Overview of Lecture: Behavioral Ecology

Read: Text ch 51

Bullet Points:
- behavior
- behaviorism, psychology
- ethology, behavioral ecology
- genes - "nature"
- environment - "nurture"
- GxE interactions
- cooperation
- mutualism; kinship
- reciprocity; manipulation
- social games
- social intelligence

"I've tried a lot of life strategies, and being completely self-serving works best for me."
We can think of **behavior** as **what an animal does and how it does it**, ... including nonmotor (latent) components of behavior such as personality, learning and memory. 

{changes of “state” that influence future behavior - like hunger, fear, knowledge, skill …

If we consider the development **{ontogeny}** of any behavioral trait, we find a series of environmental {“nurture”} and genetic {“nature”} influences that can ‘interact’ as well as ‘add up’ to influence the phenotype-trait.

**Behavioral ecology** studies how behavior is controlled and how it develops, **{ontogeny}** evolves, **{phylogeny}**. 

Natural selection favors behavior that enhances survival and reproductive success.

The debate about biological evolution and human culture remains heated. The spectrum of possible human social behaviors may be circumscribed by our genetic potential, but this is very different from saying that genes are rigid determinants of behavior. This is at the core of the debate about **sociobiology**.
Parsing the Genetics of Behavior

Science took a look at a few genes that have been in the news, with an eye toward understanding just what we do and can know about genes behind individual variation in temperament and personality. ... nailing down the genes that underlie our personalities has proven exceedingly difficult.

All we really know so far is that behavioral genes are not solo players;

For example, the same gene may influence propensities toward depression, overeating, and impulsive behavior, making it difficult to tease out underlying mechanisms.

Each gene comes in a variety of flavors, or alleles, with varying degrees of sequence variation.

One allele might contribute to a winning personality whereas another may raise the risk of mental illness.

Environment plays a strong hand, bringing out, neutralizing, or even negating a gene's influence.

And genes interact with one another in unpredictable ways.
In a prospective-longitudinal study of a representative birth cohort, we tested why stressful experiences lead to depression in some people but not in others. A functional polymorphism in the promoter region of the serotonin transporter (5-HTT) gene was found to moderate the influence of stressful life events on depression.

Individuals with one or two copies of the short allele of the 5-HTT promoter polymorphism exhibited more depressive symptoms, diagnosable depression, and suicidality in relation to stressful life events than individuals homozygous for the long allele.

This epidemiological study thus provides evidence of a **gene-by-environment interaction**, in which an individual's response to environmental insults is moderated by his or her genetic makeup.

**Fig. 2.** Results of regression analysis estimating the association between childhood maltreatment (between ages 3 and 11 years) and adult depression (ages 18 to 26), as a function of 5-HTT genotype.

... the **G x E interaction** ... showed that childhood stress predicted adult depression only among individuals carrying an **s allele**:

{depression “emerges” from an interaction}
Behaviorism originated with the work of John B. Watson, an American psychologist ... not concerned with the mind ... only with behavior. In this way, men could be studied objectively, like rats ...

Watson's work was based on the experiments of Ivan Pavlov ...
... he rang a bell as he fed some dogs ...
Pavlov then rang the bell without bringing food, but the dogs still salivated. They had been *classically* "conditioned" to salivate at the sound of a bell.

E. L. Thorndike ...

and is more likely to occur if its consequences are satisfying.

B.F. Skinner, ... developed
the theory of "operant conditioning"
{and ‘the Skinner box’}

Three fundamental ideas in behaviorism, that justified the arbitrary use of rats & pigeons as models of humans were that

1. humans (& other animals) are born with minds
2. we are conditioned by experiences written on our blank slates, and
3. the conditioning process
Comparative Psychology & Ethology

Various animals mature and they come with different programs to attend to and learn different things at different ‘critical’ times and places.

‘Biological constraints’ include … a pigeon will learn to peck a button to get food but it cannot be trained to …. however, it can learn easily to hop on a lever to stop an electric shock …

Animals are especially prepared to learn taste aversions, associating nausea with stimuli associated with novel foods. John Garcia showed how preprogrammed rats are: they quickly associate taste w/ x-ray induced nausea, but light & sound w/ electric shock, but

Ethology (Lorenz, Tinbergen & von Frisch) began treating behaviors (& learning) as adaptive traits, like other bits of phenotype - wings, guts, eyes etc. … that have phylogeny, ontogeny, proximate mechanism & ultimate function.

Imprinting: learning that is limited to a ‘sensitive period’ in an animal’s life; generally irreversible.
If we consider the development \{**ontogeny**\} of any behavioral trait, we find a series of environmental \{**“nurture”**\} and genetic \{**“nature”**\} influences.

A simple path model of the evolution of behavior:
(Boyd & Richardson1985)

Other complications include ‘**maternal effects**’ ex: womb environment and gene-environment correlations (parents influence social env)

- It is very difficult to tease apart the effects of genes, esp w/o carefully controlled experiments.

- Even w/ experiments, difficult if genes & env ‘interact’
  - diff genotypes react to diff env’s differently: (effects not additive)
NEWS OF THE WEEK
Michael Balter, Science 16 July 2010: Vol. 329. no. 5989, pp. 266 – 267
Probing Culture's Secrets, From Capuchins to Children

Derek Lyons presented new data on a phenomenon in young children that he and others think may be the key to humans' faithful transmission of complex culture: or the tendency to copy the actions of an adult even when.

No other animal has been shown to copy in this way. ... a landmark 2005 study demonstrated that when young chimpanzees and children are shown how to retrieve a reward from a box using a series of both relevant and irrelevant steps, the chimps skipped the unnecessary steps, whereas children tended to imitate everything.

Lyons and his co-workers reported in 2007 ... children were shown how to retrieve toy turtles from transparent plastic containers using irrelevant steps such as tapping the container with a feather and relevant steps such as opening the container's door.

The children continued to overimitate even when they were led to believe that the experiment was over or when they were explicitly told to avoid "silly" extra steps. The only way to avoid overimitation, Lyons found, was to convey that...

Why do children do this?
In Voles, a Little Extra DNA Makes for Faithful Mates
Elizabeth Pennisi Science 10 June 2005:Vol. 308. p. 1533

Prairie voles are renowned for being faithful mates ...
On page 1630, E Hammock & L Young report that...the amount of junk DNA affects how male voles treat their mates.

Prairie voles have longer microsatellites near the gene encoding...and as a result they make more of the receptor than do their more promiscuous cousins - meadow voles. {between species}

Last year, Young's team ... caused meadow voles to emulate the faithful ways of prairie voles

Now, Young & Hammock have found that...influence expression of the gene and overall behavior {within species}.

They paired and bred voles with long microsatellites and found that the resulting males spend more time licking and grooming their pups and more time with their partners than did males with short microsatellites.

Genetic variation in the vasopressin receptor 1a gene (AVPR1A)
H Walum et al. 2008 PNAS 2008 105:14153-14156

{ genotype your boyfriend }
It is difficult to tease apart effects of genes & env., esp if genes & env ‘interact.’


Wild chimpanzees … fish for termites with flexible tools they make out of vegetation, …

We find distinct sex-based differences, akin to those found in human children, in the way in which young chimpanzees develop their termite-fishing skills.

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**Fig 1** Sex differences in wild chimpanzees learning termite-fishing.

*a* % time at the termite mound spent termite-fishing by young chimps.

*b* Daughters' techniques (top) correlate strongly with their mothers'.


\[\text{lines have } \pm \text{ slope } \sim 1\]

Females spent more time than males watching their mothers fish for termites

**sons' techniques (bottom)** do not correlate with their mothers'


\[\text{lines have flat slope } \sim 0\]

Males spent more time playing at the termite mound

A similar disparity in the ability {?} of young males & females to learn skills has been demonstrated in human children.

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**Girl chimps learn faster than boys**

Daughters pick up their mother's skills, while sons play rough and tumble.

15 April 2004

**MICHAEL HOPKIN**

Young female chimpanzees are better students than males, at least when it comes to catching termites, according to a study of wild chimps in Tanzania's Gombe National Park. While daughters watch their mothers closely, the boys spend more time monkeying around.

**boys learning?**

The discovery mirrors differences in the learning abilities of human children, says the research team behind the study. Girls tend to catch on faster than boys when learning skills such as writing and drawing, they say.

These manual tasks are not dissimilar to the chimps' technique of using a stick to fish for termites, argues Elizabeth Lonsdorf, now at Lincoln Park Zoo in Chicago. Successfully extracting termites from their nest requires a dextrous turn of hand, she says.
Sex differences in children's toy preferences are thought by many to arise from gender socialization. {nurture}

However, evidence from patients with endocrine disorders suggests that biological factors during early development (e.g., levels of androgens) are influential. In this study, we found that vervet monkeys (Cercopithecus aethiops sabaeus)

For each trial, six toys were placed in the group cage, one at a time, in a random order ... for 5 min. These toys were categorized as "masculine" toys, "feminine" toys, or "neutral" toys on the basis of evidence that boys are more interested than girls in balls and cars (the "masculine" toy set), girls are more interested than boys in dolls and pots (the "feminine" toy set), and boys and girls are approximately equally interested in books and stuffed animals (the "neutral" toy set). Videotapes were coded for the duration of contact and approach to each of the toys. Percent contact scores equaled contact with each individual toy divided by total contact with any of the six toys × 100.
The percent of contact time with toys typically preferred by boys (a car and a ball) was greater in male vervets (n=33) than in female vervets (n=30) (P<.05), the percent of contact time with toys typically preferred by girls (a doll and a pot) was greater in female vervets than in male vervets (P<.01).

... contact time with toys preferred equally by boys and girls (a picture book and a stuffed dog) was comparable in male and female vervets.

The results suggest that sexually differentiated object preferences arose early in human evolution, prior to the emergence of a distinct hominid lineage.

{gene-environment correlation: genes choose env?}
Darwin, C. R. 1872.  
_The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life._  
London: John Murray. 6th edition;  

CHAPTER VI.  
DIFFICULTIES OF THE THEORY.  pg 162  

Natural selection will never produce in a being any structure {or behavior} more injurious than beneficial to that being ...

"I've tried a lot of life strategies, and being completely self-serving works best for me.”  

"Every man for himself!"
Some animals behave altruistically (unselfishly), in ways that appear to reduce the number of offspring they produce. **How could altruistic behavior have evolved by natural selection?**

**Altruism:** donor pays **cost**, receiver gets **benefit**.

How can altruism be an Evolutionary Stable Strategy & resist cheaters? **What ultimate benefits** compensate for the immediate **costs**?

Four kinds of compensating **benefits** - not mutually exclusive:

1. I’ll scratch your back and you scratch mine simultaneously. I’ll groom you if you let me eat the tasty tics I find. Ex: cooperative hunting & defense; market exchanges.

2. many more nieces & nephews, if slightly fewer sons & daughters. Haldane - Drown self to save 8 cousins (ancestral paternity)? **Hamilton’s rule:** **cost to self** < **benefit to kin** × r (coeff of relatedness)

3. **Direct:** If you scratch my back now, I’ll scratch yours later. **Indirect:** via third party observers; reputation, audience effect. Note that cash on delivery turns reciprocity into mutualism.

4. **Manipulation:** (a) just plain tricked (nest parasites) (b) offer that can’t be refused - bribes & punishment.
11 September 2003 JOANNE BAKER

Baboon dads defend offspring in fights.

**Picky paternal protection** ...

Baboon fathers rush to protect their kids in fights, a DNA study has revealed

Somehow the males spot their sons even in spats between the offspring of mothers both of which they have mated.

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True paternal care in a multi-male primate society.


Although male parental care is rare among mammals, adult males of many cercopithecine primate species provide care for infants and juveniles .... in the form of grooming, carrying, support in agonistic interactions, and protection against infanticide.

For these behaviours to be interpreted as true parental care, **males must selectively direct care towards their own offspring** and this care must result in fitness benefits ...

Here we show that **adult males** differentiate their offspring from unrelated juveniles and **selectively support their offspring in agonistic disputes**.

... this can be considered true parental care.
A market deal is a **mutualistic** exchange, and if there is delay, it is **reciprocity**.

The chimpanzee's service economy: **Food for grooming.**

... **reciprocal exchange** of social services
among chimpanzees ... **rests on cognitive abilities**
that allow current behavior to be

Food sharing in a captive colony of chimps was studied ...

The success rate of each adult, $A$,
to obtain food from another adult, $B$,
was compared w/ grooming interactions between $A$ & $B$
in the 2 hours prior to each food trial.

**The tendency of $B$ to share with $A$**

**The exchange was partner-specific** ...

Food possessors actively resisted approaches
by individuals who had not groomed them.

Reciprocity and interchange in the social relationships of wild male chimpanzees.
Watts DP. BEHAVIOUR 139: 343-370 Part 2-3 FEB-MAR 2002

Grooming and agonistic support: a meta-analysis of primate reciprocal altruism
Evolution: The good, the bad and the lonely

FRANZISKA MICHOR¹ AND MARTIN A. NOWAK²

The essence of cooperation is captured by the **public-goods game**. Each individual can decide whether or not to invest in a common pool. The common pool is increased by some amount and then equally distributed among all group members regardless of whether or not they made a contribution. The optimum outcome for the **group** occurs if everybody cooperates.

**But the temptation is to 'free ride':** those who don't contribute (defectors)

Self-interest is self-defeating! **("The Tragedy of the Commons")**
This social dilemma threatens public enterprises such as social security, conservation of environmental resources or group defence against external threats.
The well-known 'prisoner's dilemma' is a public-goods game for groups of two people.

Two players w/ two tactics: cooperate, defect

Mutual cooperation beats mutual defection: $2 > 1$
but there is a temptation to defect: $3 > 2$
& fear of being made a sucker: $0 < 1$

Cooperation is too risky in a single play

In repeated play w/ same partner:
is, on average, a winning strategy.
cooperative dilemmas, or “public goods” problems, involve situations in which individuals incur a cost to create a benefit for the group. Think of recycling, buying a hybrid car, valor in combat, voting, and donating blood. The dilemma arises from free-riders who enjoy the group benefits without paying the costs. 

Free-riders can profit and proliferate, leading to the eventual collapse of cooperation. On pg 108 of this issue, Gürerk et al. take an important step in understanding how self-sustaining cooperative institutions may have emerged. In their experiment, the “players” choose between two different “institutions.” In one, sanction free SFI players can contribute money to a group project. The sum of all contributions is augmented by a fixed percentage and then is divided equally among all players, regardless of their contributions. The other “sanctioning” institution SI is very similar, except players can pay to punish (reduce the payoff of) other players. Players could, choose their institution for the next interaction. Initially, most players picked the institution without sanctioning. After a few interactions...
The Competitive Advantage of Sanctioning Institutions


The uniqueness of human cooperation necessitates investigations that reach beyond the explanations of cooperative behavior of nonhuman animals. Profound empirical evidence shows that the possibility of

Would a sanctioning institution deliberately be adopted when individuals can choose between a sanctioning \{SI\} & sanction-free \{SFI\} institution?

We show experimentally that

in a competition with a sanction-free institution.

Despite initial aversion, the entire population migrates to the sanctioning institution and strongly cooperates, whereas the sanction-free society becomes fully depopulated.

The findings demonstrate the competitive advantage of sanctioning institutions and exemplify the emergence of social order driven by institutional selection.
The neural basis of altruistic punishment


Many people voluntarily incur costs to punish violations of social norms. Evolutionary models & empirical evidence indicate that altruistic punishment has been a decisive force in the evolution of human cooperation.

We used positron emission tomography to examine the neural basis for altruistic punishment of defectors in an economic exchange. 

\{a sequential Trust game \~loan & repayment w/ interest – or not\}

Fig. 2. (A) Activation in the caudate nucleus in conditions in which subjects indicated a strong desire to punish and could effectively do so relative to conditions in which there is no effective punishment or the desire to punish is absent.

Caudate activations in humans have been reported in studies that investigated reward processing; caudate activations have been observed with reinforcers such as cocaine and nicotine. Increases in monetary rewards \{received\} are positively correlated with caudate activations.

We also found increased blood flow in the thalamus \{when\} subjects expressed a strong desire to punish & could punish.

Our findings support the hypothesis that people derive satisfaction from punishing norm violations.

Fig. 3. (A) Positive correlation between caudate activation at coordinates [10, 26, –2] and the amount of money spent on punishment.

The punishment of defectors is an altruistic act in the \textbf{biological} sense because, it is costly for the punisher and induces the punished individual to defect less in future interactions with others. \{or expect future interactions w/ self=punisher?\}

However, our results suggest that it is not an altruistic act in the \textbf{psychological} sense. which requires that the act be driven by an altruistic motive.

that is not based on hedonic rewards. \{“I’m going to enjoy this!” – ult. function?\}
we use the “Trust Game”
and the Prisoner's Dilemma Game
to elicit norm-violating behavior.
We then allow participants in the second stage
to pay to inflict costs on individuals who have acted “untrustworthy”

Varying conditions of anonymity, we find that
the presence of an audience - even if only the experimenter –
causes an increase in moralistic punishment.
A new generation of experiments reveals that group-living animals have a surprising degree of intelligence.

In the past decade, the field of animal cognition has taken off, galvanized in part by a once-obscure idea that **the development of social skills drove the evolution of general intelligence**. The thinking is that the need to remember and track peers sharpened social animals' ability to do other useful cognitive tasks, such as remembering where and when particular fruit trees were ripe for the picking, or learning tool use from a particularly creative peer.

Of course, humans are masters of social intelligence. Researchers using rigorous tests in animals are finding numerous examples. Crows deceive each other, as do apes; hyenas keep track of social hierarchies. The new studies are providing provocative evidence that **perhaps humans aren't as special as we might like to think**.
Chimpanzees Are Rational Maximizers in an Ultimatum Game
K Jensen et al. 2007 Science 318: 107 - 109

Traditional models of economic decision-making assume that people are self-interested rational maximizers. Empirical research has demonstrated, however, that people will take into account the interests of others and are sensitive to norms of cooperation and fairness. In one of the most robust tests of this finding, the ultimatum game, \textit{human} individuals will reject a proposed division of a monetary windfall, at a cost to themselves, if they perceive it as unfair. Here we show that in an ultimatum game, humans' closest living relatives, chimpanzees \textit{are not sensitive to fairness.} ... unlike human subjects, chimps will accept any number of raisins

These results support the hypothesis that ... aversion to inequitable outcomes, which play key roles in human social organization, distinguish us from our closest living relatives.
Savage Chickens

by Doug Savage

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