Socially Biased Learning



Social learning as an adaptation

Darwin, Wallace, Romanes...

When is it advantageous to learn with conspecifics?

Things have to be learned fast (ex: predator avoidance)

Things that are costly to learn (ex: poisonous food)

Things that are too variable for genetic assimilation...

...but not TOO variable: adults are individuals who acquired behavioral patterns that allowed them to survive in the environment where juveniles are.

"Socially Biased Learning" X "Social learning"

Fragaszy & Visalberghi 2001: "Social Learning" x "Individual Learning"?

ALL learning is "individual"...

... but sometimes, individual learning is channeled, constrained, facilitated, or otherwise tweaked by social interactions.

Occurrence of Socially Biased Learning Ontogeny and Phylogeny

SBL is restricted to "social" species?

Social influences do not depend on direct social interaction (consequences or remains of others' behavior)

Birds and mammals: development and parental care

Occurrence of Socially Biased Learning SBL in asocial species?

Hamsters: solitary and social species (Lupfer et al 2003)





Golden hamsters (*Mesocricetus auratus*) and dwarf hamsters (*Phodopus campbelli*) interacted with a conspecific demonstrator that had recently consumed a flavored food. When given a choice between their demonstrator's flavor and another flavor, the dwarf hamsters preferred the flavor their demonstrator had eaten. Golden hamsters did not prefer their demonstrators' diets when the demonstrators were unrelated adults or littermates, **but they did when the demonstrator was their mother**.

Figure 1. The experimental setup. The arrow indicates the direction in which the demonstrator moved.

Wilkinson et al 2010

Social learning in a nonsocial reptile (Geochelone carbonaria)

Socially Biased Learning in asocial species?

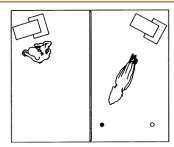
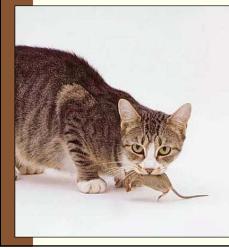


Fig. 1. Schematic of the experimental apparatus and protocol. An *Octopus vulgaris* is shown (right side of the figure) attacking a ball (the red one) and acting as a demonstrator for the other animal (observer, left side) that is standing outside of its home and watching its conspecific during the whole session through a transparent wall. Each tank had an independent supply of running water. Octopuses were allowed to visually interact for 2 hours before the start of the observational phase. Mean duration of the trials, which depended on the demonstrator's performances, was 40 s, and intertrial intervals were fixed at 5 min.



Fiorito & Scotto 1992 Observational Learning in *Octopus vulgaris*

Looking for evidence of social learning





Learning what to eat – or not (Rattus norvegicus)

Galef 2005

Poison avoidance Steiniger (1950):



Difficulty in poisoning a rat colony: some rats ate only small amounts of poisoned food, survived and started avoiding that food; new generations rejected the poisoned bait: did they learn to avoid it?

x Galef & Clark (1971): ... no; rats do not learn which foods to avoid, BUT which to eat - and are reluctant to ingest foods not introduced by older members (but the result is the same...)

Learning what to eat - or not (Rattus norvegicus)

Galef 2005

Prenatal influences

Hepper (1988): garlic (pregnant mothers) x onion

Taste cues in mothers' milk

Galef & Sherry (1973): flavored milk + poisoning

Cues during weaning

Galef & Clark (1973): co-feeding + scent marks

Cues after weaning

Behavior observation (Galef et al 1983, 2003) Breath: scent + carbon disulfide (Galef et al 1988)

Learning how to get food

Rats (*Rattus rattus*): pine cone opening

- · No individual trial-and-error learning
- · No observational learning
- · No effect of mother milk
- Cross-fostering: infants adopted by proficient females
- No learning from exposition to fully peeled pine cones
- Learning by exposition to PARTIALLY PEELED cones



Terkel 1996

Learning how to get food

Tool use



Galapagos woodpecker finches (Tebbich et al 2001) Hyacinth macaws (Borsari & Ottoni 2005)

→NO evidence of SBL

New Caledonian crows? (Hunt 2000, Hunt & Gray 2002 X Kenward *et al* 2005, 2006)

Chimpanzees, capuchin monkeys...

Learning to choose a mate

Mate choice copying

Fish: guppies (Poecilia):



Dugatkin 1992: confined females observing a male paired with a female X solitary male; observer later preferred to mate with paired ("chosen") male.

(not all guppies' species, but)

Other species: Brown & Laland 2003

Social learning and mate choice in birds

Song (dialects) and partner choice



Quails, Coturnix japonica

Kirkpatrick 1987 Galef & White 1998

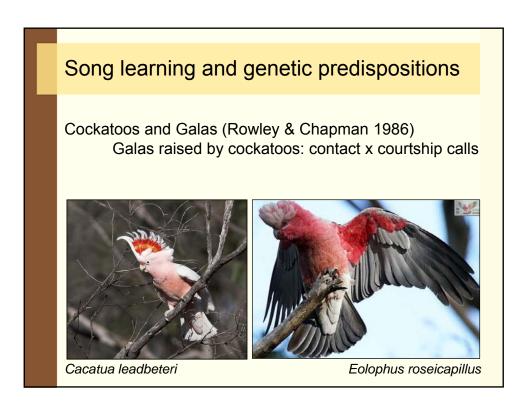
Cowbirds, Molothrus ater

Adult males learn [and females prefer] local songs (Freeeberg 1996, 2004)

laboratory: observationally transmitted preferences for males

Females "model" young males' song (West 2000)

Birdsong learning Peter Marler P. Slater Figure 2 Timelines for song learning a. In many seasonal species, such as the white-crowned speries, the sensory and sensorimotor phases of herming can be separated in time. The initial vocalizations, or 'subcong', produced by young birds are variable and generic across individuals, askin to the babbling of human infants. Subsong gradually evolves into 'ptastic song', which remains highly variable from one rendition to the next, but also begins to incorporate some recognizable elements of trutor songs. Plastic song is group subjects to incorporate some recognizable elements of trutor songs. Plastic song is group subjects where the duril the bird 'crystallized' song is Zetora finisches evolution to the next, but also begins to incorporate some recognizable elements of trutor songs. Plastic song is group subjects where the duril the bird 'crystallized' song is Zetora finisches evolution to the next, but also begins to incorporate some recognizable elements of trutor songs. Plastic song is progressively refined until the bird 'crystallized' song is Zetora finisches evolution to the next, but also begins to incorporate some recognizable elements of trutor songs. Plastic song is progressively refined until the bird 'crystallized' song is Zetora finisches evolution to the next but also begins and their two phases of learning overlap extensively. c. Open learners', such as canaries, can continue or recapitulate the initial learning process as adults. Brainard & Doupe 2002



Song learning and genetic predispositions

Zebra finches (Fehrer et al 2009): song culture as a *multi-generational phenotype*, partly encoded genetically in an isolate founding population, influenced by environmental variables, and taking multiple generations to emerge.



Zebra finch isolates, unexposed to singing males during development, produce song with characteristics that differ from the wild-type song found in laboratory or natural colonies. In tutoring lineages starting from isolate founders, we quantified alterations in song across tutoring generations in two social environments: tutor-pupil pairs in sound-isolated chambers and an isolated semi-natural colony. In both settings, juveniles imitated the isolate tutors, but changed certain characteristics of the songs. These alterations accumulated over learning generations. Consequently, songs evolved toward the wild-type in 3–4 generations. Thus, species-typical song culture can appear de novo.

Janik & Slater 2000
The different roles of social learning in vocal communication

Contextual Learning: a pre-existing signal comes to be associated with a new context as a result of experience with the signals of other individuals. CL can occur in both the signaler and the receiver:

- **Usage Learning**: the individual learns to use the same signal in different contexts to encode different messages;
- Comprehension Learning: a receiver can learn to associate a pre-existing signal with a new context (...) and thus, extract a new meaning from it.

Production Learning refers to instances where the signals themselves are modified in form as a result of experience with those of other individuals. (to which the expression 'vocal learning' has traditionally been applied in studies of bird song).

Janik & Slater 2000

The different roles of social learning in vocal communication

INNOVATION AND INVENTION

Innovations can be achieved either by production or by contextual learning. **Invention** can involve social learning but does not need to do so.

Tyack 1997: bottlenose dolphins - novel signals for individual

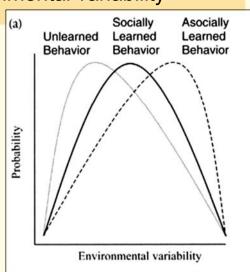
recognition?



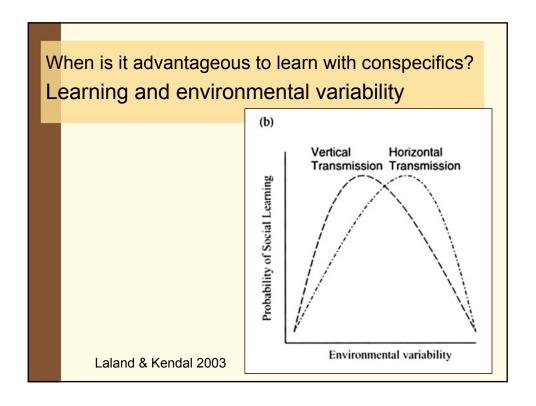
Janik 2000

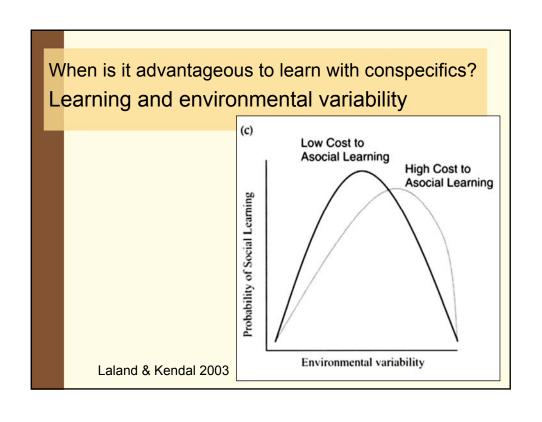
"Signature whistle" of bottlenose dolphins (Tursiops truncatus)

When is it advantageous to learn with conspecifics? Learning and environmental variability



Laland & Kendal 2003

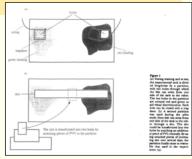


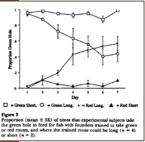


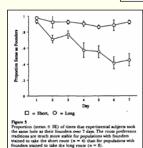
Potential costs of social learning

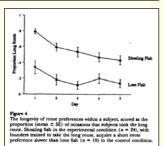
Laland & Williams 1998

Social transmission of maladaptive information in the guppy









Whom and when to copy

Mathematical/theoretical modeling of social learning "biases":

Copy the majority? (Boyd & Richerson 1985) ("conformity bias")

Copy the successful? (Boyd & Richerson 1985)

Copy the older? (Kirpatrick & Dugatkin 1994)

Copy the dominant?

Copy those doing better? (Schlag 1998)

Copy if dissatisfied? (Schlag 1998)

Humans: "Prestige Bias" (Henrich)

Scrounging and Socially Biased Learning

Ottoni, Resende & Izar 2005



Capuchin monkeys: observation of nut-cracking by juveniles: "comensalism" (*tolerated scrounging*) as a proximal motivation? (an *age-dependent* strategy...)

Behavior observation x **endosperm leftovers** in nut cracking sites (*local enhancement* + reinforcement: "niche construction")

Young observers/scroungers seem capable of choosing the most proficient nutcrackers – which not only optimizes [adult-dependent] feeding, but also the conditions for SBL

Scrounging x learning: frequency-dependent?

Pigeons unable to simultaneously scrounge & learn socially?

Giraldeau & Lefebrye 1987

Pigeons that learned socially to produce seed by removing the stopper from a test tube would switch from producing to scrounging and back again as a function of whether there were producers active in the population. Scroungers and producers maintained a frequency-dependent balance.

Giraldeau & Beauchamp 1999



Watching the best nutcrackers: Observation targets' choice by infant and juvenile scroungers Ottoni, Resende & Izar 2005

Observation rates X social affinities?

X Spatial Social Proximity	Partial Tau K _r =.125, p _r =.8486	NS
X Dominance	Partial Tau K _r =.148, p _r =.1824	NS
X Age (X ² : p<.0001)	Partial Tau K _r =.076, p _r =.3123	NS
X Proficiency*	Partial Tau K _r =.232, p _r =.0495	S
[*Prof. X Cracking Abs.Freq.: Partial Tau K,=.114, p,=.2569		

(it does not require a complex "cognitive" explanation: reinforcement is sufficient!)

Ottoni et al. (2009): When the behavior entered the "tradition phase", with highly proficient adult males, the correlations with Age & Dominance became significant (in this situation, youngsters can use a "rule-of-thumb": "follow dominant male").

Modes of Social Information Transfer

Social Information Transfer (King 1991, 1994): does not discuss *mechanism*: increase in behavioral homogeneity due to social interaction and its persistence in time.

Stimulus/Local Enhancement

Imitation and Emulation

(Functional) Teaching (or "scaffolding")

Social biases on learning Visalberghi & Fragaszy (1990):

Social facilitation: an increase in the probability of the emission of a behavior (already present in the repertoire of the individual) as a consequence of the presence of other individuals exhibiting the same behavior (increases behavioral homogeneity of behavior by promoting motivational homogeneity; ex: mobbing)

Stimulus/local enhancement (Thorpe 1956): individual's attention attracted to elements of the environment as a function of other individual's activity – increasing probability of interaction of that element [Whiten & Ham 1992: enhancement ≠ observation learning]

Galef (1988): "S. Facilitation + St. enhancement = Social Enhancement" Heyes (1993): "imitative" X "non-imitative" social learning

Imitation: novel behavior acquired by its observation in another individual's repertoire

Stimulus Enhancement Local Enhancement



Observation of behavior x Attention orientation to environmental elements

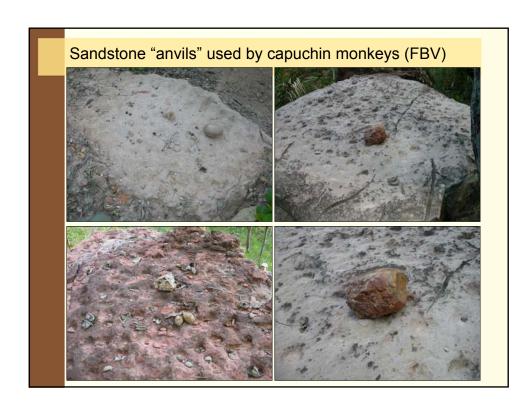
Contact with environmental alterations resulting from other individual activities even in the immediate absence of the agent

The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools Fragaszy et al 2013

All investigated cases of habitual tool use in wild chimpanzees and capuchin monkeys include youngsters encountering durable artefacts, most often in a supportive social context.

Enduring artefacts associated with tool use, such as previously used tools, partly processed food items and residual material from previous activity, aid non-human primates to learn to use tools, and to develop expertise in their use, thus contributing to traditional technologies in non-humans.

Therefore, social contributions to tool use can be considered as situated in the three dimensions of Euclidean space, and in the fourth dimension of time. This notion expands the contribution of social context to learning a skill beyond the immediate presence of a model nearby.



Imitation and Emulation

Imitation: lack of agreement between authors:

(strict sense): a **novel** behavior in the individual's repertoire is copied through the **observation of another individual's behavior**

For some authors (ex: Tomasello), imitation implies an understanding of the observed individual's **goals** ("joint attention" etc) and/or "**metarepresentation**" of others' mental states (Whiten, Ham, Byrne)

Emulation (Tomasello 1987, Whiten & Ham 1992): a more "restricted" process than true imitation: copy of the final result of the behavior (but not of all procedural details).

Imitation and "over-imitation" (see lecture 7...)

Imitation and Emulation

Learning by imitation: a hierarchical approach Byrne & Russon (1998)

"Program-Level" Imitation: "a broader description of subroutine structure and the hierarchical layout of a behavioural "program.""

A high-level, constructive mechanism, adapted for the efficient learning of complex skills and thus not evident in the simple manipulations used to test for imitation in the laboratory (ex: food processing by gorillas) [a possible reconsideration of "emulation"...]

"Action-Level" Imitation: "a rather detailed and linear specification "of sequential acts" Seldom observed in great ape skill learning, and may have a largely social role, even in humans

Teaching in non-human animals?

Anecdotal reports (since Romanes)...

Rodrigues Islands'
frugivore bats:
Experienced female
demonstrates
birth posture (head up)
to another
(primiparous?)
female?

T. Kunz 1997



Pteropus rodricensis

Teaching (strict sense)

Intentional information transfer by the model

X Youngster's readiness to watch older individuals

Humans

ToM, Imitation (Tomasello 2001)?

"Natural Pedagogy" (Csibra & Gergely 2011)

Chimpanzees?

- Captivity: the infant Loulis learning Sign Language (Fouts 1998)
- Wild: mother "demonstrates" correct "hammer" use (Boesch 1991) (?)

Other mammals and birds:

"Functional teaching" as "species-specific" patterns? (= "scaffolding", ~ Fixed Action Patterns?)

Teaching in wild chimpanzees?

(scant evidence...)

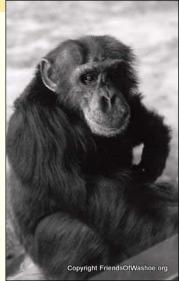


Boesch 1991: Teaching in wild chimpanzees

Teaching in language-trained chimpanzees

Loulis, adoptive son of Washoe learned sign language from the mother and an age peer; Washoe "molded" his hands into signs (as done to her...)

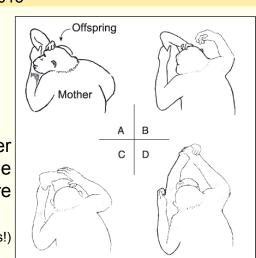
Fouts 1998



Ontogeny of a Social Custom in Wild Chimpanzees: Age Changes in Grooming Hand-Clasp at Mahale Nakamura & Nishida 2013

A mother "molding" the offspring gesture

(~ Washoe and Loulis!)



"Scaffolding"

Terkel 1996 (Rattus rattus)

Opening of pine cones for seed extraction through the removal of the "scales"





"Functional Teaching"

Caro & Hauser (1992) - Functional definition of "teaching":

- (i) an individual, A, modifies its behavior only in the presence of a naïve observer, B;
- (ii) A incurs some cost or derives no immediate benefit; and
- (iii) as a result of A's behavior, B acquires knowledge or skills more rapidly or efficiently than it would otherwise, or that it would not have learned at all.
- "Opportunity teaching" (put pupil in condition conducive to learning)
 X "Coaching" (encouragement + punishing)

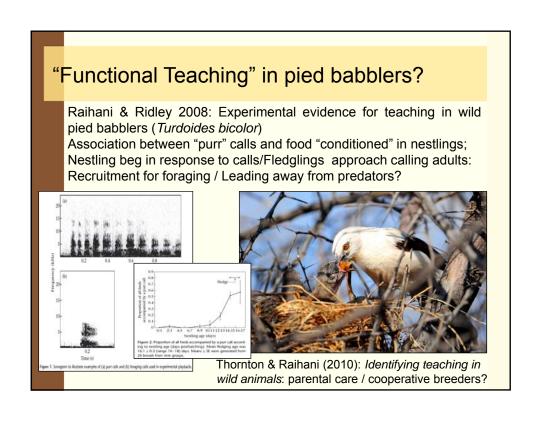
Lessons from animal teaching

Hoppitt et al 2008

"(...) we endorse Caro and Hauser's definition with one caveat. Their requirement that there be a cost or no immediate benefit to the tutor is only partially successful in ruling out behaviour with alternative functions. For instance, parental provisioning is costly and can transmit dietary preferences to offspring, but it might have evolved because selection benefits parents that provide nutrition to their young, rather than because provisioning functions to teach.

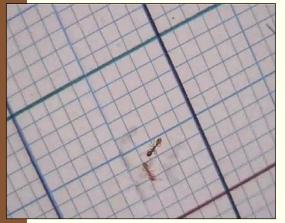
Consequently, for cases where behaviour increases the inclusive fitness of the tutor irrespective of whether knowledge is transmitted to the pupil to be regarded as teaching, we would require evidence that the tutor's behaviour has been modified by selection to promote learning."

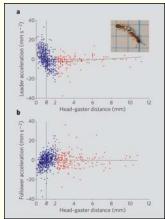
"Functional [opportunity] teaching" in meerkats Thornton D young Proportion fed intact 0.5 pups 0.4 0.3 0.2 n = 10 0.1 Handling of dangerous prey (scorpions) according Expt to pups' age older Proportion fed dead pups 0.4 Adults' behavior controlled 0.2 by infants' vocalizations Control



"Functional Teaching" in ants

Franks & Richardson 2006: Teaching in tanden-running ants (*Temnothorax albipennis*): leaders and followers adjust velocities, leaders wait while followers stop and (presumably) search for landmarks.





Hoppitt et al 2008

Honeybees' waggle dance as teaching?

"According to the criteria of and Hauser, Caro waggle dance of honeybees $(\ldots),$ historically not considered as teaching, could be seen in a similar light to tandem running in ants. (...) We suggest that the waggle dance, and indeed other forms of communication in bees, constitute strong cases of teaching."



Apis mellifera

Lessons from animal teaching Hoppitt et al 2008

The evolution of teaching

Instead of being seen as a separate set of mechanisms for information transfer, teaching can usefully be regarded as introducing another dimension to social learning: whether the role of the demonstrator is active or passive. Teaching will often arise as signals, or responses, given by tutors that take advantage of pre-existing social learning mechanisms.

We expect that specific forms of teaching will have evolved from the ancestral condition of the equivalent form of inadvertent social learning. For example, teaching by local enhancement is only likely to evolve in a population that exhibits inadvertent local enhancement. This is because, to teach in this way, a tutor need only evolve signals or other behaviour necessary to increase the likelihood or efficiency of local enhancement in the pupil.

Lessons from animal teaching Hoppitt et al 2008

Table 2. Parallel classification of processes involved in social learning based on 'inadvertent' information and social learning based on 'inadvertent' information and social learning based on 'inadvertent' information and social learning based on 'inadvertent'

Туре	Inadvertent social learning	Teaching
Local enhancement	A demonstrator inadvertently attracts an	The behaviour of the tutor functions to attract
	observer to a specific location, leading to the	a pupil to a specific location, leading to the
	observer learning.	observer learning.
	Naïve guppies follow informed individuals to	Tandem running in ants [15], in which leader
	food [56].	ants slow down to ensure followers keep in
		touch (Box 3).
Observational	The behaviour of the demonstrator	The behaviour of the tutor functions to expose
conditioning	inadvertently exposes an observer to a	a pupil to a relationship between stimuli,
	relationship between stimuli, allowing the	causing the pupil to form an association
	observer to form an association between	between them.
	them.	
	Blackbirds learn to recognise predators	Adult babblers expose nestlings to the
	through observing birds mobbing unfamiliar	relationship between the 'purr' call and food
	objects [69].	[20].
Imitation	After observing a demonstrator perform a	The behaviour of the tutor functions to
	novel action, an observer learns to reproduce	demonstrate a novel action, causing the pupil
	that action.	to learn how to perform it.
	Birds learn to produce novel sounds through vocal imitation [70].	A human tennis coach demonstrates a shot.
Opportunity	The products of the behaviour of the	The behaviour of the tutor functions to
providing	demonstrator provide the observer with an	produce products which provide the pupil
	opportunity to engage in operant learning	with an opportunity to engage in operant
	that would otherwise be unlikely to arise, for	learning that would otherwise be unlikely to
	example by providing an easier, less	arise, for example by providing an easier, less
	dangerous or more accessible version of the	dangerous or more accessible version of the task
	task.	
	Black rat pups in Israel steal semiprocessed	Adult meerkats provide pups with dead,
	pinecones from their mothers [23].	disabled or live scorpions depending on the
		pups' age [14].
Coaching/inadvertent	The response of a demonstrator to the	The response of the tutor to the behaviour of
coaching	behaviour of the observer inadvertently acts	the pupil functions to encourage or
	to encourage or discourage that behaviour.	discourage that behaviour.
	Female cowbirds respond to preferred male	Mother hens attract their chicks away from
	songs with 'wing stroking,' which acts to	food the mother perceives to be unpalatable
	reinforce that song in the male [25].	[24].

Lessons from animal teaching

Hoppitt et al 2008

The evolution of teaching

As with altruism, we would expect teaching behaviour ultimately to benefit the tutor's inclusive fitness, either through kin selection or because the tutor benefits directly from the pupil learning. In the case of kin selection, teaching will evolve according to Hamilton's rule: if the fitness cost to the tutor (c) is less than the fitness benefit to the pupil (b), multiplied by the degree of relatedness between them (r), or c < br.

Teaching is more likely to evolve in species where the average relatedness between interacting individuals is high, or to occur selectively between individuals of high relatedness. This could explain why teaching appears to be present in many **eusocial insect** colonies, where the average relatedness tends to be higher than in other animal populations.

Lessons from animal teaching

Hoppitt et al 2008

The evolution of teaching

The benefits of teaching clearly depend on the resulting increase in the probability that pupil learning occurs, or increase in the rate or efficiency of learning X the probability that learning occurs associally or via an inadvertent demonstrator.

Therefore, we only expect teaching to evolve when the equivalent form of inadvertent social learning is relatively ineffective or when there are few opportunities for social or individual learning.

This might explain why teaching is rare in chimpanzees and other non-human apes [extremely capable social learners]. Young chimpanzees generally feed alongside their mothers for extended periods of their life, which potentially provides youngsters with considerable opportunities for social learning, with little selective advantage to active information transfer.

Socially Biased Learning and behavioral traditions

Fragaszy DM & Visalberghi E (2001). Recognizing a swan: socially-biased learning. *Psychologia* 44:82-98:

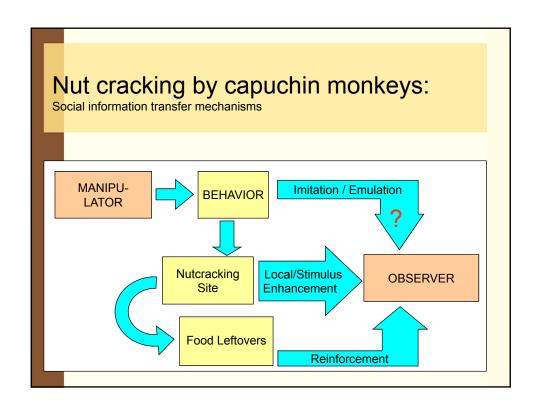
Any form of SBL can sustain the establishment of traditions(not only imitation)

"Emotional Contagion" and associative learning example: snake avoidance by rhesus monkeys (Mineka & Cook 1988)

Conditioned Modulating Experiences

example: "occasion setting" (in Terkel 1996 rats):

Infants' responsivity to pine cones altered by the mother's presence



Heyes 2012 What's Social About Social Learning?

"A great deal is known about the adaptive functions of social learning, including its role in the social or cultural transmission of behavior, but very little is known about the cognitive mechanisms that make social learning possible.

Social learning has been isolated from cognitive science, not just by the usual barriers to cross-disciplinary integration, but by the long-standing and largely implicit assumption that it depends on social-cognitive adaptations—learning mechanisms distinct from those mediating asocial learning.

Social and asocial learning depend on the same basic cognitive mechanisms; these mechanisms are adapted for the detection of predictive relationships in all natural domains; they are associative mechanisms (...) and they mediate human as well as nonhuman social learning."

Heyes 2012 What's Social About Social Learning?

Then what is special about social learning?

"I suggest that social learning is distinctive when input mechanisms— perceptual, attentional, and motivational processes—are biased or tuned to a particular channel of social information (...) this kind of tuning can be achieved phylogenetically or ontogenetically, by evolution or via developmental processes.

Heyes 2012 What's Social About Social Learning?

Social and Asocial Learning Come in the Same Varieties

Animal learning theory (concerned primarily with asocial learning): three basic types of learning according to the kind of experience that provokes a change in behavior:

- Exposure to a single stimulus
 (S learning, e.g., habituation and sensitization)
- Exposure to a relationship between two stimuli (S-S learning, or Pavlovian conditioning)
- Exp. to a relationship between a stimulus and a response (S/R; instrumental learning, habit formation).

Heyes 2012 What's Social About Social Learning?

Social and Asocial Learning Come in the Same Varieties

- St. Enhancement corresponds to single stimulus Learning.
- Observational Conditioning corresponds to S-S Learning.
- Observational Learning corresponds to S/R Learning.

Socially mediated exposure to an R-S or S-R relationship sometimes results in the observer exhibiting behavior that is topographically similar to the behavior of the demonstrator; in these cases, observational learning is also known as "imitation".



