bs148h 27 November 2007
Read: Text ch 51

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

We can think of behavior as what an animal does and how it does it, including nonmotor components of behavior such as including nonmotor components of behavior such as (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 (proximate cause) and how it develops, (ontogeny) evolves, (phylogeny) and contributes to survival & reproduction. 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.


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... "law of effect"... a given behavior is learned by trial-and-error, 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 that are blank slates, and
2. we are conditioned by experiences written on our blank slates, and
3. the conditioning process is a general process 'law of effect'... a given behavior is learned by trial-and-error, and is more likely to occur if its consequences are satisfying.

Comparative Psychology & Ethology

Various animals mature 'pre-programmed' instincts and they come 'programmed to learn' ('innate school marm' - Lorenz) 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 peck a button to avoid electric shocks;... 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 & Richardson 1985)

Other complications include 'maternal effects' ex: womb environment and parental influence on social env.

It is very difficult to tease apart the effects of genes, even with carefully controlled experiments. Even w/ experiments, difficult if genes & env 'interact' - diff genotypes react to diff env’s differently: (effects not additive)

In Voles, a Little Extra DNA Makes for Faithful Mates

Prairie voles are renowned for being faithful mates but some individuals are more faithful than others. On page 1630, E Hammock & L Young report that fidelity and other social behaviors in male prairie voles seem to depend on the length of a particular genetic sequence (regulatory?) DNA between their genes. In the mid-1990s, researchers discovered that DNA between their genes affects how male voles treat their mates.

Prairie voles have longer microsatellites near the gene encoding a receptor (V1aR) for the brain chemical vasopressin, and as a result they make more of the receptor than do their more promiscuous cousins - meadow voles. (between species)

Now, on page 1630, Young & Hammock have found that variations in V1aR-associated microsatellites among individual prairie voles influence expression of the gene and overall behavior. They paired and bred voles with long microsatellites and found that the resulting males (w/ ~19 more base pairs of 'junk') spend more time licking and grooming their pups than did males with short microsatellites.

In this study, we found that vervet monkeys (Cercopithecus aethiops sabaeus) are similar to those documented in children.


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. In this study, we found that vervet monkeys (Cercopithecus aethiops sabaeus) are similar to those documented in children.

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 books and stuffed animals (the "neutral" toy set), and boys and girls are approximately equally interested 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 dolls 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), while 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 prior to the emergence of a distinct hominid lineage. (gene-environment correlation: genes choose env?)


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 ...

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 costs?

Four kinds of compensating benefits - not mutually exclusive:

1. **Directly selfish**:
   - 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. **Indirectly selfish**: increases copies of genes in future through many more nieces & nephews, if slightly fewer own children.
   - Haldane - *Drown self to save 8 cousins* (ancestral paternity)?
   - Hamilton's rule: *cost to self < benefit to kin* × *r* (coefficient of relatedness)

3. **Utilitarian selfish but risky delay between cost and benefit**:
   - 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. **Tricked**:
   - (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.

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


... reciprocal exchange of social services among chimpanzees ... rests on cognitive abilities that allow current behavior to be contingent upon a history of interaction.

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 was if A had groomed B than if A had not done

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

Notice that the well-known 'prisoner's dilemma' is a public-goods game for groups of two people.

Two players w/ two tactics: cooperate, defect

The essence of cooperation is captured by the public-goods game:

Other players can work together to create a resource
The optimum outcome for the group occurs if everybody cooperates.

But the temptation is to those who don't contribute (defectors) always get a higher pay-off than cooperators who do contribute.

If everyone defects, however, no one will enjoy the public goods. 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.

Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back.

Altruistic food giving among genetically unrelated individuals is rare in nature. The few examples that exist suggest that when animals give food to unrelated others, they may do so on the basis of mutualistic or reciprocally altruistic relationships.
We present the results of four exp's designed to tease apart the factors mediating food giving among genetically unrelated cotton-top tamarins ...

In exp 1 we show that individuals give significantly more food to a trained 'stooge' who than to a 'stooge' who

Exp's 2-4 show that altruistic food giving is mediated by prior acts of altruistic food giving by a conspecific.
... tamarins give (less) food to unrelated others when the food received in the past represents

{both get food when partner pulls}
or when a human gives them food ...
{controls for ?}
By contrast, if one tamarin gives another food without obtaining any immediate benefit, then the recipient is more likely to give food in return.
... tamarins ... discriminate between altruistic and selfish actions, and

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Grooming and agonistic support: a meta-analysis of primate reciprocal altruism

The quest for cooperation is as old as evolution itself.
In the Origin of Species, Darwin noted that mutual cooperation beats mutual defection but increase that of others.
Yet cooperation is abundant in nature.

The standard explanations that have been developed for this include: {kin selection, group selection} and reciprocity. {+ mutualism}

The essence of cooperation is captured by the public-goods game:
Each individual can decide whether or not to invest some money 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 those who don't contribute (defectors)
always get a higher pay-off than cooperators who do contribute.

If everyone defects, however, no one will enjoy the public goods. Self-interest is self-defeating! ("The Tragedy of the Commons")

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Notice that 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: strategy is, on average, a winning strategy.
Discriminating cooperators and cheaters is important to stabilize reciprocity. Enhance memory for faces of cheaters.

Abstract:

... students were asked to rate the attractiveness of photo reproductions of Caucasian males. Each of the photo reproductions was presented with a fictional descriptive sentence giving information on the depicted individual's social status (high or low) and character (history of cheating, irrelevant information, or hist. of trustworthiness). A week later subjects again rated photos-half repeated and half new-this time, without descriptions. Subjects were asked to report which of the photos they remembered from the previous week. ... The predicted bias - that subjects would preferentially recognize faces initially presented as those who had been punished, the bias was mitigated when the face was presented as a person of high status; ... The results support the idea that we have evolved highly selective attention and storage mechanisms for processing social information, and that both character (cheating potential) and status are important features in the engagement of these mechanisms. 

The neural basis of altruistic punishment


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

The punishment of defectors is an altruistic act in the biological sense because it is costly for the punisher and induces the punished individual to defect less in future interactions with others. However, our results suggest that it is not an altruistic act in the psychological sense, which requires that the act be driven by an altruistic motive that is not based on hedonic rewards. 

The Competitive Advantage of Sanctioning Institutions

Gürerk et al., Science 7 April 2006: Vol. 312, no. 5770, pp. 108 - 111

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 sanctioning norm violators stabilizes human cooperation at a high level, whereas cooperation typically collapses in the absence of sanctioning possibilities. Would a sanctioning institution deliberately be adopted when individuals can choose between a sanctioning (SI) & sanction-free (SFI) institution? We show experimentally that a sanctioning institution is in a competition with a sanction-free institution. The findings demonstrate the competitive advantage of sanctioning institutions and exemplify the emergence of social order driven by institutional selection.
Audience effects on moralistic punishment
Kurzban R, DeScioli P, O'Brien E
EVOLUTION AND HUMAN BEHAVIOR 28 (2): 75-84 MAR 2007

We report two experiments in which we induce participants to commit moral violations and then present third parties with the opportunity to pay to punish wrongdoers.

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.

Chimpanzees Are Rational Maximizers in an Ultimatum Game

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, (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 ... are ... unlike human subjects, chimps will:

{Fair offer}

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.

Silk and her coauthors test the hypothesis that sociality among baboon females has a direct impact on their reproductive fitness.

... females who are significantly more social (indexed principally by the amount of time that others spend grooming them) have more than the average number of infants surviving to 12 months of age.

The sociality of adult female baboons is positively associated with infant survival and thus with overall fitness. In evolutionary terms, sociality is good for you.

Bergman et al. investigated whether adult female baboons are capable of evaluating the status of another individual in terms of both rank and kinship ...

... both human and animal subjects are more attentive to stimuli that are “surprising” ...

baboon subjects stared [at] hidden loudspeakers for significantly longer when played a pair of calls signaling ... across different matrilines ...

{subord in mat B gives threat call & dominant in mat A gives subord scream}

... baboons can categorize the world in a hierarchically embedded fashion