

Animal Behavior = Cause + Development + Evolution + Function

KEYWORD CONCEPTS	TIME FRAME	
	Pattern	Process
HIERARCHICAL LEVEL IN BIOLOGY	(e.g. "Snapshot" or slice in time)	(e.g. "Video" of changes over time)
Proximate		
(e.g. "micro lens" on individuals, neuronal networks; genotypes P= C+D)	Cause	Development
Ultimate		
(e.g. "macro lens" on populations, gene pools; proportions of genotypes U=E+F)	Function	Evolution

EXPLANATION:

These four basic perspectives were defined as questions by Dr. Niko Tinbergen, a Nobel prize-winning scientist who is known as one of the "fathers of ethology".

Each perspective is analogous to a "lens" that both focuses and filters each scientist's view of the reality of animal behavior. These four scientific perspectives contrast with <u>Folk Psychology</u>, which is not considered a scientific basis for the study of behavior.

The Folk Psychology perspective is illustrated in many videos that explain animal behavior in anthropomorphic terms (beliefs, desires and emotions of humans) which has its place in communicating with the general public. This is why it is important to learn about the people and sources that shape our understanding of animal behavior, and to exercise critical thinking in what is a "scientific source" compared to a "folk psychology source".

FOLK PSYCHOLOGY (FP)

Intuition | "right brain" | Beliefs, Desires, and Emotions | Anthropomorphism

What is an intuitive Folk Psychology view of behavior?

Anthropomorphic explanations based on the mental model that animals have desires, beliefs and emotions like people do (FP is a "right brain" mode), e.g.

- desires (I want X...);
- beliefs (I think if X then Y...);
- emotions (I feel happy...sad...)

What are some example statements?

- The dog wanted to go outside.
- The dog believed that if he barked, his companion would open the door
- The dog was happy when his companion opened the door.

Why is FP rejected by scientists as circular reasoning?

- circular explanations are not logical from an analytical Scientific Perspective (SP is a "left brain" mode)
- "for the good of the species" (as if a species had a desire to survive, or could look into the future)
- "design for a higher purpose" (as if natural selection is a god or engineer, with intent for future development)
- "to pass on their genes" (as if an individual had a conscious desire to perpetuate its genotype, and knew it should do so for future generations)
- those scientists who reject circular reasoning, accept explanations in term of chance and relative probabilities (e.g. Einstein!)

When is FP appropriate?

FP is appropriate when used in the context of "right brain" activities

- public outreach programs at zoos and reserves (people who have not received training as scientists
- when scientists brainstorm about developing an hypothesis that could be tested by collecting data
- problem solving in individual case studies (best when integrated with "left brain" activities)

PROXIMATE CAUSE (PC)

Structure | "micro lens" on individuals | "Snapshot" or slice in time

What is proximate cause?

- Structure or phenotype of a behavioral trait (physiology, form and movement)
- "snapshot" of behavioral mechanisms at the individual level of biology
- stimulus=> response, as modified by
 - o external context (other outside cues in addition to the stimulus)
 - o internal state (mood, hormones, neurotransmitters, etc.
- internal mechanisms linking perceptions with behavioral responses,
- interaction of internal state and external stimuli;
- scientists' mental models about cause (stimulus) and effect (behavior)

What are example questions from the PC perspective?

- Did the dog turn away because he did not hear me or because he smelled a cat?
- What is the stimulus for a given behavioral response?
- What is the variation in a behavioral trait among individuals?
- What goes on inside and outside the animal affecting the probability that it behaves in a certain way?
 - How do seasonal changes in hormone levels (internal state) influence the probability of males fighting?
 - How does the context of females in the area influence the probability of males displaying?
- Is a male more likely to escalate when his rival is smaller?
- Is a cat more likely to pay attention to a bird when it has been food deprived?
- Do all male sticklebacks respond to the color "red" with the zig-zag dance?
- Within the neural network of the brain, is attack behavior inhibited at the level of the frontal cortex or the hippocampus?

Why did Tinbergen consider PC to be scientific?

- Hypotheses about cause and effect can be tested, and rejected if not supported by the evidence
- The form, or structure, of a behavioral trait can be analyzed just like any other physiological or anatomical trait
- In the logic of natural selection, if there is no variation in a trait then that trait is not likely to change as a result of evolutionary processes
- Behaviors are controlled by physiological systems that interact with stimuli in the outside world

PROXIMATE DEVELOPMENT (PD)

Ontogeny | "micro lens" on individuals | "video" or maturational change in a lifetime

What is proximate development?

- "video" at the individual level of biology
- age-related changes in behavioral traits of individuals (Nature/Nurture); how much is learning, how much is instinct?
- developmental changes in behavior related to maturation and age;
- mental models re. processes of change in individuals' patterns of behavior related to age (eg. internal information includes genetic and hormonal effects on neuronal networks; external information includes the social and physical environments)

What are example questions from a PD view?

- At what age should a puppy be socialized to humans?
- What about this behavior is instinct and what is learned?
- Where is this behavior on the continuum of fixed (heritable) to flexible (learned)?
- Is the variation in this behavior highly heritable or due to individual experience?
- How does the behavior of animals change with age as a complex interaction of internal and external information?
- How does Nature (genetic information) and Nurture (environmental information) interact in development of a particular behavioral trait?
- How similar are the behaviors of close relatives raised apart?
- How different are the behaviors of unrelated individuals raised together?
- How does variation in a behavioral trait in adults suggest hypotheses about the relative importance of genotype and environment during development?
- Is there a sensitive period in development when imprinting is more likely?

Why did Tinbergen consider PD to be scientific?

- Hypotheses about the heritability of behavior can be tested, as can hypotheses about changes in behavior related to developmental changes with age
- Ontogeny in modern terms is understood in terms of controller genes that affect the timing during development when other genes are turned on or off
- If the variation in a behavioral trait is not heritable, then it will not be influenced by the process of natural selection

ULTIMATE FUNCTION (UF)

Purpose | "macro lens" on populations | "snapshot" in time (1 generation)

What is the ultimate function perspective?

- "snapshot" of the relative fitness of genotypes in one generation
- an hypothesis stated in terms such as "those that did X had relatively higher fitness than those that did Y"
- fitness is in terms of relative rates of survival and reproduction of genotypes within a population (cannot be measured for an individual outside the context of a genetic population)
- function of variation in behavioral traits, in terms of differential survival and reproduction
- mental models re. variation in behavioral patterns at the population level

What are example questions from a UF viewpoint?

- Are dogs with hip dysplasia less likely to reproduce?
- How does variation in behavioral strategies and tactics influence the relative fitness of individuals in a population?
- How do fitness costs and benefits compare for different strategies in a population?
- Which strategies would have higher fitness under a given set of conditions?
- How would the proportion of genotypes be different in another population with different environmental costs and benefits (in terms of fitness)?
- Which strategy would pass on more genes compared to another?
- How would the proportion of genotypes be different in another population with different environmental costs and benefits (in terms of fitness)?
- Why did strategies co-evolve within a species?

Why did Tinbergen consider UF to be scientific?

- Heritable variations of traits can be compared within a population, to test which which genotype survives and reproduces better in a certain environment
- The same trait can be compared in different environments, to test how survival and reproduction change depending on the environmental conditions
- According to the logic of natural selection, only if heritable variations in a behavioral trait result in differential reproduction or survival will that trait be subject to natural selection over evolutionary time scales

ULTIMATE EVOLUTION (UE)

Phylogeny | "macro lens" on populations | "video" of change over generations

What is the ultimate evolution perspective?

- *informal*: "video" of change in species over many generations; shaped over ecological or geological time scales (e.g. millions of years)
- *forma*: comparison of behavioral traits in several species to induce hypotheses about phylogenetic history (convergent, divergent, inertia)
- *scientific model*: processes of change in behavioral patterns at the population level over many generations

What are example questions from a UE viewpoint?

- Why are there differences in behavior of closely-related species? (divergence)
- Why are there similarities in behavior of species from diverse taxonomic groups? (convergence)
- Why are there similarities among related species, and differences among diverse taxonomic groups? (phylogenetic inertia)
- Which is the "precursor form" that might have occurred in ancestral species, and which is the "derived form" in modern species of a particular genus or family?
- What changed in the environment (over ecological/geological time scales), which might have influenced the gene pool of populations to change over many generations?

What is Convergent evolution?

- **Analogy**: different species=> similar traits
- conceptual map: two lines that merge into one
- *informal*: the result of long-term change where different environments converge to be more similar; clues to develop hypotheses about similar function in species as different as birds and mammals
- *formal:* When two species from completely different taxonomic groups evolve similar traits as a result of similar "selective pressures" in their environments

What is Divergent evolution?

- **adaptive radiation**: similar species=> different traits in different environments
- conceptual map: one line that forks into two lines
- *example:* bats have diverged into insect-eating, fruit-eating, nectar-feeding and blood-sucking lineages
- *formal:* When two similar species evolve different traits due to divergent changes in their environments
- *hypothesis*: the trait of blood-sucking in bats was derived from the precursor trait of nectar-feeding in an ancestral species

What is Phylogenetic inertia?

- **Homology:** similar species=> similar traits
- conceptual map: two parallel lines
- *example*: all species in the taxonomic family of pelican-like birds have a similar "prelanding call" although some genuses differ in the form of courtship behaviors
- Informal: the environments diverged, but there was not the "raw genetic material" for selection of divergent traits
- *Formal:* When the traits of two species with similar ancestors remain similar, despite changes in their environments and divergence of other traits

What are "precurser" vs. "derived" traits?

- *conceptual mapping*: a precursor trait is at the stem of a branch in the evolutionary tree; the derived traits are at the tips of the branches
- **precursor**: the form of a trait in an ancestral species known from the fossil record; we hypothesize a trait is a precurser when it is similar in all the species that diverged from a shared ancestral species;
- **derived**: the form of a trait in a modern species; we know the derived traits because we see them in the species alive today, and we can compare them in terms of similarities and difference; if they are different, we hypothesize it is due to a phylogenetic history of divergence within a lineage; if they are similar we hypothesize phylogenetic inertia within a lineage; the tips of the branches on the evolutionary tree
- *example*: in Galapagos finches, "insect eating" was derived from the precursor behavior of seed eating; the hypothesis is that the ancestral species was a heavy-beaked seed eater that foraged on the ground, all modern species show this heavy beak and ground-foraging where seeds are available, but seeds are not always available on the islands where the insect eating species live
- *tip*: in developing an hypothesis about phylogenetic history, pick the trait that is similar among genera and call it the ancestral trait; look for traits that are different among species and call them the derived traits

How is natural selection (NS) related to evolution?

- Natural selection is an hypothesis about evolutionary processes resulting in changed proportions of genotypes within populations; we say an evolutionary adaptation is the end product of the process of natural selection
- memory aid: NS= VHDP
- IF there is **Variation** in a behavioral trait within a population (i.e. PC perspective), and
- IF Heritability of this variation is high (i.e. PD perspective), and
- IF Differential fitness results from this variation (i.e. UF perspective)
- THEN the **Proportion of genotypes** will change within the population, over generations(i.e. UE perspective)