
- Livingstone and Hubel discovered what are called cytochrome oxidase blobs, or
 CO blobs, which are regions of cytochrome oxidase containing neurons that are distributed at roughly equal intervals over the primary visual cortex
- The neurons in the CO blobs respond exclusively to colour information and show little or no response to shape, orientation or movement
- The CO blobs are arranged in columns that project down into layers 2 and 3 of the primary visual cortex
- o The neurons in the CO blobs respond in an opponent fashion
- Recordings from neurons in CO blobs show that they have donut shaped receptive fields, where one colour presented to the centre of the receptive field increases the firing rate of the cell and the complementary colour decreases the rate
- The opposite firing pattern occurs if the colours strike the surround of the receptive field
- Colour information is then passed from the CO blobs of the primary visual cortex to the visual association areas or the extrastriate cortex, where it is analyzed further in the ventral stream
- Here, information from colour is integrated with other information, like shape

Colour Blindness

- One interesting case where a woman was colour blind in one eye, but not the other
- She was shown wavelengths of light between 400 nm and 700 nm to her colour blind eye and asked to match the colour that she perceived to a range of colours that she looked at with her normal eye
- For the colour blind eye, all wavelengths between 500 nm and 700 nm appeared to be the same shade of yellow (roughly 570 nm) in her normal eye
- When her colour blind eye was presented with wavelengths between 400 nm and 500 nm, her normal eye perceived them as the same bluish colour of around 470 nm
- So this woman was red-green colour blind in one eye and only able to see blues, yellows and shades of grey
- Types of Colour Blindness

- Although colour blindness is sometimes caused by an injury to the colour detecting regions of the visual cortex by trauma, it is usually an inherited condition
- Total colour blindness
 - When a person sees everything in shades of grey
 - Very rare
- Three types of colour blindness
 - Protanopia, deuteranopia, tritanopia
 - Both protanopia and deuteranopia occur when someone confuses red and green and they see the world in shades of yellow, blue and grey
 - These people have normal visual acuity, suggesting that their problem is not that they're lacking a number of cones, but that they're lacking the colour photo pigment in the cones
- Protanopia/Deuteranopia
 - People with protanopia have red cones that are filled with the photo pigment for green, while people with deuteranopia have green cones that are filled with the photopigment for red
 - Either way, these individuals don't have any way of responding differently to red and green
 - If however, there is even a slight difference in the way each cone's photopigment absorbs light, that person will be able to tell green from red, even if these colours would look different than the reds and greens that a person with normal vision would see

Tritanopia

- Involves the yellow-blue system and occurs rarely
- Since the faulty gene is not carried on the X chromosome, it is equally prevalent in males and females
- It is thought to occur because the blue cones, which are much less frequent in the retina to begin with, are either lacking or defective
- So these people see the world in shades of reds, greens and greys
- To them, the sky looks bright green and a banana would look pink

Colour Perception Live Lecture

- Visual Spectrum just part of a continuum
 - Gamma rays at the far end of the continuum (10⁻¹² m)
 - o Radio waves at the other end of the continuum (10³ m)
- Humans are sensitive to infrared wavelengths
 - Even though we can't see them, we can feel them (as heat)
 - Touch receptors have evolved to sense infrared wavelengths
- For rattlesnakes, heat and vision are the same
- Cones are sensitive to different ranges
 - We need at least two different types of cones (for comparison)
 - Dichromats

- Species who only have two types of cones
- Trichromats
 - Species who have three types of cones (humans)
- Humans
 - Fovea contains the three types of photoreceptors
 - Short wavelengths (blue) firing cones
 - Medium wavelengths (green) firing cones
 - Long wavelengths (red) firing cones
 - A lot of overlap between the three
 - Some people have four types of photoreceptors
- Trichromatic and Opponent Process theories
 - Trichromatic theory says that there must be three kinds of receptors that respond to red, green and blue
 - Opponent Process theory talked about opponent process receptors
 - Receptors that respond to red/green, blue/yellow, dark/light
 - New theory which incorporates both theories
 - Retinal cones contain three different receptors that respond to green/red/blue wavelengths
 - Signals from retinal cones passed on to ganglion cells, which is eventually passed on to brain
 - o Ex. Red light being shone on to person's eyes
 - Red retinal cone will send an excitatory signal to red/green ganglion cell, which passes to visual cortex, showing perception of red
 - Ex. Green light being shone
 - Green retinal cone will send an inhibitory signal to red/green ganglion cell, net effect is perception of green
 - o Ex. Blue light being shone
 - Stimulates blue responding cones in retina, inhibitory signal sent to blue/yellow ganglion cell, leads to perception of blue
 - Ex. Yellow light being shone
 - Causes about equal stimulation of red and green retinal cones
 - When red retinal cone activated, sends excitatory signal to both red/green ganglion cell and blue/yellow ganglion cell
 - When green retinal cone activated, sends excitatory signal to blue/yellow ganglion cell and inhibitory signal to red/green ganglion cell
 - Net effect on red/green ganglion cell is nothing because excitatory signal and inhibitory signal cancel out
 - Net effect on yellow/blue ganglion cell is excitatory signal sent to the brain, showing yellow
- McCollough Effect
 - After looking at red horizontal stimulus and green vertical stimulus, when looking at a black and white stimulus, spaces in between the lines will look pink and green respectively
- Colour-Graphine Synesthesia

- Immediate pop-out just due to form of shapes
- Even though numbers are all black, some forms would look one colour and some forms would look another colour
- Number of cone types determines the colour experience
 - o Deuteranopia
 - Cones are insensitive to medium wavelengths (green)
 - Tritanopia
 - Cones are insensitive to short wavelengths (blue)
 - Blues and greens are confused
 - Yellows are also affected, may appear read
 - Achromasy
 - Totally colour blind
 - Only photoreceptors they have are rods
 - Can only see black, white and shades of grey
 - Have poor visual acuity and strong aversion to bright lights
- Colour and Fitness
 - Diurnal species
 - Probably evolved colour perception
 - Nocturnal species
 - Don't really need colour perception
 - Adaptive Significance: Foraging Hypothesis
 - Species of marmosets, some are dichromats and some are trichromats
 - Hypothesis is that trichromats should have advantage in identifying forage and food
 - Took some cereal, dyed it either orange, red or green and scattered cereal around enclosure of marmosets
 - Results showed that trichromats overall found more cereal pieces if they were orange or red, but found just as much green cereal as dichromats
 - Adaptive Significance: Facial Hue Hypothesis
 - Individuals can detect differences in facial hue from factors such as oxygen and blood
 - Finding was that a redder face is better
 - All participants, whether they were male or female, liked a woman's face to be redder than a male's face
 - Redder faces indicate higher levels of oxygenated blood
 - Skin colour distribution is an index of health.

Lecture 11: Depth, Perception and Motion

March 6, 2011

- We need to make split-second decisions about depth and distance everyday
- We can make these split-second decisions because we can create a mental image of a three-dimensional world, based on a combination of top-down and bottom-up processing

Monocular and Binocular Cues

- How do we transform flat, two-dimensional visual images projected onto our retina into an accurate 3-D mental image of the environment
- Psychologists have identified two main classes of cues that we use to perceive depth in our environment
 - o **Binocular cues**, which are depth cues that require two eyes
 - Monocular cues, which are depth cues that you can get using one eye
- Two types of binocular cues to depth perception

Convergence

- Results from the way our eyes turn inwards to fixate on a specific point
- Ex. If you look at your finger at arm's length and then slowly bring it towards you while focusing on your finger
- As your finger approaches your face, you'll feel your eye muscles training
- The feedback that we receive from these eye movements gives us information about depth
- Convergence as a depth cue only works for objects that are relatively close because with objects that are far away, the eyes don't have to turn in at all to fixate on the same point
 - Path of sight for two eyes becomes parallel

Retinal Disparity

- Caused by the fact that our eyes, which are located about 6 cm apart, will each see slightly different visual scenes
- Ex. If you point to an object in the distance and then open and close one eye at a time
- You will see your finger jumping around and pointing to a different object when you look with each eye
- These are the two different scenes that each eye is receiving
- When these two scenes are combined in the brain, the resultant perception is depth
- Our visual systems are equipped with a class of neurons that fire maximally only when each retinal image is slightly different

Three types of monocular cues

Accommodation

- Involves changes in the shape of the lens as you focus on objects at different distances
- When objects are near, we make a different accommodating response than when objects are farther away

- However, the lens can only change so much in shape and because of this, accommodation is only an effective cue for depth up to about 2 metres
- For all points beyond this distance, the lens is a constant shape and so we have to rely on other depth cues

Motion

Motion Parallax

- Refers to the fact that when we pass by a scene, objects in the scene pass by us at different speeds, depending on how far away these objects are relative to us
- Objects that are close to us appear to speed by much faster than objects that are farther away

Optic Flow

- Refers to the changing optical projection of a scene that is caused by the motion of the observer, as well as motion of objects within the scene
- As you get closer, an object will get bigger and it will get smaller as you move away from it
- Not only does the size of the object that you're focusing on change as you move toward or away from it, so does the entire visual scene
- Objects that are close to you will seem to move more in the visual scene and change more in size than objects that are farther away and these changes in size and motion can give cues to depth

Pictorial

Interposition

- When you have an object that partially blocks another, it is perceived as being in front of the other object
- Most effective when the objects are familiar and you know what their shapes should be
- Can still provide information about depth if objects are unfamiliar because of Gestalt principle of **closure**
- Ex. If you have two circles that are partially overlapping, you will tend to see the partially blocked shape as a circle and not as a crescent because of the principle of closure
- As a result, you would perceive the full circle being in front of the partially blocked circle instead of seeing a full circle beside a crescent shape

Relative Size

- If you have two objects that are the same shape but different sizes, then the larger shape will be perceived as closer
- If you know what size a car should be, if you see an image of a tiny car, you will know that the car is far away
- · Relates to the concept of optic flow

 We avoid collisions with other cars by monitoring the rate of expansion of the approaching car on our retina and keeping this rate constant

Linear Perspective

- Ex. A railroad track
- Even though you know the tracks are parallel, they appear to converge at a single point on the horizon
- This provides a cue to depth because objects that are farther away decrease in size and spacing between objects

Texture and Haze

- Sometimes called aerial perspective
- Ex. If you're looking at a gravel road, then you will easily be able
 to see the texture of the rocks under your feet, but as you look in
 the distance, you will just see the same rocks becoming a uniform
 grey colour with little texture
- Ex. When we're looking at objects that are farther away, it will be harder to see the outline and texture of objects compared to objects that are closer to you

Shading

- Cannot give us information about how far away the object is from us, but can tell us what part of the object is close to us and what is farther away
- We are used to light coming from above, like the sun, so we automatically use the pattern of light striking an object to tell us whether the object surface is coming toward us or receding away from us
- If the light is striking the bottom of the object, then it is receding from us and if the light is hitting the top of the object then it is coming towards us

Elevation

 Objects that are higher up in a picture or closer to the horizon are seen as farther away than objects that are lower in a picture

Evolution of Depth Perception

- The effect of eye placement on depth perception
 - The types of cues that an animal can use to perceive depth depends a lot on where the animal's eyes are placed on its head
 - Prey animals typically have eyes that are on the side of their heads, like rabbits and fish
 - These animals have very limited depth perception from binocular cues and must rely on monocular cues
 - Predator animals typically have both eyes facing front, like cats and primates
 - These animals are able to use both binocular and monocular cues

- In addition to providing information about distance between predators and prey, the binocular cue of retinal disparity is excellent at detecting camouflage
 - Retinal disparity allows you to group together features or objects that are at the same distance
- The necessity of multiple depth cues
 - The reason we have so many different depth and distance cues is because we needed a visual system that was flexible and capable of processing distance and depth in many different situations
 - Ex. Motion parallax and optic flow only work as cues for depth if you or the scene around you is moving
 - Texture only works as a good depth cue if the surface has a consistent texture and if none of that textured scene is blocked from view
 - Accommodation, convergence and retinal disparity only work for objects that are less than approx. 30 feet from you
 - o Elevation only works if the scene is relative flat
 - Relative size and haze are most effective if the objects are familiar
 - Linear perspective requires parallel and straight lines that recede in the distance
 - Interposition only works if there are more objects placed in front or behind other objects
 - Shading is a poor cue if the light source comes from directly in front or behind the object

Development of Depth Perception

- Depth perception has been extensively studied in infants using the visual cliff
- The visual cliff is an apparatus that creates an illusion of depth sing an elevated platform
- On one half of the platform, there is a checkerboard pattern directly under the glass surface
- On the other half of the platform, the checkerboard pattern is a few feet under the glass surface, creating an illusion of a sudden drop-off
- The infant is then placed in the middle of the platform and the mother stands at the either ends and calls the infant to crawl to her
- About 90% of infants, ranging from 6 to 14 months, readily cross to the shallow half, but fewer than 10% were willing to venture out into the deep half
- Suggests that infants who can crawl and who are at least 6 months of age can perceive depth in the visual cliff and have the sense to avoid it

Innate Vs. Learned

- Innate
 - Some researchers believe that depth perception is not due to experience with crawling because infants as young as two months, far too young to crawl, show an increase in heart rate when they're placed on the deep side, but not when they're placed on the shallow side

- This increase in heart rate suggests that they have an innate fear of the deep side
- When animals that can walk right after birth are tested on the visual cliff, they show a reluctance to walk to the deep side
- Taken together, these results suggest that experience with moving around in your environment is not necessary to learn basic depth perception

Learned

- Infants younger than two months actually show a decrease in heart rate on the deep side and no change in heart rate on the shallow side
- A decrease in heart rate is indicative of curiosity or interest and shows that very young infants react differently to the deep and shallow sides
- This difference may be due to experience with crawling
- Infants who are more experienced crawlers are less likely than agematched infants with little crawling experience to cross to the deep side
- This suggests that there is some increase in either the perception of depth or in fearing drop-offs with more crawling experience, regardless of age
- Furthermore, infants who were too young to crawl, but were given 30 to 40 hours of experience with a walker showed more fear of heights than they did before trying the walker
- These results seem to indicate that fearing heights is caused by interaction between genes and the environment

Introduction to Motion Perception

- To be effective, our visual system has to be able to compensate for our own movements to perceive movement of objects in the environment
- Movement can also be an excellent cue to perceiving forms

<u>Process of Motion by the Visual System</u>

- The signals that leave the eye and project to the LGN are carried by two main classes f ganglion cells
 - The parvo- and magno- streams
- Parvo cells are highly involved in detecting colour, pattern and form
- Magno cells, which are crucial for detecting changes in brightness as well as motion and depth, are found throughout the retina, although the ones found in the periphery are most sensitive to movement
- From the retina, some of the magno cells send axons along the secondary pathway, or to the superior colliculus, then onto the pulvinar of the thalamus, before finally reaching the parietal lobe
- This secondary pathway is important for detecting location of objects in space, as well as controlling the direction of eye gaze so that it shifts towards the object
- Most of the magno cells however, send their axons along the main pathway to the LGN

- Information from magno cells is processed in two of the layers of the LGN, while the remaining flour layers are reserved for input from the parvo cells
- From the LGN, information from the magno cells goes on to layer IV of the primary visual cortex, where there are some cells that respond to the direction of motion of images on the retina
- Ex. Some complex cells are particular about the direction of movement and will only fire
 if a bar stimulus is moving from right not left, but not if it is moving from left to right
- The Waterfall Illusion
 - If you stare long enough at a waterfall, with time you will adapt to the downward motion
 - If you then look at a stationary scene, you will experience everything appearing to move upwards
 - This after effect occurs because the MT neurons selective for a particular direction fatigue
 - Consider two sets of MT neurons, one sensitive to upward motion and one sensitive to downward motion
 - Your brain computes overall motion direction by comparing the output of these two populations of neurons
 - If your upward motion selective neurons are firing more than your downward motion selective neurons, you will perceive upward motion
 - After staring at the downward motion of the waterfall for a long time, your downward sensitive MT neurons will become fatigued and inhibited
 - This means that even though your upward motion sensing neurons are still just firing at baseline level, they're responding more relative to your tired downward motion sensitive neurons
 - The net result is that you will perceive upward motion that does not exist
- Evidence for neural processing of motion
 - The input from the parvo and magno cells that arrives in the primary visual cortex is treated as three separate types of information that correspond to colour, form and movement
 - The movement information goes on to the extrastriate cortex, where it is processed in visual area 5 or V5 before it reaches the parietal lobe
 - The extrastriate cortex is where information gets segregated into two streams according to what type of information is being processed
 - Ex. Colour and form are processed in the ventral or "what" stream, which goes from the primary visual cortex to the extrastriate cortex and then on to the temporal lobe
 - Movement information, is processed in the dorsal or "where" stream, which begins in the primary visual cortex and ends up in the parietal lobe
 - Studies with monkeys have shown that area V5 of the extrastriate cortex, also known as area MT, has neurons that are sensitive to movement information
 - If a monkey suffers damage to area MT, then it won't be able to perceive stimuli that are moving

- Because the information that is being processed in area MT has to be up to date in order to correctly process movement, the axons that transmit information from the magno cells are thick and heavily myelinated
- This increases the speed with which visual information can be transmitted to area MT
- Compared to other regions of the extrastriate cortex, area MT is designed to respond much sooner to any input

Motion Agnosia

- One patient, L.M. suffered brain damage in area V5 of the extrastriate cortex and lost her ability to detect movement
 - To her, things that were moving appeared frozen and they would seem to jump from one place to another
 - She couldn't pour herself a cup of tea because she wouldn't see the tea rising slowly in her cup, but instead would see a solid spout of tea coming from the teapot one second and the next second she would see tea spilling over her cup and onto the counter
 - She did however, have normal vision for everything else and could read, recognize objects and name colours
 - Even though her only problem was with perceiving movement, she was still able to perceive form from movement
 - So if she was shown a blackened out person with lights on their joints, she would be able to recognize these lights as a person, even though she could not perceive the lights moving at all
- Another patient, R.A. had brain damage to a different region of the extrastriate cortex

Lecture 12/13: Form Perception

March 12, 2011

Gestalt Principles

- A group of psychologists in Germany called Gestalt Psychologists began to study how people perceive the world around them
- With respect to perception, they firmly believed that "the whole is different than the sum of its parts"
- They believed that people tended to perceive the whole stimulus rather than just putting together a collection of the stimulus' discrete parts
- The Gestalt movement was in part a reaction to the structuralist approach at the time, which suggested that everything could be reduced to basic elements
- Ex. Consider the perception of movement you experience when watching a movie made by flashing slightly different static pictures every second

- There isn't continuous movement in or across any of these frames, but we still perceive continuous movement as we watch the rapid sequence of still pictures
- Motion is an emergent property of the sequence of pictures
- The perception of the movie in its entirety is something more than the collection of thousands of still photographs
- Gestalt psychologists also proposed laws of organization that described how we group visual input in certain ways
- These laws of organization are called the **Gestalt principles** and it is thought that they
 are innate or that we acquire them rapidly
- There are six of them
 - Figure-ground
 - The ability to determine what aspect of a visual scene is part of the object itself and what is part of the background
 - Ex. Viewing a vase of flowers against a flowery wallpaper
 - In the simplest scenario, you would have a small, enclosed region that is completely surrounded by a larger region, which would be the background
 - The figure would tend to have distinct borders or edges that give it a perceptible form and is perceived as being in front of the background
 - Background is typically formless or made up of multiple forms
 - This seemingly simple process can be more difficult if the cues that are used to make these figure-ground decisions aren't clear, as is the case with reversible figures
 - Ex. Picture of two people about to kiss or a wine glass in the middle

Proximity

- Says that elements that are close together in space tend to belong together
- Ex. A field of daisies
 - The daises aren't all uniformly spaced apart, but tend to have regions where they've clustered close together in some areas and fewer in numbers in other areas
 - You will naturally see the regions of high daisy density as one group of daisies because of their proximity to each other, rather than grouping together some daisies from one cluster with some from another cluster

Closure

- Refers to the fact that if there are gaps in the contours of a shape, we tend to fill in those gaps and perceive a whole object
- Ex. Picture of a truck crashed into a telephone pole
 - Although the telephone pole is in front of the truck and blocking part of the contour of the truck, you don't perceive the object as being two separate pieces of a truck
 - Instead, you automatically fill in the missing part that you can't see and perceive the truck as a whole object

- Ex. A rectangle with gaps in it
 - You will perceive it as a rectangle even if there are obvious gaps in it
 - In fact, your tendency to fill in the gaps may be so strong that you might even think you see faint lines across the gaps

Similarity

- The tendency for us to group together elements that are physically similar
- Ex. A grid of alternating columns of X's and O's
 - You will tend to see the columns of the same elements, either all X's or all O's, as belonging together, rather than grouping together a row of "X O X O"

Continuity

- Principle that lets us perceive a simple continuous form rather than a combination of awkward forms
- Ex. The letter "X" tends to be perceived as two continuous lines "/" and "\", that cross in the middle, rather than seeing a combination of "." And ""

Common Fate

- The idea that things that change in the same way should be grouped together
- Ex. We tend to group elements together if they are moving together in the same direction at the same time
- If we look at a school of fish and see them moving together in the same direction, we will tend to group them together
- This tendency is strong enough to lead us to a perception of the group of elements as a kind of object on its own
- Can also explain why we can suddenly see a camouflaged animal once it moves, like a moth against the bark of a tree
- When the most is still, it is almost impossible to see where the wings of the moth end and the bark begins
- But as soon as the moth moves, there are elements within the moth's pattern that are moving together in the same direction and at the same time
- These moving elements with a common fate allow the contour of the moth's shape to be perceived and the moth seems to pop out against the tree

Pattern/Object Recognition

Expectations

- What a person expects to see can influence what they do see
- o Ex. Ambiguous picture

- If someone said they were excited about attending an upcoming costume ball, most people would see the picture as a costume ball scene
- If instead someone said they were excited to go to Marineland to see the trained seal show, most people would have interpreted the same picture as something completely different
- Processes of Object Recognition
 - The preliminary steps in object recognition involve identifying what aspect of the scene is the figure and what is the background
 - Once that is established, the parts of the figure are identified and grouped together into a single object
 - Recognizing an object is really a combination of two processes
 - The first of these is **bottom-up processing**, where the features that are present in the stimulus itself guides object recognition
 - Ex. You recognize a cow as being a cow because it has four legs, goes "moo", has an udder, a big nose, ears and eyes
 - So bottom-up processing says you recognize what you see by analyzing the individual features and comparing those features to things with similar features that you have in memory
 - The other process is top-down processing, where your own beliefs or expectations are the primary influence for determining what you're seeing
 - Ex. B/13
 - Asked to read a series, first row is letters and second row is numbers
 - The "B" and "13" are identical, but you read them as "B" and "13"
 - Another example is with an effect called priming
 - In a priming experiment, the experimenter measures how fast a participant can read a word that is flashed on a screen
 - If you tell the participant that the next word is an animal, you'll find a priming effect because words like dog or duck will be recognized a lot faster here than words like log or puck
 - This shows that processing of a word is more efficient if the participant is primed to expect a word from a certain category
 - Top-down processing can't work alone because you need some input from the stimulus itself before your expectations about that stimulus can influence your recognition of it
 - Bottom-up processing can't explain everything alone either because expectations certainly do influence our perceptions

- Seems most reasonable to think that both of these processes must be involved and that we're dealing with bi-directional activation, where processing occurs in both directions at once
- In this way, the features of the object in combination with our expectations guides object recognition

Theories of Object Recognition

- Biederman's Geon Theory
 - Suggests that we have 36 different geons, or simple geometrical forms, stored in memory
 - These would be forms like a cone, a sphere and a cylinder
 - According to this theory, using just these 36 geons, it is possible to recognize over 150 million different objects
 - Ex. An ice cream cone is just a cone and a sphere
 - Some problems with the idea that we store 36 geons to recognize everything
 - There are certain stimuli, like faces or crumpled pieces of paper, for which it is difficult to determine what geons would be used, yet we have no difficulty recognizing these stimuli
 - Also, there is evidence that some forms of brain damage lead to very specific deficits
 - Ex. People suffering from these brain injuries may not be able to recognize different types of fruit, but they can name different types of tools
 - If geons were involved in object recognition, you might expect deficits in recognizing all types of object based on their shapes and not a specific category of objects
 - However, it is possible that geons could be processed at a different level of processing separate from the area of brain damage

Template Theory

- Suggests that we store many different templates in memory and when we come across an object, we compare that object to all the templates in memory
- If a match is found, then it is a familiar object and the person could name it by activating connections to other language areas in the brain
- If no match is found, then it is an unfamiliar object and a new template is stored in memory
- Most psychologists don't find the idea of templates very compelling because we would have to store an incredible number of different templates to recognize all of the different objects that we encounter
- Ex. A mother's face has many different facial expressions, hairstyles, lighting conditions and points of view
- You would need countless dedicated mother templates and that's just to recognize one person

Prototype Theory

- Overcomes the storage problems of the template theory
- Says that we store the most typical or ideal example of an object
- This system is much more flexible because you don't need an exact match between the observed object and what is stored in memory
- This is how we can easily recognize common objects that we've never seen before, like a new dog or coffee mug
- However, we can also recognize specific individual objects, like our favourite coffee mug, or our own dog
- So it's likely that we have more than one type of representation for each object, like an ideal prototypical dog and also all the dogs that we are personally familiar with
- The Importance of Parallel Processing
 - We are able to recognize objects as quickly and efficiently as we do in part because much of the neural processing of object information is done in parallel
 - Different brain systems process different components of the visual signal simultaneously
 - At this time, no particular theory can provide the complete explanation for the remarkable success of our ability to recognize objects
 - o It's one particular task that we are much better at performing than computers
 - \circ Ex. Simultaneous processing of both form and colour \rightarrow it's a puppy

Perceptual Constancies

- Perceptual constancy refers to our ability to perceive an object as unchanging even though the visual image that the object produces is constantly changing
- Five types of perceptual constancy
 - Shape constancy
 - Refers to the fact that we perceive objects to have a constant shape, even though the actual retinal image of the shape would change as your point of view changes or as the object changes position
 - Ex. You perceive the shape of your door to be rectangular, but it really only produces a rectangular retinal image if you're looking at it straight on and the door is closed
 - As soon as you move or the door opens, the shape of the retinal image is no longer perfectly rectangular, but you still perceive the door as having a constant rectangular shape
 - Location constancy
 - Objects are constantly moving around on our retinas as we move our eves
 - Despite this constant movement, we perceive the objects around us as stationary and this is called location constancy

■ Ex. When we drive in a car, the entire scene is moving very fast on our retinas, but we don't perceive the objects in the scene to be moving

Size constancy

- We tend to see the size of objects around us as unchanging even though as these objects vary in distance from us, the size of the retinal image that they produce can vary quite a bit
- Ex. As your friend walks away from you, you don't think that he is shrinking before your eyes
- You perceive that he is still the same size, but that he is getting farther away from you

Brightness constancy

- Refers to our ability to know that the brightness of objects around us does not change even though the object may reflect more or less light depending on the ambient light conditions
- Ex. Black still looks black and white still looks white regardless of whether we are inside under relatively low illumination or outside on a bright sunny day
- Although this is our perception, the black object outside is reflecting ore light than the white object inside

Colour constancy

 Has to do with the way that we perceive objects around us to have a constant colour even though the light stimulus that reaches the retina may change with different illumination conditions

Explaining Perceptual Constancies

Existing Knowledge

- How do we account for all of these perceptual constancies
- Some of it probably depends on our knowledge about objects, which can provide a top-down influence on how we see those objects
- We know that most objects don't change
- Ex. Our friend is a constant size, our dog is a certain colour

Cues in scenes

- Our visual system has a way of picking up cues in the rest of the scene and using those as clues to perceive constancy in an object
- Ex. We might use depth cues to both determine that our friend is far away and shape how we perceive our friend in that context
- We use the depth cues to keep us from seeing our friend as shrinking in size as he moves farther away
- So even though he is producing a retinal image that is considerably smaller than the lamp post in the foreground, you know from other cues in the scene that he is just far away and of normal height
- Ex. When you're driving a car and approaching a bus that stopped in front
 of you, you don't see the bus as moving toward you
- Again, your brain is integrating the motion of all the elements in the scene

- If the bus was moving toward you, everything else in the background would remain stationary
- When everything in the scene is moving toward you, the brain can use this information to determine that the movement is actually yours and adjust how you perceive the scene accordingly
- Perceptual constancy occurs because we know that certain properties of objects do not change and our perceptual system automatically factors in other cues in the environment that give us information about the objects of interest

Visual Illusions

- Although our brain is tuned to recognize a variety of objects in different situations, sometimes it makes mistakes
- The reason visual illusions occur is because our perceptual strategies, which work most of the time, are used in these particular situations where, in fact, they don't belong
- We think we see one thing when in reality, what we're looking at is something quite different
- Many of our perceptual constancies can be overcome by simply removing the relevant contextual information
- Ex. If we place our dog with the reddish cast in a scene in which no other objects have a reddish cast, then we would fail to recognize the dog as our own
- Muller-Lyer Illusion
 - One explanation of this illusion is that it is an example of misapplying size constancy and inaccurately interpreting depth
 - The angled lines on top of the vertical lines each look like a corner, but the one
 with upside down "V""s look like a corner that is pointed toward you, whereas
 the one with the right side up "V" s look like a corner that is receding away from
 you
 - Since the two lines give exactly the same retinal image, but the first one is assumed to be closer to you than the second one, the first one is perceived as shorter
 - Interestingly, people from cultures who live in round huts and aren't surrounded by right angles are much less susceptible to the Muller-Lyer illusion and are more likely to say that the two lines are of the same length
 - This provides some support for the explanation of the Muller-Lyer illusion is at least partly due to cultural and experience dependent processes
- The Ames Room
 - The **Ames room** is a specially constructed room that looks like a normal rectangular room, except that it is actually trapezoidal in shape
 - One corner is actually much farther away from your point of view than the other corner

- So if you have two people of equal height standing in each corner, the one standing in the farther corner looks much smaller than he person standing closer to you
- But since you believe and perceive the room to be a normal rectangular room of normal height, you interpret the scene as though each person is the same distance from you
- When your brain applies the compensatory computations that normally lead to size constancy, it can be tricked by the cues normally used for distance constancy
- If you perceive the distance to be the same between you and the two ends of the room, then the two people will be perceived as different sizes
- o The one who is in reality closer to you will be seen as larger

Ponzo Illusion

- Most people say that the top horizontal line is longer than the bottom line, when in fact they are both the same
- The illusion likely occurs because the two vertical lines are converging, which gives a sense of depth
- You tend to perceive the top of the lines, where they have converged the most, as farther away than the bottom of the lines where they're further apart
- You're again using depth cues to gauge size and because the top horizontal line is perceived as being farther away, you will see that line as longer than the bottom line, which looks closer to you
- o Again, retinal size is the same, but the perceived distance differs

Conclusion

- Visual illusions show us how our experiences and culture can influence how we perceive events in the world
- They show us that perception is an active process, in which perception is shaped by our prior experiences and not just by the scene immediately in front of us

xFeature Detectors

- Recall that the brain uses a division of labour, with each region along the visual pathway processing relatively specific information and then passing it on
- Form recognition follows a similar strategy
- Magno and Parvo cells
 - First, magno and parvo cells in the retina transducer the light stimulus into a neural implse
 - Recall that magno cells are found mainly in the periphery of the retina and are used for detecting changes in brightness as well as motion and depth
 - Parvo cells, on the other hand, are found throughout the retina and are important for detecting colour, pattern and form
 - These ganglion cells, with their small receptive fields, are the crucial first step to object recognition

- From the retina, the axons of these cells exit the eye via the optic nerve, travel to the LGN and end up in the primary visual cortex in the occipital lobe
- The cells in the primary visual cortex are very particular about what will make them fire and these cells are called **feature detectors**

Hodgkin and Huxley

- o Recorded the electrical activity in an individual neuron of a squid
- Paved the way for other researchers to use this technology to see how individual neurons respond to specific stimuli

Lettvin et al.

 Discovered a neuron in the optic nerve of a frog that responded only to moving black dots and they called these cells "bug detectors"

Hubel and Wiesel

- Spent years extending this work in their studies of cells in the visual cortex of cats and monkeys
- Began exploration of visual cortex by trying to learn what type of stimuli the individual cortical cells responded to
- They did this by putting microelectrodes in the cortex of a cat to record the electrical activity of individual neurons as the cat was shown different types of visual stimuli, such as flashes of light
- The problem was that they weren't getting much response from the neurons, until one day when they presented the cat with a slide that had a crack in it
- When the line that was projected from that crack moved across the cat's visual field, the neuron started to fire like crazy
- They realized that neurons must respond to stimuli that are more complex than diffuse flashes of light
- They began using lines of different orientations and thickness that moved in different directions and they found that each neuron is very specific about what will make it fire the most
- These cells fire maximally to stimuli of a certain shape, size, position and movement and this defines the receptive field for that cell

Simple cell

- Simple cells respond maximally to a bar of a certain length and orientation in a particular region of the retina
- Receptive field for a simple cell is organized in an **opponent** fashion, making it sensitive to the location of the bar within the receptive field
- o Ex. A simple cell responds the most to a horizontal bar
 - If that same bar is moved outside that particular region and/or changes orientation, then the cell will be inhibited and actually fire less than baseline

Complex cells

- Respond maximally to a bar of a certain length or orientation regardless of where the bar is located within the receptive field
- Doesn't care where in its receptive field the bar is located and it will even continue to fire if the bar is moving within the receptive field

- Some complex cells do care about the direction of this movement
- Hypercomplex cells
 - Respond maximally to bars of a particular orientation that end at specific points within the receptive field
 - Ex. Hypercomplex cell fires the most to a horizontal bar of light that appears anywhere in the "on" region of the receptive field, but gives only a weak response if the bar touches the "off" region
 - So these cells have an inhibitory region at the end of the bar, making them sensitive to the length of the bar
- Topographical Organization
 - The layout of the visual scene is preserved in the visual cortex
 - Neighbouring objects in your visual field are processed by neighbouring areas of your brain
 - But this mapping from visual field to brain is not exact because the largest amount of cortex is devoted to processing information from the central part of the visual field, which projects onto the fovea
 - Nevertheless, each region of the cortex receives some input from a small piece of the visual field and within each region, there are cells that analyze specific features of the scene
 - For a particular part of the visual field, there are neurons that fire maximally if there is something in the scene that has a line of a certain orientation, length and movement
 - Other neurons respond maximally if there is something in that tiny portion of the visual scene that is a specific colour
 - Other neurons respond most when there is a line that moves in a certain direction
 - Cluster of cells in the region of the cortex right beside this region are doing the same analysis for the neighbouring part of the visual scene
 - An important benefit of this parallel processing strategy is speed

Ventral Stream

- Processing of visual input in primary visual cortex involves specific cells responding to relatively specific features from a small portion of the visual field
- For the visual scene to make any sense, this information has to be combined to form a meaningful whole
- This combination begins in the extrastriate cortex, also known as the visual association cortex, which surrounds the primary visual cortex
- The extrastriate cortex has multiple subregions that each receives a different type of information from the primary visual cortex about the visual scene
- Ex. One subregion of the extrastriate cortex will receive information about the colours in the scene, another about any movement in the scene and another about different line orientations in the scene

- It is in the extrastriate cortex where the information begins to be segregated into two streams according to the type of information that is processed
- One stream is the dorsal stream (where stream), which processes where objects are located in the visual scene and how they are moving within that scene
- The dorsal stream takes information from the primary visual cortex to the parietal cortex, which processes spatial information
- The other stream is the ventral stream (what stream), which processes information about what the object is, including form and colour
- The ventral stream takes information from the primary visual cortex and sends it to the temporal cortex, where all the bits of feature information come together
- Columns in the Temporal Cortex
 - Temporal cortex is arranged in vertical columns that are oriented perpendicularly to the surface of the cortex
 - Neurons in the temporal cortex respond to a very specific stimuli that are much more complex than the stimuli to which the neurons in the primary visual cortex respond
 - These stimuli include images like hands, faces, apples or chairs
 - Within each cortical column, there are five layers of neurons, with each layer responding to complex stimuli that come from same category
 - o However, each layer responds to slightly different features within that category
 - Ex. One column of neurons might respond best to apples and layer 1 might prefer red apples, layer 2 might fire maximally to green apples, layer 3 to yellow apples, layer 4 to small apples and layer 5 to big apples
 - Do not think that every object is coded by a specific neuron
 - An object is represented by unique activity patterns across many cells in several different brain areas

Development of Pattern/Object/Face Recognition

- Many researchers have used the preferential looking method to determine what kinds of patterns infants can perceive by measuring which of two patterns infants look at the most
- Infant Pattern Recognition
 - o It turns out that infants prefer to look at patterns more than plain stimuli
 - Infants prefer the ones that have a lot of high contrast with sharp boundaries between light and dark regions
 - Infants will look the longest at the most complex stimuli that they are able to perceive
 - Ex. If presented with a checkerboard pattern, a newborn will prefer to look at the pattern with bigger squares

- o If the squares are too small, the newborn's poor visual acuity will make it look like a uniform grey surface, which isn't very interesting
- By 2 months of age, when the infant's visual acuity has improved, they will now prefer to look at a smaller-squared checkerboard because it is more complex
- Some researchers believe that because infants under 2 months of age see so poorly and look at such a limited part of the object, they may be unable to perceive whole forms at all
- Ex. If you show a young infant a triangle or a star and measure where they look, they will tend to stare at one corner and not at the entire shape, whereas infants over 2 months of age are beginning to focus on the entire shape
 - Shows that newborns are naturally attracted to certain key features of a stimulus, like angles and edges, but not necessarily the object as a whole
- By 3 months old, infants can perceive a whole form when given only parts of the form
 - Ex. If you're shown a picture of four circles with right angle wedges missing, you
 can't help but see a square in the middle, even though the square isn't really
 there
 - o Infants can see this too by 3 months because if you habituate them to a picture of a real square and then show them the four-circle square, they will stare less at the four-circle square than if you showed them a different four-circle shape
- Being able to distinguish two objects that are touching or overlapping is more difficult because it requires the ability to use cues like pattern and colours to tell what parts of an object belong together and what parts are separate and from another object
- Young infants cannot use cues like colour or texture to tell one object apart from another until they are almost 5 months old, especially if the objects are standing still or if they move together
- But if one object moves independently of the other, infants as young as 3 months old know that there are two separate objects and not a single larger object
- When an infant is finally able to perceive an entire form, he has to recognize form as being the same under different viewing conditions
 - He must have some sense of perceptual constancy
 - Some studies suggest that infants are starting to get a handle on brightness, colour and shape constancy by as young as 4 months of age
- Ganrud's Size Constancy Study
 - Ganrud tested infants of various ages for size constancy to see if an infant understood that an object doesn't change in size when it is viewed at different distances
 - Infants were shown a teddy bear at a specific distance and were then shown a second teddy bear at a farther distance
 - The second bear was either the exact same bear, which would produce a smaller retinal image than the first bear, or a larger bear that would produce the exact same retinal image as the first bear
 - Infants between 4 to 5 months of age treated the identical bear that was viewed at two different distances as familiar, but they stared much longer at the larger bear that was viewed from a greater distance

- This suggests that infants at this age had some sense of size constancy and understood than an object that is farther away should produce a smaller retinal image
- Some researchers have argued that even newborns prefer to look at faces over any other pattern and that this innate preference has evolved to ensure that as infants, we orient toward other people and not other objects in our environment
 - This could serve to build a necessary social bond with our caregivers
 - In face preference studies, infants as young as 4 days old are shown different patterns, colours, shapes or even a scrambled face and the infants prefer looking at faces
 - Interestingly, by 2 months old, infants prefer to look at attractive faces over unattractive faces and what an infant considers to be an attractive face actually coincides with what adults consider to be attractive
 - Furthermore, 2 month old infants will look longer at their own mother's face than faces of other people
 - By 5 months old, they can begin to detect different emotional expressions, such as happiness or sadness
 - All of these studies suggest that we are born with a readiness to perceive and prefer face stimuli compared to other stimuli
- Other studies have found that infants show no preference for faces over other complex stimuli and if there is a face preference, it emerges gradually from all the early experience we have with faces
 - The argument is that infants do not have a preference for faces, but really have a preference for complex stimuli that have a lot of contrast between light and dark, such as the eyes and mouth, as well as moving parts
 - In fact, studies that used non-face stimuli that were matched to the face stimuli for complexity showed that infants did not prefer the face stimuli
- Studies that tracked where an infant was looking when shown a picture of a face revealed that infants under 2 months of age focused mainly on the outer contours of the face, such as the hairline or chin
 - o It wasn't until the infant was over 2 months old that she looked at regions within the face, like the eyes and mouth
- All of these studies suggest that it is our early experience with faces that develops our preference for them and that at birth, we simply have a preference to look at complex, high-contrast stimuli, whether these are faces or not

Normal and Abnormal Visual Development

- Visual system provides us with a perfect example of how normal development requires an interaction between innate abilities and environmental stimulation
- If we didn't have the innate architecture in place, then no amount of environmental stimulation would improve our vision
- We are born with a certain readiness in our brains for vision and we need early visual experiences for those brain centers to develop normally

- Furthermore, there is a critical period early in life during which these early visual experiences must occur to reserve these brain centers for the function of vision
- If that early experience isn't there, then those brain centers may take on other functions and the individual will forever have abnormal vision
- Cat Studies using Cylinder Environments
 - One study raised kittens in a cylinder that had vertical stripes painted on the walls only
 - These kittens failed to develop proper feature detectors for horizontal stripes and as a result, where unable to see horizontal edges and objects in their environment
- Dr. Deda Gillespie
 - Found that if 1-month old kittens were kept in the dark for as little as 3 to 4 days,
 then the visual regions of the brain already began to degenerate
 - If a 1 month old kitten is left in the dark for an entire week or longer, then the damage to the visual brain regions is severe and permanent
- These studies show how crucial it is for early visual experience because without it, the brain starts making other plans for those areas that went unused
- Humans Born with Cataracts
 - Having cataracts is like having a thick cloud in the lens of your eye, which allows only diffuse light to reach the retina and results in a complete loss of the ability to perceive any objects, patterns or details
 - Treatable by surgery to remove the cloudy lens and replace it with an artificial lens
- Using the preferential looking method, if you show a baby with a card with stripes on one side and plain gray on the other and if they choose to look at the stripes, we know that they can see the stripes
 - Over trials, we make the stripes thinner and thinner
 - The thinnest stripes babies prefer over gray provide a measure of their vision
 - Experiments tell us that babies can see right from birth and that vision improves rapidly over the first few months of age
 - o By 6 months of age, acuity is 5 times better than it was at birth
 - Tells us that even humans go through an early period in development when they need a certain amount and type of visual input for visual development to proceed normally

Visual Agnosia and Prosopagnosia

- If you suffer damage to the primary visual cortex, you will lose vision in some parts of your visual field, but the parts that you do see will seem normal and you will be able to perceive objects in those intact areas of your visual field
- Extrastriate damage
 - If you damaged your visual association cortex, your entire visual scene might be intact and you would probably be able to see all the objects in the scene, but you would have difficulty in recognizing some or all of the objects

Called visual agnosia

- Object Agnosia
 - A type of visual agnosia
 - The inability to perceive objects
 - A person suffering from object agnosia is unable to identify different objects by sight, even though they can see those objects perfectly, have normal visual acuity and are able to recognize and name the objects by touch
 - o Ex. Oliver Sacks and his patient Dr. P
 - Dr. P once reached for his wife's head and tried to pick it up to put on his head
 - He confused his wife's head with his hat
 - Occasionally, the type of object that the person can't recognize is very specific
 - Ex. A person may not recognize different tools, but can recognize different fruits and vegetables
 - Many people with object agnosia can still read, which shows that recognizing words involves different brain mechanisms than recognizing objects

Prosopagnosia

- Another type of visual agnosia
- Occurs when a person can recognize regular objects, but can't recognize faces
- Will know that they are looking at a face and they will be able to see eyes, a nose and a mouth, but they won't be able to put those individual features together and perceive whose face it is, even if they're looking in a mirror
- These people have to rely on other cues to recognize other people, like their voice, smell or the way they walk
- People with prosopagnosia can also have difficulty recognizing other specific stimuli, but can recognize categories of objects
- Ex. They would be able to recognize a dog and a car, but wouldn't be able to pick out their own dog or their own car

Form Perception Live Lecture

- What do infants know about faces
 - Infants as young as three months of age, prefer looking at human faces compared to other objects
 - Is preference for faces innate
 - Already a lot of environmental input, have seen faces for three months already
 - Infant's visual acuity is quite poor
- Researcher at McMaster is experimenting on newborns minutes after they are born
 - o Took a ping pong paddle and drew three squares to make it look like a face
 - Took another ping pong paddle and drew three squares, but didn't make it look like a face
 - Same amount of data, complexity, good control

- Results showed that these babies preferred faces
- Strong evidence for innate
- Holistic Face Processing
 - Eyes and mouth inverted on upside down Barack Obama photo
 - When you're looking at it upside down, you don't know how dramatic the change is
 - Only when the photo is right-side up do you see the extent of the change
 - The Inversion Effect
 - Face presented for a very brief duration
 - Then you are shown two faces and asked which face is the same as the face you just saw
 - Easy to do when all the faces are right-side up
 - Harder to do when first face is shown upside down
 - Two strategies for face processing
 - Configural or Holistic view
 - Whole is greater than sum of parts
 - Take in whole face at once
 - Featural process
 - Process individual features of face along
 - More evidence supports holistic view
 - The Composite Face Effect
 - Shown two faces, asked if they are same or different
 - Only focus on the top half of face
 - Bottom half is always going to be different, random faces
 - Told to ignore bottom half of face
 - Results show that people cannot ignore bottom half of face, they have no choice but to take in all the information
 - Another experiment was the exact same, but top and bottom half of faces were slightly misaligned
 - This group could much easier ignore bottom half of face
 - Suggests that if you have a properly aligned face, no choice but to take it all in as a whole
 - Greeble Experts
 - Greebles → Objects with face-like qualities
 - Have genders, families and specific names
 - People were asked to familiarize themselves with the Greebles, took 7-10 hours
 - Then, experts were asked to look at a new Greeble, "pimo" and "pimo's quiff"
 - The quiff was shown in isolated parts, studied configuration and a transformed, wrong configuration
 - Results showed that experts could identify quiffs much easier when they were isolated
- The value of face processing

- Paul Eckman → Lie to Me
- When you are lying, will unconsciously express fear and disgust

Lecture 14: Audition

March 19, 2011

The Auditory Mechanisms of Different Species

- Auditory mechanisms vary across different species according to specific needs
- Sound Frequency
 - o Different species can hear different ranges of frequencies
 - Ex. Dog whistle
 - Humans can perceive sounds that lie anywhere between 20 and 20,000 Hz
 - Whales, dolphins and dogs have a wider hearing range, while frogs and birds have a narrower range
 - At the lower frequency detection extreme are fish, while at the higher frequency detection extreme are bats and rodents
 - Audible frequency range is determined in part by evolution of structures of auditory system
 - One key structure is the basilar membrane, which contains the hearing receptors
 - Sounds of different frequencies are processed along different areas of basilar membrane
- The Basilar Membrane
 - Varies in length across species
 - It is shortest in amphibians and reptiles, longer in birds and longest in mammals
 - A longer basilar membrane allows processing of a wider range of frequencies

The Stimulus: Sound Waves

- Sound travels in waves, although sound waves travel much slower and require some medium to travel through
- Sound waves are initiated by either a vibrating objet, like vocal cords or a guitar string, or by forcing air past a small cavity, like a pipe organ
- This causes air molecules surrounding the source of the sound to move, causing a chain reaction of moving air particles
- These alternating bands of more and less compressed air molecules interact with eardrum to begin auditory processing
- A band of compressed air molecules causes your eardrum to get pushed slightly inwards whereas a band of less dense air particles causes the eardrum to move outwards
- Changes in air pressure over time that make up a sound wave can be graphed as a sine wave
- The three physical characteristics of the wave, amplitude, wavelength and purity, when applied to sound waves, translate into the three psychological properties of loudness, pitch and timbre

- Amplitude: Measure of Loudness
 - Variations in amplitude or height of sound wave affect the perception of loudness
 - Since waves of greater amplitude correspond to vibrations of greater intensity, higher waves correspond to louder sounds
 - Loudness is measured using a logarithmic scale of decibels (db)
 - o In this scale, the perceived loudness of a sound doubles for every 10 dB increase
 - A whisper is at around 27 dB, a normal conversation at 60 dB and the front row of a rock concert at around 120 dB
- Frequency: Measure of Pitch
 - Sound waves also vary in the distance between successive peaks, called wavelength or frequency of sound and this property affects the perception of pitch
 - Pitch is measured in hertz (Hz), which represents the number of cycles per second or the number of times in a second that a sound wave makes one full cycle from one peak to the next
 - So if many wave peaks are condensed into one second, then this sound will be of a high frequency and result in a perception of a high pitched sound
 - Similar to light, the audible zone of frequencies that humans can detect represents only a portion of the possible frequencies that can be produced
- Timbre: Measure of Complexity/Purity
 - Most sounds we hear everyday are complex sounds that are composed of multiple sound waves that vary in frequency
 - Timbre refers to the complexity of a sound
 - Ex. When you pluck a guitar, it vibrates as a whole (fundamental), but also vibrates at shorter segments along the string (overtones)
 - The final sound you hear is a mixture of the fundamental tones and all the overtones and this combination is timbre
 - So a piccolo and a bassoon may both play the same note, but because each instrument produces a unique combination of fundamental frequency and overtones, they still sound different to us even though each instrument is producing same frequency and amplitude

The Ear

- Structure of Ear
 - Can be divided into the external, middle and inner ear and each area conducts sound in a different way
 - Incoming changes in air pressure are channelled through the external ear, onto the middle ear and amplified so that it can be detected as changes in fluid pressure by inner ear
 - These changes in fluid pressure are then finally converted to auditory neural impulses
- The External Ear

- o Made up of the pinna, ear canal and eardrum
- The pinna is the folded cone that collects sound waves in the environment and directs them along the ear canal
- Since the ear canal narrows as it moves towards the eardrum, it functions to amplify the incoming sound waves, much like a horn
- The eardrum is a thin membrane vibrating at a frequency of the incoming sound wave and forms the back wall of the ear canal

The Middle Ear

- Begins on the other side of the eardrum, which connects the ossicles, the three smallest bones in the body
- The ossicles consist of the hammer, the anvil and the stirrup
- The amplification of vibrating waves continues here in the middle ear
- Vibrating ossicles are about 20 times larger than the area of the oval window to which they connect to create a lever system that amplifies the vibrations even more
- The additional amplification is necessary because the changes in air pressure originally detected by the external ear are about to be converted to waves in the fluid-filled inner ear

The Inner Far

- Vibrating oval window connects to the cochlea of inner ear
- Cochlea is a fluid-filled tube about 35 mm long, coiled like a snail shell
- Cochlea contains the neural tissue that is necessary to transfer the changes in fluid to neural impulses of audition

- The Cochlea

- The **oval window** is actually a small opening in the side of the cochlea and when
 it is made to vibrate, it causes the fluid inside the cochlea to become displaced
- The round window, located at the other end of the cochlea, accommodates for the movement of the fluid by bulging in and out accordingly

The Basilar Membrane

- Inside the cochlea is a flexible membrane, called the basilar membrane that runs the length of the cochlea like a carpet
- So when the basilar membrane is pushed downwards, the fluid inside the cochlea causes the round window to bulge out and when the basilar membrane is forced upwards, the round window bulges inwards
- Although the cochlea itself gets narrower toward the end, the basilar membrane gets wider
- Because the length of the membrane varies in both flexibility and width, sounds
 of different frequencies cause different regions of the membrane to vibrate
- Higher frequency sounds cause the end nearest the oval window to vibrate whereas lower frequency sounds cause the end nearest the round window to vibrate

Hair Cells

o Basilar membrane houses auditory receptors, which are called hair cells

 As membrane moves in response to waves in the fluid, the hair cells also move and this movement is finally converted to neural impulses that the brain can understand

Auditory Pathway: From Receptors to Auditory Cortex

- When activated, hair cells along basilar membrane release a neurotransmitter
- Hair cells form synapses with bipolar cells, whose axons make up the cochlear nerve, a branch of the main auditory nerve
- Although the outer hair cells outnumber the inner hair cells by about 4 to 1, it is the inner hair cells that mainly contribute to signal in the cochlear nerve
- Some important differences between inner and outer hair cells
 - Each inner hair cell communicates with roughly 20 afferent fibres, which means that signal from each inner hair cell has exclusive rights to 20 direct links to the brain
 - The outer hair cells have to share one direct link to the brain with about 30 other outer hair cells (slower)
 - The axons that synapse with outer hair cells are thin and unmyelinated, whereas axons that carry information from inner hair cells are thick and myelinated
 - The arrangement of these connections suggest that even though there are far fewer inner hair cells than outer hair cells, inner hair cells are primarily responsible for transmitting auditory signal to brain

Cochlear Nucleus

- Neurotransmitter released by hair cell is capable of triggering EPSPs in the cochlear nerve fibres, which then sends this signal to the cochlear nucleus in the hindbrain
- Cochlear nucleus has separate dorsal and ventral streams
- In visual system, recall that ventral stream processes object recognition and dorsal stream processes location of object
- Similar processes occur with auditory system
- Another similarity in how brain processes visual and auditory information has to do with how raw information is organized along neural pathways
 - Recall that spatial organization of our visual world is maintained at all levels along our visual pathways
 - Ex. Neighbouring locations in space fall on neighbouring regions on our retina and this spatial organization is still true at the level of the LGN, primary visual cortex and extrastriate cortex
 - This type of organized neural representation of the visual world is called topographical
- Same principle applies with auditory sense, it is called tonotopic organization

- Recall that frequency is coded along different regions of basilar membrane because sounds of different frequencies displace the hair cells in these different regions
- The hair cells connect to the cochlear nerve such that neighbouring regions of hair cells remain together and this organization is maintained all the way through auditory pathway to primary auditory cortex
- So if we looked at how the primary auditory cortex responded to sounds of different frequencies, we'd see that the region of the basilar membrane that is closest to oval window and responds the most to low frequency sounds is represented at one end of area A1
- Whereas the other end of basilar membrane that is closest to round window and responds best to high frequency sounds is represented at other ends of area A1
- With this type of organization, information about similar frequencies is processed together

Auditory Localization

- In addition to being able to identify what the source of a sound is, we're also able to localize where a sound is coming from in space through auditory localization
- Our skills in auditory localization rely on the fact that our sense organs are separated in space
- Process is a little different from visual localization
- In vision, recall that location of an object in the environment directly corresponds to image of object on the retina
- In audition, there is no spatial map
- Auditory localization is calculated from the neural representation of incoming sound
- With vision, we saw that retinal disparity occurs because each eye sees a slightly different image, which gives us cues for the perception of depth
- Similarly, the fact that our ears are located on opposite sides of our head results in interaural differences in sound that give us cues for auditory localization
- The first interaural cue is the difference in time it takes for the sound to reach each ear
 - Can be measured in sub-milliseconds
 - Dependent on the direction of incoming sound, specific neurons in the superior olivary complex respond to these slight differences in the timing of arrival of the action potential from each ear in response to same sound
- Intensity difference at each ear
 - For very close sounds, there is a detectable loss of intensity because the sound wave has to travel farther to reach one ear than the other
 - o For sounds that are further away, this difference is less detectable
 - Instead, ears rely on difference in intensity caused by head which casts a "sound shadow" that diminishes the intensity at the distal ear, much as light is diminished within the shadow you cast in sunlight
 - Since input from each ear travels to both sides of the brain, these differences in intensity can be directly compared to calculate the location of sound

- Some neurons in superior olivary complex respond specifically to these intensity differences from each ear, while others respond specifically to interaural differences in arrival times for sounds
- When a sound is directly in front or directly behind you, it strikes both ears at the same time and you will have difficulty locating the source of the sound
- In this case, rotating your head will cause slight changes in sound intensity reaching each ear and you will be able to localize the sound

Pinna cues

- Another type of acoustical cue is the sound direction produced by the characteristic folds and ridges of our pinnae
- Pinna diffracts incoming sound waves to make significant changes to frequency content of sound that reaches inner ear
- Some frequencies become amplified, while others become attenuate
- These changes are collectively called pinna cues and are required for accurately localizing the elevation of a sound source
- Because everyone has a unique ear shape, pinna cues are particular to the individual and are sometimes called "earprints"
- When pinna cues are altered (by placing plastic molds into pinna cavities), dramatic disorienting effect on localization ability, despite the fact that interaural difference cues are still available
- Over the course of weeks, subjects can adapt to new pinna cues and localization becomes normal again

Echolocation In Bats

- Bats are very visually adept
- They use a system of **echolocation**, through which a bat is able to form a perceptual image of the objects in the surrounding environment by emitting a sound and then analyzing the time and frequency information that is contained in the returning echoes
- The bat first emits a burst of sound waves of a very high frequency, which bounces off the object and returns to the bat's ears
- The bat's brain analyzes the slight differences in frequency content and timing of the returning sound waves to determine the characteristics of objects in its environment
- An object that is close to the bat will return echoes sooner in time than objects that are farther away
- Objects that are moving will have echoes that are Doppler-shifted compared to stationary objects
- Objects that are textured will produce echoes that vary slightly in their return times relative to echoes from objects that are smooth
- In response to selective pressure exerted by bat's abilities at echolocation, some prey have evolved a sense of hearing designed especially for detection of bat calls
- The interaction of selection pressures of predator and prey is called co-evolution

- Adaptation of traits of one species can directly affect the adaptation of traits in another species
- Across many generations of predation and selection by echolocating bats, moths have evolved the ability to hear sounds that match the frequency range used by most bats when they're hunting insects using echolocation
- Being able to detect the bat has certainly helped moths because their chance of survival increases when they can hear the bat coming in advance and can respond by engaging in a defensive flight pattern

Lecture 15: Music Perception

March 20, 2011

Introduction

- Music is more than just a collection of individual notes that are strung together in a certain order
- Instead, when you hear music, you perceive it as an organized whole
- This organized whole can form an acoustic pattern that is so salient that you can hum the tune after hearing it only once
- The acoustic pattern is easily recognizable, even if it is played in a different key or with different instruments
- This suggests that what's important to the perception of this pattern is the relation between the notes and not the individual notes themselves

Auditory Scene Analysis

- The same Gestalt principles used to organize a visual scene also apply to organizing an auditory scene
- Ex. Incoming stream of sounds are separated into figure and ground (figure-ground)
 - We can consider the "ground" (background) to be whatever sounds you're not focusing on, such as the random sounds of a subway station itself
 - The "figure" is the sound of a particular arriving train or a specific voice on the subway platform that you are paying attention to
 - However, the sounds that make up the figure and ground are not permanent and will change as you focus your attention
 - Ex. You may be listening to your friend while ignoring the drone of the random sounds around the subway station, then have your attention suddenly drawn to the PA system announcing that your train will be arriving late
 - You have switched the figure and ground and the friend that you were previously listening to has become background noise to the PA system

Proximity

 The principle of proximity organizes sounds that occur close together in time or space

- If you played a series of high and low tones both spaced apart in time you would perceive two separate tones
- However, if you played the tones closer together in time, you would hear a single tone

Similarity

- Allows you to group together auditory input that is similar, such as sounds that are of a similar frequency of timbre
- Allows you to pick out and group a series of sounds as all belonging to one particular voice among many voices

Continuity

 The principle you would use to follow along with one song, even if you simultaneously heard another song playing with the same instruments

Closure

 Principle that allows you to understand a conversation, even if every other sound was muffled or missing

Pitch Perception

- Pitch perception, or how the frequency of a sound wave affects our perception, has been studied extensively
- Recall that the lowest frequency we can hear is 20 Hz and the highest is about 20,000 Hz
- Recall that sound waves enter the ear canal, vibrating the eardrum, further amplified by the ossicles, which cause a wave in the fluid in the cochlea
- This movement of the fluid causes the hair cells along the basilar membrane to move, sending a signal that is sent down the auditory nerve to key regions in the brain
- There are two theories required to explain pitch perception along the entire frequency range that we can hear
 - Frequency theory is so named because it was thought that the entire basilar membrane vibrates at the frequency of the incoming sound wave
 - This causes impulses of the corresponding frequency to travel up the auditory nerve, effectively allowing the brain to decipher frequency by counting the number of neural impulses
 - In accordance with the predictions of the theory, physiological evidence indicates that the hair cells on the basilar membrane do indeed vibrate together

Problems

- It was learned that axons are incapable of firing more than 1000 impulses per second
- This would work fine if all of the sounds that were important to our reproduction and survival were less than 1000 Hz
- Although a single axon can't fire more than 1000 impulses per second, groups of auditory nerve fibres can fire a series of impulses that as a team, can signal to the brain the frequency of sound waves up to 5000 Hz

- Called the volley principle and it extended the audible frequency range for the frequency up to 5000 Hz
- But still not enough to cover the entire frequency range that reaches 20000 Hz
- So theory cannot explain how we perceive pitches between 5000 and 20000 Hz
- Although the hair cells along the basilar membrane move together as the frequency theory predicts, they in fact move as a traveling wave that forms a peak at a particular place along the basilar membrane
- Place theory of pitch perception states that the brain can decipher the frequency of the sound wave by being tuned to the specific place of the peak of its traveling wave along the basilar membrane
 - Recall that each inner hair cell has roughly 20 direct links with the brain, which would allow the region of each inner hair cell on the basilar membrane to be represented very specifically in the auditory cortex
 - When a sound causes a wave in the basilar membrane, high frequency sounds maximally displace the hair cells closest to the oval window, where sound initially enters the cochlea
 - On the other hand, low frequency sounds produce a wave that peaks at the opposite end of the cochlea
 - This results in tonotopic representation of pitch and this organization is maintained all the way to the primary auditory cortex, with neighbouring regions of the cortex responding maximally to neighbouring frequencies
 - Tonotopic map contains a map of different locations on the basilar membrane in the primary auditory cortex
 - Tonotopy in Primary Auditory Cortex
 - Neurons are arranged in such a way that high frequency sounds activate neurons at one end of the cortical area and low frequency sounds activate neurons at other end and each neuron is maximally sensitive to sounds at a certain frequency
 - Although each hair cell is maximally responsive to a specific frequency, it will still respond to a range of frequencies
 - Much like how visual receptors respond maximally to light of a specific wavelength, but will also respond to a range of wavelengths of light
 - Direct evidence for tonotopic coding of pitch and support for the place theory comes from animal studies that have used drugs that can damage the hair cells
 - In one experiment, Stebbins and colleagues administered the drug and then tested the monkeys' ability to perceive different frequencies of sound
 - When the cochleae was later observed, they found that even brief exposure to the drug damaged hair cells near the entrance to the cochlea at the oval window

- With longer exposure to the drug, damage to the hair cells extended toward the other end of the basilar membrane
- The behavioural tests showed that monkeys with damage to the hair cells near the oval window were unable to perceive high frequency sounds
- More damage along the basilar membrane translated into a growing inability to hear progressively lower frequency sounds
- Taken together, these results demonstrate that different frequencies are represented at specific places along the basilar membrane, with high frequencies at the entrance of the cochlea and lower frequencies at the opposite end of the cochlea
- Problems with place theory
 - As the frequency of sound gets lower, the location of the peak of the wave along the basilar membrane gets more and more variable
 - For very low frequencies under 50 Hz, the peak actually disappears completely
- So the place theory alone cannot account for the full audible range of hearing, much like the frequency theory
- It turns out that both theories are needed to explain the full range of hearing
- Frequency theory is useful to explain how we hear low frequencies that are below 1000
 Hz and place theory explains how we perceive high frequencies above 5000 Hz
- Both mechanisms are theoretically used for frequencies between 1000 to 5000 Hz,
 which is coincidentally the range of frequencies that we discriminate most effectively

Bird Song

- Bird song is defined as the music-like vocalizations that are made primarily by the male of a species during the breeding season in order to attract a female or defend his territory from other males
- Songbirds have evolved two key brain regions to deal with the complexities of producing song
 - o The high vocal centre (HVC) and the robust nucleus of the archistriatum (RA)
 - As males are the primary producers of song, both of these regions are larger in males than females
 - The sex differences are controlled in part by hormones
 - A female given testosterone will show an increase in the size of these brain regions and will begin to sing like a male
 - These key brain regions are further modified by experience
 - Males that are particularly at song have enlarged HVC and RA brain regions
- Birdsong is an excellent collaboration between inherited and learned components during development to produce a species-typical behaviour

- Birds may inherit a genetic predisposition to sing, but they must learn and practice to produce correct songs
- Evidence for Learning
 - Marler and Tamura analyzed the songs of white-crowned sparrows that lived in three different local regions
 - Their findings confirmed that songs were at least partially learned because the same species birds living in these different regions had different dialects
 - Although their songs were similar and these birds would understand each other,
 they had different accents and would be recognized as strangers

Evidence for Inheritance

- Marler and Peters conducted a simple experiment to make the point
- They took two closely related species of sparrow, the swamp sparrow and the song sparrow, and raised them in isolation, while exposed to tape recorded birdsongs from both species
- Results showed that each species learned to produce the song of its own species, even though each group was equally exposed to the auditory input from both species
- This suggests that there is some genetic hardwiring that guides learning toward the birds' own species-specific songs
- Birds usually hatch in the spring or early summer and are only exposed to the specific bird song from the father until the end of summer
- The young bird then gets no more exposure to the song and has to remember it for nearly a year, when they must reproduce the song in the following spring with accuracy
- The ability to retain something as complex as a song for such a duration suggests a rather special form of learning
- Development of Bird Song
 - Birds start out by producing subsong, which consists of vocalizations that don't sound like the final adult song
 - It's "baby talk" for birds
 - Gradually, the bird enters a period of plastic song, when the song is now recognizable as belonging to its own species
 - However, it may still not have all of the elements of the adult song and the song itself is still changing
 - Shortly after plastic song, the bird enters the final stage of crystallized song, when the song is perfect and the bird makes no further changes to the song for the rest of its life

Template Model of Song Learning

- According to the template model, songbirds inherit a rough template for their species-specific song
- At some point after hatching, they have a sensitive period for learning their own song from the sounds around them, which refines their template in memory
- Before their song crystallizes, they practice their song, trying to match the sounds they produce to their refined template
- Here, they may use auditory feedback or social cues from others

 Another example of how inherited and learned components interact during development to produce the final bird song

<u>Infant Music Perception</u>

- There is a lot of evidence that infants are quite capable of perceiving many of the intricate details of music
- Ex. 2-3 month old infants notice changes in tempo and also recognize changes in timing between successive notes
- By 7 months, infants can recognize a specific Mozart sonata among other pieces of music and remember it over a two-week period
- They can also identify when a musical passage has been tampered with to create a less pleasing sound
- Dr. Trainor
 - Studying whether multisensory interactions between music and movement are also present in young infants
 - Investigating not only whether musical rhythms make us move, but whether the way we move affects how we interpret or perceive auditory rhythms
 - They created am ambiguous rhythm pattern to investigate this
 - It is 6 beats long, but has no accented beats
 - o People interpret this rhythm in one of two main ways
 - One way is as a march with accents every second beat
 - The other way is as a waltz with accents every third beat
 - They reasoned that if movement affects what we perceive, then if we bounce some infants on every second beat, but bounce some infants on every third beat while they listen to this ambiguous rhythm pattern, maybe the movement will influence whether they perceive it as a march or a waltz
 - After the bouncing experience, they wanted to test whether infants thought that the ambiguous rhythm they heard was a march or a waltz
 - One of the challenges in working with infants is that they can't ask them in words what they heard
 - So they employed the preferential looking method
 - The infant sat between two speakers and they flashed a light on one side of the infant
 - When the infant looked at the light, it remained on, illuminating a toy and one version of the rhythm pattern played
 - The infant controlled how long they listened to the pattern because when they looked away from the light and toy, the light went out and the rhythm pattern stopped
 - For the next trial, they flashed a light on the other side and this time the infant got to listen to the other version of the rhythm pattern
 - Again, they got to hear the version for as long as they looked at the light and toy

- By repeating a series of these trials, they were able to determine which version
 of the rhythm pattern infants spend longer listening to, that is, which pattern
 they preferred
- They found that they preferred listening to the rhythm pattern that matched how they were bounced
- They have shown that even in young infants, there are multi-sensory contributions to the perception of music and that they way we move affects what we hear

Musical Training and the Brain

The Mozart Effect

- Rauscher and Shaw found almost a 10-point increase in the spatial reasoning score of college students after listening to 15 minutes of Mozart's music
- This controversial finding is still being challenged today and has sparked a lot of research that has looked at the effect musical training has on the brain
- Studies have found that musical training is related to measureable changes in the brain
- Ex. Various studies have reported that in the brains of musically trained students more auditory cortex is devoted to processing musical scales and more somatosensory cortex is devoted to processing input instruments
- Some studies have also reported that a larger planum temporale (important for processing complex sounds), a larger Broca's area (involved in language processing) and a larger Heschl's gyrus (contains primary auditory cortex)
- Evidence for Musical Brain
 - In one study, violinists, pianists and control subjects with no formal musical training were presented with different test tones from a violin, piano or pure tones
 - The brains of musicians responded very different to the test tones compared to those of non-musicians, reflecting plastic changes made over years of formal training
 - However, in an interesting twist, the responses of non-musicians could be made more similar to the performance of musicians if they were given some pitch discrimination training before the experiment began
 - This suggests that the adult brain retains plasticity and is capable of change in a way that is related to the amount of musical training
 - Another study by Pantev et al. found that the cortical representations of musicians are especially tuned to the sound of their specific instrument
 - These findings provide strong evidence that brain differences between musicians and non-musicians are more likely due to their different experiences with music, rather than a specific genetic predisposition to music
 - It is more likely that existing connections become better at transmitting information in the brain's physiology
 - These stronger connections are very rapid, perhaps within hours

Audition and Music Live Lecture

- Sound Sensations
 - Similarities to Vision
 - Except that frequency is inverse of wavelength
 - Sound Waves
 - Longitudinal waves
 - Ex. Speakers
 - Move in and out
 - When they move out, compress air molecules in front of it (compression)
 - When they move in, allow air molecules expand (rarefaction)
 - o Frequency is interpreted as pitch
 - When a tuba plays a sound at 100 Hz, it also plays it at 200, 300, 400, 500
 Hz
 - But auditory processing allows us to put it all together to hear one pitch
 - Even if we take away the 100 Hz, so all we can hear is 200, 300, 400, 500
 Hz, the sound we hear is still 100 Hz
 - Called the Case of the missing fundamental
 - Level of processing that develops very early
 - Amplitude is measure of loudness
 - Timbre is measure of complexity/purity
 - A mixture if the fundamentals and harmonics make up the timbre
 - Dependent on relative loudness of harmonics to fundamental
 - What makes two people's voices sound different
 - Loudness
 - Logarithmic scale (decibels)
 - 70 dB to 80 dB is not ten times as loud, it's twice as loud
- The Ear
 - Human Ear
 - Amplification
 - In middle ear
 - Middle ear composed of three bones (hammer, anvil, stirrup)
 - Takes sound waves from tympanic membrane and amplifies it so that when it reaches the oval window, sound is much bigger
 - Hair cells need to move very little in order to send signals to brain
 - Hearing your own voice
 - Why don't we go deaf hearing our own voice
 - When we speak, muscles attached to the bones stop the middle ear bones from moving so we don't amplify the signal coming from our own mouth
 - Stapes and stapedius muscle
 - Where do they hear
 - Some insects have hearing organs on abdomen (grasshopper)

- Cockroach has sensory organs on anus
- Noise Induced Hearing Loss
 - Caused by destruction of hair cells in inner ear
 - Lose ability to turn physical signals into impulse signals
 - Musicians are particularly impacted by noise induced hearing loss
 - For musicians such as violinists, tend to show hearing loss related to their instrument
 - Tend to have left ear hearing loss because closest to instrument and hearing loss on range of their instrument

Music

- Finger-tapping
 - If you ask someone to tap along with rhythm, people actually tap before they hear the noise
- o Peter Janata
 - The more we like a piece of music, the more we move along with it
 - The more we move along with it, the more pleasurable we feel about it
 - Stimulating reward pathways in brain and releasing dopamine
- o Rhythm Perception in DJs
 - Blue line is when DJs are allowed to move to rhythm
 - Red line is when they are asked to sit perfectly still
 - Results show that the more offset the beat is, the more accurate DJs can notice it
 - Also, DJs who were allowed to move were more accurate
 - Next result showed that DJs are outperforming control subjects
- o Amusia
 - An inability to discriminate pitch
 - Also known as tone deafness
 - Musicians tend to be better at spatial tasks
 - So amusics are worse at spatial tasks
- Williams Syndrome
 - Causes distinct facial morphings
 - High cheekbones, upturned noses
 - Causes severe cognitive delays
 - These people tend to be drawn to music and become very proficient at it
 - Ex. Gloria Lenhoff
 - IQ is 54
 - World famous opera singer
- Music and Emotion
 - Acquired Amusia and Emotion
 - One person in Montreal acquired Amusia because of leaking capillary in brain
 - No longer to sing songs she used to know
 - But could still distinguish between "happy" and "sad" songs

Lecture 16: Hunger and the Chemical Senses

March 26, 2011

<u>Introduction to Hunger and Satiety</u>

- Seeking out food and drink is a fundamental goal-directed behaviour because your moving body needs regular nourishment to function optimally
- During most of the human evolutionary past, food sources were scarce and behaviours were motivated by the constant need to obtain energy and nutrients essential for survival
- Feeding behaviours may be motivated by hunger and satiety signals, but are guided to a large extent by the interaction of the senses of taste and smell

Hunger and Satiety

- Overnight, you have fasted for the longest period of your daily cycle
- Many signals and complex interactions between the brain and digestive system that drive your feelings of hunger to consume food and drink and satiety signals which lead you to stop consumption
- Glucose and Glycogen Balance
 - When you are fasting, one of the main reasons you feel hungry is low blood glucose levels
 - o Glucose is important for keeping your body's functions operating and is the preferred source of energy for the brain
 - Unlike other organs and tissues, the brain cannot use fat energy stores for fuel, which makes regulating glucose levels a top priority
 - You are very sensitive to the level of glucose in your blood and this directly relates to your feelings of hunger
 - To keep your brain constantly supplied with energy, your body can store glucose in the form of glycogen, which can be released in between meals
 - Some glycogen is stored in the muscles, but the main supply is in your liver where it can be readily converted back into glucose when your circulating blood glucose levels are low
 - This glucose-glycogen balance is mediated to a large degree by the liver and a pancreatic hormone called insulin
 - After a meal, the pancreas secretes insulin to promote the uptake of glucose by cells in your body for immediate use, but also to stimulate storage of excess glucose as glycogen
 - o As time goes by, your blood glucose levels will correspondingly begin to dip
 - When these levels get low enough, the liver begins to breakdown its stored glycogen into glucose, releasing it back into circulation
 - In this way, liver and pancreas help to buffer extreme swings in blood glucose levels

- As this cycle continues and the time since your feast increases, your glycogen reserves in the liver will decrease and a status signal is sent to the brain
- At some point, the glucose and glycogen levels get too low and you will feel hungry
- In the time between a meal and the next morning, your glycogen stores are being depleted
- Eating a bowl of cereal increases your blood glucose levels for now and helps to replenish your glycogen stores for later

NPY

- Another hunger cue you were likely to experience this morning came from Neuropeptide Y (NPY)
- High levels of NPY activity in the hypothalamus are associated with increased appetite and food seeking behaviours (ex. heading to the kitchen)
- NPY affects feeding behaviour similarly in fish, reptiles, birds and other nonhuman mammals

Satiety and the Liver

- Just as your liver and send signals to your brain to trigger hunger, it can also send signals to the brain that trigger satiety
- Ex. If you take a dog that is eating and you inject glucose into a vein that connects directly to the liver, the dog will stop eating
- However, when the same glucose dose is injected into a different vein, such as one that does not connect to the liver, the dog will continue eating
- The liver monitors glycogen stores and blood sugar levels
- Low blood glucose and low glycogen levels serve as signals of hunger, while high glucose levels and high glycogen stores are signals of satiety

CCK and Meal Duration

- The small intestine also has a role to play in feelings of satiety
- As your breakfast moves from your stomach to your gut, the small intestine produces Cholecystokinin (CCK), a hormone that is responsible for feelings of satiety or fullness after a meal
- o Receptors in the brain detect CCK, which serves as a signal to stop eating
- Scientists have found that if you inject individuals with CCK, they report feeling satiated sooner
- In another study, researchers administered CCK to rats leading to shorter than average meal durations compared to controls
- Interestingly, these rats who received CCK ate more total meals per day than the controls and so the total daily food intake was actually the same for both groups
- This shows that CCK is a short-term satiety signal
- CCK appears to regulate short-term feeding behaviours, but not long-term energy consumption

Long-Term Weight Regulation

- Animals need to consider more than their current nutritional needs, they also need to store some excess energy for use in times when food is scarce
- Whenever possible, long-term energy storage takes place in the form of fat (adipose tissue)
- Both short-term and long-term mechanisms interact to regulate overall energy balance and body-weight
- Adipose Energy Stores
 - Why do animals store most of their excess energy in the form of fat instead of storing it all as glycogen, which is a quickly transferable source of energy
 - For one thing, fat has more than twice the energy that carbohydrates like glycogen have
 - For every 1 gram of fat, there are 9 units of kilocalories, while carbohydrates only contain 4 kilocalories per gram
 - o Unlike glycogen, fat is found in virtually all parts of the body
 - For the long term, fat is a better choice for storing more energy
 - But fat or adipose tissue is more than just a passive energy storehouse
 - It is an active component of your regulatory physiology and was fairly recently classified as an endocrine organ as well

Leptin

- Adipose tissue secretes a hormone called leptin, which is involved in long-term energy balance and correlated with fat mass
- When leptin levels rise, they act on receptors in the hypothalamus to reduce appetite and consequently, food consumption decreases
- Leptin production is controlled by the OB Gene
- In genetically altered knock-out mice lacking an OB Gene, leptin production stops
 - In this state, mice are missing a key hormonal signal to regulate appetite and become extremely obese
 - This condition can be reversed if mice are given regular injections of leptin, causing their eating behaviour and weight to return to normal
- These studies suggest that a contributing factor for obesity in humans may involve defective OB genes or receptors
- This inference is not supported in clinical findings however
- If you were to give an obese animal who has normal leptin levels additional leptin, there is no weight loss to return leptin levels to normal
- It appears that humans and other animals are capable of becoming leptin resistant
 - Beyond a certain point, leptin's ability to inhibit appetite is reduced
- For most of evolutionary history, access to calories was a limited resource for humans
- It is more than likely that the primary adaptive function of leptin was to serve as a n indicator of low energy stores, rather than as a signal to directly reduce food intake

- Low levels would signal to increase foraging effort or minimize activity in order to conserve energy
- Rarely would an individual have very high levels of leptin suffer from negative effects associated with excess adipose tissue

NPY

- Leptin acts to inhibit the actions of NPY
- NPY mediated increase in appetite is prevented by leptin, leading to decreased appetite and energy consumption
- o Together, leptin and NPY interact to regulate weight to optimal levels
- Evidence in rats suggests that NPYergic neurons can specifically affect rewarddriven feeding for high calorie foods such as sucrose
- In one series of experiments, NPY was injected directly into the brain of rats who were satiated by previous food consumption
- This revealed interesting results
 - First, there was an increase in the intake of sucrose
 - Second, rats will begin to work harder for a cue associated with sucrose
 - Third, rats also increased the consumption of saccharin (similar taste to sucrose, but without calories)
 - Finally, these rats will also preferentially choose a diet of carbohydrates over protein or fat
- This line of research suggests that NPY action promotes unconditional and conditional behaviours that specifically lead to increased carbohydrate consumption
- Rats that showed a higher baseline preference for carbohydrates showed the greatest preference for carbohydrates following the NPY injection
- These studies suggest an interesting implication for genetic predisposition toward carbohydrate consumption

- Endogenous Opioids

- Another hypothesis on overeating
- Endogenous opioids have morphine-like actions within the body and also contribute to palatability and reward-driven feeding
- Blocking the opioid receptors with a drug called naloxone reduces intake of rewarding foods such as saccharin and sucrose
- Consistent with the hypothesis, knock-in mice which have been genetically modified to lack the opioid receptor show lower preference for saccharin than do control mice
- Some researchers speculate that overeating in some people may be reflective of a maladaptive opioid-mediated reward-driven feeding
- Energy balance and body weight regulation by the hormones and mechanisms seems to be asymmetric
- The body defends itself against weight loss more strongly than it does against weight gain
- This asymmetry can be understood from an evolutionary perspective, where calories and nutrition were less certain

Summary

Molecule/Hormone	Source	Function
Glucose	Food, glycogen	Primary fuel for brain
Glycogen	Liver, muscles	Stored form of glucose
Insulin	Pancreas	Stimulates glucose metabolism and glycogen synthesis
CCK	Small intestine	Responsible for short-term satiation, terminating meals
NPY	Hypothalamus	Stimulates appetite, food consumption
Leptin	Adipose	High levels inhibit NPY, appetite
		Low levels promote feeding, energy conservation

<u>Taste Preferences and Food Selection</u>

- Through the course of evolution, foods that are bitter or sour are associated with flavours not commonly enjoyed because they are often indicative of toxins or noxious foods
- Special acquired tastes for bitter and sour must be learned through experience
- Foods that are sweet, salty or savoury are associated with flavours that are craved because they are more often indicative of foods that are safe, nutritious and rich in energy such as fruits and protein
- Individuals who could detect these taste differences had a survival advantage as they were better able to avoid dangerous foods, while accessing reliably sources of energy for good health
- Two lines of evidence suggest that certain taste responses are universal and basic to human behaviour
 - o Particular tastes will elicit the same reaction in infants from all over the world
 - Fully healthy infants as well as those with extensive brain damage, exhibit the same characteristic responses to tastes
 - Experiment
 - Infant subjects are given a neutral solution to taste
 - When given a sweet or salty solution infants show characteristic acceptance responses and smile

- When given bitter or sour solutions infants show a characteristic rejection response and are altogether unhappy
- Interestingly, these same responses are mirrored by the infant without a cortex and by the infant with hydrocephalus, suggesting that these responses are governed by lower regions of the brain
- The perception and response to particular tastes are adaptive mechanisms, controlled by older regions of the brain that enable you to discriminate foods that are safe and nutritious from foods that are potentially spoiled or toxic
- Taste preference is also shaped by cultural influences which presumably were shaped by local food availability
- In addition to the universal taste preferences that infants display, the foods that you enjoy are learned by experience
- Taste Sensitivity
 - One reason for individual differences in taste may have to do with the number of taste buds on your tongue
 - Highly sensitive tasters have more taste buds than the average person
 - Generally, women tend to be more sensitive to some sweet and bitter tastes than men
 - This increases even more so during the first trimester of pregnancy, corresponding to the period during which the fetus is most sensitive to toxins and harmful substances
 - Enhanced taste sensitivity would have allowed for better nutrition and toxin avoidance during pregnancy and beyond
- Taste Preferences
 - Preferences for salty, sweet and rich foods can be detrimental in a fast food nation
 - Taste preferences have yet to adapt evolutionarily

Introduction to Chemical Senses

- While visual, auditory and tactile sensory systems deal with physical stimuli like light, sound waves and touch, your sense of taste and smell are unique in their ability to detect chemical stimuli
- The chemical senses of taste and smell depend on receptors that can interact with molecules of food particles to provide you with the pleasurable experience of eating
- Together, taste and smell influence your perception of flavour
- Ex. When you're sick, food tastes bland
 - o It's because of the clogged sinuses and impaired sense of smell

How Taste is Processed in the Brain

- Chewing on an apple grinds the whole fruit pieces into a pulp of saliva and molecules of water, sugar and carbohydrates
- Taste buds containing taste receptor cells detect and respond to the dissolved apple molecules

- Each taste bud has anywhere from 50 to 150 taste receptor cells
- About two thirds of your taste buds are located on your tongue, with the remaining on the soft palate and the opening of the throat
- 5 Taste Receptor Cell Types
 - You can discern 5 different tastes: sweet, salty, bitter, sour and umami or "savoury"
 - Each of these tastes gives you information about the nutritional quality and content of foods
 - Sweet signifies energy-rich foods like fruits and their sugars
 - o The ability to taste salt helps you to identify and ingest essential electrolytes
 - Sour and bitter tastes warn you of harmful, spoiled or potentially poisonous foods
 - Umami taste detects the amino acids glutamate and aspartate
 - The old view that different regions of the tongue respond uniquely to one particular taste has been modified
 - In fact, all areas of the tongue are able to detect the 5 basic tastes
 - Specifically, each taste bud contains some proportion of all 5 taste receptors
 - From each of these taste receptor cells, afferent neurons send signals to the brain for processing to create your perception of taste
- After a taste receptor cell fires an action potential, the information is sent from the main gustatory nerve to the brainstem, where it diverges into two main pathways
 - One pathway travels through the medulla to the thalamus, from which the information is sent to both the primary somatosensory cortex and the gustatory cortex
 - In the primary somatosensory cortex, the feel and texture of food in your mouth is processed along with where on the tongue the taste is sensed
 - Regulates sense of food texture
 - Gustatory cortex is primary taste area of brain with sets of neurons that respond to each of the 5 basic tastes
 - Passes information to orbital cortex, which is near region where olfactory information enters olfactory cortex
 - Orbital cortex is where smell and taste information is combined to result in flavour
 - Second pathway goes on to pons and then to hypothalamus and amygdala
 - Thought to be involved in other aspects of feeding behaviour, such as satiety, which complements the actions of the CCK mechanism of satiety
- The Nose and Taste
 - If you plug your nose and eat two jellybeans, you can taste the sweetness, but you can't differentiate between the flavours of the jellybeans
 - Molecules from the two jellybeans would bind with receptor on the taste receptor cells that detect sweetness
 - The subtle differences between the 2 jellybeans are not perceived by the taste buds and instead are broadly categorized as the taste of "sweet"

- The more sophisticated ability to sense flavour comes from an interaction with taste and smell that occurs in the nasal pharynx at the back of the throat
- It is here that the subtleness of the flavours comes out
- When your nose is blocked, either by pinching it or by stuffed sinuses from a cold, the contribution of smell is reduced
- You're only left with the taste of food and deprived of its flavour

How Smell is Processed in the Brain

- Humans often have difficulty naming all the different smells that can be detected
- Of the five senses, your sense of smell is unique in that it has a direct link to the cortex, without being routed through the thalamus first (suggests olfaction is a very old perceptual system)
- This may be because smell is an important system for alerting you to significant events in the environment
- Airborne molecules that you perceive by smell can communicate information over extremely long distances, which can have advantage for finding food and mates or avoiding potential predators
- Smell signals are transmitted to higher regions of the brain (pyriform cortex)
- Olfactory Receptor Cells
 - As you breathe, the chemical molecules enter the nasal cavity and dissolve in the mucus of your nose
 - This allows the chemical molecules to interact with the olfactory cilia, tiny hair-like structures that cover the receptor surface of the nasal cavity, or the olfactory epithelium
 - o Each olfactory receptor cell receives input from between 10-20 cilia
 - Olfactory receptor cells respond to a range of stimuli
 - A specific smell does not activate a unique receptor cell, but rather activates a unique pattern of firing across receptors in the olfactory bulb
 - Once an action potential is triggered in an olfactory receptor cell, it travels down the axon and synapses with cells in the olfactory bulb of the brain
 - Here, the cell form synapses with dendrites of other cells called glomeruli, each of which receives input from thousands of olfactory receptor cells
 - The signals from the glomeruli are transmitted to higher regions of the brain (pyriform cortex)
- Glomeruli and Olfactory Cortices
 - The output from glomeruli is sent to different areas of the brain, most of which goes to the hypothalamus and areas of the limbic system that deal with basic drives and emotions
 - Some of the output also goes to the primary olfactory cortex in the temporal lobe, as well as the secondary olfactory cortex in the frontal lobe

Hunger and the Chemical Senses Live Lecture

Biological factors (1XX3)

- Study of eating behaviours in a group of lab rats who had access to different diets
 - Neuroscience
 - One group had standard rat food
 - Another group was placed in a "buffet bar", which contained a lot of unhealthy foods like frosting, bacon (23 hours a day)
 - Become obese and addicted to the human food
 - Even when researchers paired the food with electric shock, rats would still eat it
 - Changes in rat's brain was analogous to a rat addicted to cocaine
 - Third group had more limited access to this buffet bar (1 hour)
 - Development
 - There are genetic/environmental factors to underweight/overweight
 - Evolution
 - Access to calories has been a limited resource
 - A struggle to just maintain a positive energy balance
 - But now, almost unlimited access to calories, but inherent taste preferences still remain
 - About 10,000 years ago, agriculture started so humans didn't have to worry about their next meal
 - Portion sizes have changed drastically as well, over the last 20 years

- 1X03

- The Awful Popcorn Study
 - People were given free buckets of popcorn that was 5 days old (stale, tasted bad)
 - One group of subjects got medium popcorn and another had extra large
 - Later, everyone rated that the popcorn was terrible, but the people who had extra large ate 53% more popcorn
- The Bottomless Soup Study
 - Four students had a bowl of soup and told to eat as much as you want and told that they were going to discuss some issue
 - For two subjects, there was a normal bowl of soup and for the other two subjects, they had bottomless soup (tube under table refilling bowl)
 - Later, subjects were asked how much soup they ate and how full were they
 - The latter two ate 73% more soup, but all subjects reported same amount of fullness
- Social Influences
 - Subject comes in and sees a box of cookies
 - Confederate in the same room and either eats 0,1,2,3 cookies

- Subjects follow the confederate
- Therefore, social considerations affect how much you eat
- Understanding Complex Human Behaviour
 - Attractiveness and Body Size
 - Women choose a smaller body size when asked what they think is attractive and what is ideal
 - But men think attractive women is bigger than what women think
 - Dating Sites
 - Self-presentation goals
 - Appear attractive
 - Appear honest
 - Gendered goals
 - Females → prefer taller men
 - Men → prefer slender, younger women
 - What people actually do
 - Lie frequently
 - Lie subtly
 - Females → lie about age and weight
 - Males → lie about height
 - General results
 - People are usually honest about age
 - Height
 - o Females are generally honest
 - Men are generally shorter than they say
 - Weight
 - Men are generally honest
 - Women generally heavier than they say
- Multisensory Integration
 - Hollow face experiment
 - When you see the hollow face, your brain is thinking it sees two eyes, a nose, a mouth
 - Brain thinks that it must be a normal face
 - "McGurg" Effect
 - When they see the mouth moving, they hear "Da da"
 - What he's actually saying is "Ba ba"
 - But because there is a conflict between mouth movements and what you hear, you think he's saying "Ba ba"
- Multisensory Integration and Synaesthesia
 - Colour graphine synaesthesia
 - People see letters and numbers with corresponding colours
 - Time-space synaesthesia
 - Can see a "calendar" around them and tell what day a specific date is
 - Names and Flavours
 - Some people have synaesthesia between auditory and taste

- Ex. When she hears "Amanda" she tastes unripe banana
- o Defining traits of synaesthesia
 - Involuntary and automatic
 - Consistent
 - Highly memorable
 - Laden with affect
 - Spatially extended
- o Neural development
 - Idea with synaesthesia is that we are all born with these effects, but through pruning, we lose those neural connections