Chapter 17. Cognition, Memory and Learning

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Learning, Behaviorism, and Cognition

Are some behaviors the result of innate programming of genes?

Do animals show intelligence?

Is the animal born with a *tabula rasa* and only through the experiences of a lifetime are its behaviors shaped by conditioning and interaction with its environment?

These questions span the breadth of approaches and ideas concerning the evolution of behaviors. We have already seen clear cases of innate programming or hardwiring of the nervous system. Complex behaviors are the result of relatively simple neural circuits. Fixed action patterns (FAPs) such as the response of the feeding toad to different stimuli is filtered by the receptive field (Chapter 14) and triggered by sign stimuli. In contrast, imprinting reflects a learning process that takes place within a very short period. For example a progeny that learns its mother via a vocal cue, or odor undoubtedly has some hardwired circuits devoted to this imprinting process. Nevertheless, this view cannot explain all cases of behavior. It is not just nature, but nurture.

More properly it is not simple genes, but gene interactions, emergent properties of gene interactions (epigenetics), and gene interactions in social environments that generate the full span of nurture. In Chapter 15, I introduced concepts of epigenesis with examples of endocrine maternal effects. While the role of maternal estrogens in altering offspring behavior are clear, we still do not understand how such epigenetic effects can lead to the complex forms of inheritance that transcend the simple additive effects of genes. Even for a simple trait like nurturing behavior, we do not understand the full 'evolutionary dynamic'. That is, we lack a complete understanding of how the genetic forms of inheritance interact with the maternal, paternal and indeed fully cultural forms that drive the transmission of nurturing behaviors. The expression of filiative behaviors and the tight associations that are formed (Chapter 11), should give rise to filiative behaviors in the next generation.

In this chapter, we will explore the higher-order interactions underlying behaviors -- learning and cognition. These forms will then be synthesized in the Chapter(s) on Social Evolution (19, and human evolution, 20) into a more comprehensive picture of how the cultural transmission of behaviors takes place and the consequences of a dual genetic and cultural transmission mechanism for behaviors.

The theory of learning maintains that the organism is born with relatively flexible neural circuits, but that such circuits have the capacity to be programmed by learning. We have already encountered a relatively simple example of synaptic plasticity in the programmed dominance interactions of crayfish (Chapter 8). Dominance is not hardwired, but rather dominance is shaped by repeated social interactions that can alter the kinds of neurotransmitter receptors at the gap junctions, generating a flexible (plastic) nervous system. The circuits become conditioned through trial-and-error associations. Stresses of social interactions act through the endocrine networks of positive and negative regulation (reinforcement) to either dissolve some of these neural associations or crystallize the associations in a more rigid form. Finally, whereas some behaviors could be the result of this simple learning and conditioning process, others might be the result of true intelligence and insight or at the very least, cognition. At the highest level humans use **reasoning**, **insight** and **abstraction** to make decisions (see Chapter 20). Whether or not some animals are capable of such higher-level cognitive processes is not certain. We will explore the distinction between learning and conditioning theories, and cognitive views of behavior.

Processes of learning and cognition are, by there very nature, **performance based**. An important aspect to consider in measuring performance is whether or not the animal is **motivated** to perform a behavior. We must consider motivation in our study of learning and cognition because any learning study may be confounded by a lack of motivation or differences in states of arousal among subjects.

At another level, **proximate causal mechanisms** underlying motivation may also explain differences in the behavior of individuals in the wild. For example, a subordinate in a troop of baboons is suppressed from engaging in copulation, and such suppression may be because an important causal agent, testosterone, is at lower levels or perhaps because corticosterone, a stress hormone, is at higher levels in the subordinates (Chapter 8). In contrast, levels of testosterone may be at very high levels in a dominant. Motivation is likely to be context specific with regards to social dominance status and endocrine states, as well as neuroendocrine states. A dominant has the motivational state to engage in aggressive interactions with other less dominant individuals, and learn and acquire information. Subordinates simply flee and not learn much about other rivals. However subordinates and dominants may have the motivational state to copulate with receptive females.

Finally, the proximate causal mechanisms underlying both motivation and learning may also give us powerful explanations of differences in behavior between organisms. For example, songbird males and females differ in the capacity to learn song. Such **constraints on learning** arise from the basic neural architecture of songbirds. In cases where female song may be important, for example in the formation of a pair bond in a monogamous species, the regions of the brain are elaborated by natural selection and such constraints do not hamper the learning of song in female birds. In other species, females do not rehearse a song like males. To begin this discussion we need to categorize the kinds of learning in animals. Learning is often broken down into 5 types, however, each of these forms has synonyms or in some cases antonyms that are used extensively in the literature: 1) **habituation** *vs*. **sensitization** (antonym), 2) **operant** or **instrument conditioning** (synonyms), 3) **classical** or **Pavlovian conditioning** (synonyms), 4) **observational** or **social learning** (synonyms), and 5) **insight**.

Motivation

The study of motivation entails the study of cause and effect. Behaviorists are interested in the causes of certain behaviors, and the most proximate of all causes for a specific behavior would be the **stimuli** from the external environment. The second aspect in the causal chain underlying a behavior is an internal state of the organism that **motivates** the underlying behavior. In many cases, stimuli are abundant

in the social environment, and yet the animal does not respond to a given stimulus all the time. For example, food may be present a lot of the time, but an animal is not constantly eating in the presence of food. Internal factors control the level of satiation in the case of feeding and such satiation mechanisms provide negative regulation on the feeding behaviors. We have already touched upon some of the key circuits that govern satiation and reward in Chapter 11. The **Nucleus Accumbens (NAcc)** along with the pre-limbic cortex, are key control areas for the **reward reinforcing pathway** for natural stimuli like **appetitive behaviors** that involve food reward as well as aberrant behaviors like drug abuse (MacBride et al. 1999). The receptor for **dopamine**, the neurotransmitter in this pathway, is concentrated in the NAcc (Fig. 11.9ef). This pathway plays a direct role in learning.

Of all the internal mechanisms studied, hormones, neurohormones and neurotransmitters are the most readily understood aspects of an animal's physiology that provide positive and negative regulation to reinforce or extinguish a given behavior. In addition, endocrine systems controlling a behavior can be altered and the negative regulation or positive regulation can be interrupted. Such **experiments** allow one to address the cause and effect relations between the proximate mechanisms underlying motivation. Equally important in such an endeavor is our ability to measure **natural levels of hormones** in organisms and correlate such changes with changes in an animal's motivational state.

For example, one can remove the endocrine organ responsible for testosterone production, the testes, and inject known quantities of testosterone to study how plasma testosterone precisely governs the response of males to agonistic situations (presence of rival males) or sexual stimuli (presence of receptive females). Testosterone is present over a long time course, and can be considered a general factor governing **arousal** in animal. The presence of a male or a female can be clearly identified as the external stimuli that might elicit a behavior, given that sufficient testosterone is present to allow for the underlying motivational state to be reached. Testosterone is used by both of the sexes to generate a heightened state of sexual arousal, but in females an additional hormone is required for receptivity, estrogen. Thus, hormones may require synergistic interactions to generate the motivational states.

Hormones do not necessarily have to be present for long periods to alter an animal's motivational state. For example, the "flight-or-fight" neurohormone, **adrenalin**, effectuates changes in motivational state of animals within seconds. Further downstream reactions to the stimulus that initially caused high levels of adrenalin production then are used to push an animal down one of the two alternatives: flight or fight.

The links between negative and positive feedback in the nervous system are also fairly well understood. Many protein hormones governing the reproductive cycle are produced by the pituitary or hypothalamus, which is innervated directly from the brain. The nervous system is axiomatic in effecting behaviors that are elicited by external stimuli.

Learning

Habituation and Sensitization: Non-associative learning

Habituation forms the simplest kind of learning process. Animals respond to many aversive stimuli such as being touched by a foreign object by recoiling or retracting. For example, a snail will retract into its shell in response to being touched by a probe. However, probing will cause a snail to habituate and eventually the snail stops retracting. The example of escape behavior in *Tritonia gilberti* (Chapter 16) is a classic example of a FAP, but such FAPs can be extinguished by habituation. Another example of habituation is **input filtering** (Chapter 13-14). *Anolis* lizards habituate to sinusoidal movements quite readily and such habituation usually takes place within 2 to 3 waves of stimuli. Input filtering and the more general process of habituation allows the animal to stop responding to inappropriate or noisy stimuli.

Sensitization is the flipside of habituation. In sensitization, response to external stimuli is elevated as trials progress rather than depressed as in habituation. For example, the common octopus can be trained to attack a target at the end of tank. Such a response can be increased after an individual has been fed. The octopus will be sensitized to more readily attach the neutral target in this altered state.

Associative Learning

Associative learning takes place whenever an animal learns to associate an external event with a change in its own internal state, or a change in its behavior. The first form of associative learning is **classical conditioning**. In addition, an animal can also learn to associate an act that it performs with some kind of reward. The second form of learning is **operant** or **instrument conditioning**, in which a motor action is effectuated to effectuate the delivery of a reward.

Classical Conditioning

The study of learning has been dominated by the paradigm of associative learning. For example, in **classical conditioning**, an animal is presented with a "*neutral*" *environmental stimulus*, such as the ringing of a bell, and follows up on this stimulus with a *motivationally significant event* such as feeding. The reader is undoubtedly familiar with this example in which Pavlov conditioned dogs to begin salivating in response to a buzzer, even before they were presented with the food.

What happens during the classical conditioning process?

Why does the dog begin salivating in response to a neutral stimulus?

Pavlov argued that food is **natural or unconditional stimulus (US)** that triggers a reflex response in the form of salivation, which is likewise the **unconditioned response (UR)**. Conditioning leads to the **conditioned stimulus (CS)**, a buzzer, becoming **associated** with the reflex or unconditioned response. Pavlov believed that the CS comes to substitute for the US in triggering the UR. Indeed the response of the dog includes more than just reflex action, the dog becomes excited, approaches the food dish (or site of feeding). The example of Pavlovian conditioning is one in which the US is positive, however, negative stimuli such as an electric shock could also be used.

How can such learning be viewed in an adaptive context? Processes underlying classical conditioning allow an animal to make associations between two stimuli in the external environment (cue and reward, or cue and danger) and then prepare for the upcoming event that is triggered by the predictor. Developing such correlations between external events permits the animal to make adaptive modifications of behavior.

Instrument or Operant Conditioning

Instrument or operant conditioning was popularized by the invention of the Skinner Box, by B. F. Skinner. Instrument conditioning differs from classical conditioning in that the motivationally significant event occurs after the subject **performs** some behavior rather than performing some behavior in response to a stimulus. Rats learn to press a bar by reinforcement with a pellet of food reward. Instrument conditioning is also a form of associative learning in that the rat comes to associate the bar press with receipt of a reward.
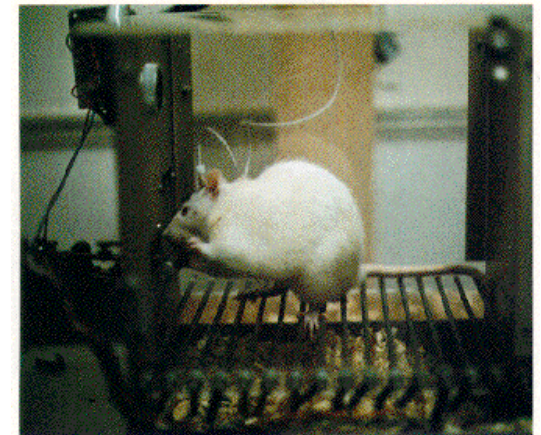

Figure 17.1 A rat learns to press a bar in a Skinner box. With each bar press the rat is rewarded with food.

Even though the Skinner box may be somewhat artificial, the principles of instrument conditioning have practical applications in nature. For example, a squirrel attempting to crack open nuts, it learns to open the nuts by a similar process. It modifies its behavior as it finds a successful technique that allows it to access the meat of the nuts faster. The foraging jay, by flipping leaves or removing bark, finds a grub reward.

Biological Constraints on Learning

To understand the arguments of nurture and nature two concepts linked the ideas of behaviorism and laws of learning:

1. General Process Theory, and
2. The Principle of Equipotentiality.

An adherent of **general process theory** would contend that all examples of associative learning involve the same basic underlying mechanism or process. This allowed learning theorists to pick model systems to study the process of learning *per se*, and to construct experiments in the laboratory, in which the artificial testing minimized the possibility of species-specific behaviors being expressed. The mechanism underlying learning theory are not proximate mechanisms, which we are used to thinking about such as neural circuitry, but rather the formal rules underlying the learning process (e.g., definition of cognition, Chapter 6).

The **principle of equipotentiality** implies that all organisms are capable of learning to associate anything. In its most extreme form, the life experiences of an organism are built upon the *tabula rasa* (the empty board). More complex associations, as the animal's life unfolds, shape experiences. A strict behaviorist would maintain that such experiences are immune to instincts. So began the debate between nurture and nature in the mid 1950's. Behaviorists on the one hand held this view of experiences. Ethologists found such arguments absurd. Evidence rapidly accumulated that organisms could not learn associations between *anything*. This evidence seemed to invalidate the principle of equipotentiality, but really had no bearing on the general process theory.

A simple example should suffice to make these distinctions. Rats are very capable of making associations between taste and nausea. However, they are incapable of making associations between sounds and nausea. Conversely rats are capable of making associations between sounds and electric shock and can learn to crouch when they hear a sound in order to avoid an electric shock, but they do not learn to associate tastes with electric shock.

The process of natural selection hones organisms to learn an association because it has survival value. In the case of taste aversion, the rat can make such associations because avoiding foods that cause nausea might have survival value. Likewise avoiding shock by crouching (or not rearing) in the presence of sounds is easily learned because rats naturally associate sounds (e.g., of a predator) with pain that an unsuccessful predation attempt entails. However, associating taste with pain is not normally found in the realm of a rat's natural experience. Conversely, color is the dominant sensory mode attached to taste aversion in the case of birds, rather than odor, which is less well developed in most birds.

Examples of Learning in "Natural Contexts"

Follow these links to review examples already considered:

1. Search Image: Operant (Instrument) Conditioning of Blue Jays (Chapter 6)
2. Taste Aversion: The Evolution of Aposematic and Mullerian Mimicry (Chapter 14)
3. Neighbor Stranger Recognition in Birds (Chapter 8)
4. Deme Recognition: Female Choice for Natal Song (Chapter 5, 12, 15)
5. Classic Song Learning (Chapter 15)
6. Spatial Mapping: Learning or Instinct of Stellar Navigation? (Chapter 12)

Adequacy of Associative Learning Theories and Complex Learning

A review of these examples provides clear evidence of some apparently ordinary abilities (e.g., color aversion) and some extraordinary abilities (e.g., star maps) that animals have for learning complex information. Some of these examples fall within the scope of associative learning paradigms. However, examples of bird song (e.g., dear enemy) and spatial learning maps appear to fall outside of this paradigm.

The case of color aversive learning of noxious prey and Müllerian mimicry that we considered can be contrasted nicely with the example of taste aversive learning of rats. Birds tend to learn aversion to noxious stimuli through associations with color. In contrast, rats learn aversion to noxious stimuli through associations with taste. Each group operates with a different sensory modality, however it appears that the *general process of learning* underlying each may be similar. Again this is not to say that the neural mechanisms are the same, but rather the principles of learning are similar. However, each group appears to be constrained in what they can learn with regards to aversive stimuli (e.g., rats do not learn visual cues, and birds tend not learn the taste cues).

In other examples, which we have studied, bird song, does not readily fall into the category of associative learning. In this case, a template of the song is formed in memory, and through a process of rehearsal, the bird learns his species-specific song. The acquisition of human language in general may involve such rehearsal learning (see Chapter 20). In songbirds, rehearsal involves a potent form of self-feedback in which the individual refines its song, in response to an internal template. The pleasure centers of the brain are most certainly involved and the neuropeptide Dopamine. The **Nucleus Accumbens** (NAcc), which along with the pre-limbic cortex, are key control areas for the **reward-reinforcing pathway** for natural stimuli like **appetitive behaviors** that involve food reward as well as aberrant behaviors like drug abuse (Chapter 11). Neuropeptides like the **endorphins** play a potent role in reinforcing the positive sense of accomplishment that is associated with operant conditioning (in humans endorphins gives rise to runner's high).

In addition, it is very clear from Chapter 8 (dear-enemy experiments in the warbler by Rene Goddard or on weakly electric fish by McGregor) that spatial components strongly interact with song learning. The cases of spatial maps indicates that even more complex kinds of learning take place in natural contexts that go beyond the scope of such associative learning experiments. The learning found in stellar maps is not very well understood. However, other forms of spatial learning such as maze running in rats appear to be associated with a specific region of the brain known as the hippocampus. Maze running paradigms have been revived in recent years because it appears that rats form **cognitive maps** of their environment, and that this map is located in the hippocampus.

The vertebrate hippocampus

In Chapter 16, I discussed the role of enriched environments in enhancing neuron growth in rodents, work that was pioneered by Marion Diamond. One of the key areas for building memory, the core component of learning, arises in the hippocampus. The hippocampus is a key brain region that I have not yet discussed, but one that contributes to many of the concepts in behavioral ecology that I have discussed. The hippocampus undergoes both plastic changes owing to use in spatial learning tasks, and also undergoes evolutionary increases in size, in those animals where spatial learning is favored under selection.

To introduce the concept of evolutionary changes in the hippocampus, simply consider the size of this neural structure in a species heavily selected for elaborate spatial ability compared to a closely related species with less of a premium on spatial memory. A very early model system (Kerry et al. 1993) in this regard is the difference between the brown-headed cowbird, *Molothrus ater*, and its icterine relatives the redwing blackbird, *Agelaius phoeniceus*, and the common grackle, *Quiscalus quiscalus*. The brown-headed cowbird is a brood parasite (Chapter 15) that must seek out and lay eggs in the nests of a host species. However, in the case of brown-headed cowbirds it is the female that must have much more elaborate spatial abilities compared to males, which in the case of brood
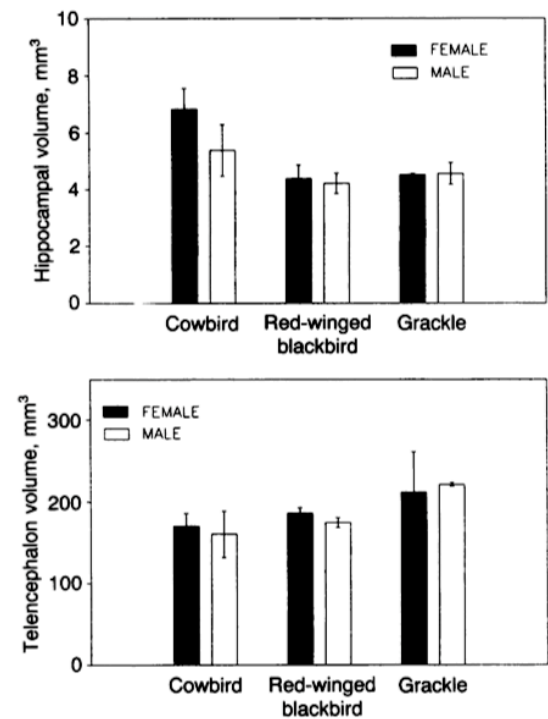

Figure 17.2. Hippocampal and telencephalic volume in three icterine species (from Sherry et al. 1993).

parasites have little need to actively defend a nesting territory. The two other icterine species, the redwing blackbird and grackle, have the more typical passerine mating system of a male that defends a territory and a female, which nests on the territory. Female brown-headed cowbirds lay at least 40 eggs over the course of the breeding season (Scott and Ankley 1980, 1983) and each egg is laid in the nest of a different host.

The female brown-headed cowbird also parasitizes the nests from among 250 different species of songbirds. The cowbird must first locate the nests before all the eggs are laid, probably relying on the songs of males of the host species. Then it periodically monitors the nest and oviposits an egg in the nest when the host begins to lay its own eggs. Therefore a selective premium is imposed on female brown-headed cowbirds to locate and keep track of many host nests. As predicted by Sherry et al. (1993) the cowbird has a significantly larger hippocampus compared to other icterines, but a normal sized telencephalon (Fig. 17.2), which is a structure unrelated to spatial learning.

Evolved changes hippocampus volume and food hoarding behavior

Another model system for studying the size of the hippocampus is species of birds that exhibit food-hoarding behavior. Food hoarders or food cachers store seeds in many locations on their feeding territory. While the behavior is not restricted to birds (e.g., squirrels are classic food-hoarders) it is best studied in birds. In particular, the titmice (Paridae), nuthatches (Siitidae), crows, jays and nutcrackers (Corvidae), woodpeckers and some raptors, store items (often a single item) in sites that are scattered across their home range (Clayton and Krebs 1995). Up to 10,000 items might be stored during the course of a year and items can be retrieved a few days to weeks after storage. Crows will often retrieve items 6 months or more after storage. Other long-term food storers in the corvidae (e.g., crow family) such as jays harvest seeds in the fall and use them throughout the winter. Therefore hoarding behavior is thought to dampen temporary fluctuations in food such as occur in winter.

Two approaches have been used to investigate food hoarding behavior and hippocampal volume. The first approach is to use the phylogenetic

Figure 17.3. The phylogeny of birds used for the phylogenetic analysis of food hoarding in association with relative volumes of the hippocampus, and of the telencephalon and also relative overall brain size. The scale for branch length is given in the bottom left (from Garamszegi and Eens 2004).

method in which pairs of sister species (e.g., as used in the brood parasite example, Fig. 17.2) are compared. In Chapter 18, we will study the phylogenetic method in greater detail. In the second method, a researcher specifically manipulates the learning environment to detect plastic changes in neurons that grow in response to the challenge (e.g., see Chapter 16, Marion Diamond' experiment on enrichment).

The phylogenetic example in food-hoarding birds is illustrative in that the method used, **independent contrasts** (Felsenstein 1985) uses a large number of species comparisons on an arbitrary phylogeny to generate data that is independent. This method is used when a large number of species comparisons, such as in Fig. 17.2) are unavailable.

The method of independent contrasts is a transformation of data, which is distributed across a phylogeny, such that data are **phylogenetically independent** (more on this in Chapter 18). What do we mean by independent. Well consider the converse pattern where the pattern of data on a phylogeny is **dependent** on closely related ancestors. Recall from the example on Müllerian mimicry that most species of *Pitohui* actually share Müllerian traits by common descent, not because they have independently evolved Müllerian colors (see Fig. 14.24).

Consider the phylogeny used to study food-hoarding behavior (Fig. 17.3). The group of birds on the first branch from the bottom is the woodpeckers, which exhibit varying degrees of specialization to food hoarding. The next branch up does not exhibit any species with food-hoarding. The following branch up is the corvidae, which again exhibits varying degrees of specialization. All corvids are food hoarders. Rather than using the raw data, which is not independent, data on hypothetical ancestors are computed and the distance along the tree among such ancestral reconstructions is used, which are independent (Chapter 19).

Garamszegi and Eens (2001) used the phylogenetic distribution of food hoarding behavior along with avian phylogeny to test whether a large hippocampus went hand-in-hand with evolution of hoarding behavior. They also tested whether other traits, which have also been linked to the hippocampus, like migratory behavior or brood parasitism confounded the pattern of brain enlargement due to food-hoarding behavior.

Moreover, they posited an intriguing hypothesis not yet considered regarding evolutionary changes in other brain regions besides the hippocampus (e.g., general brain size). The hippocampus does not act in isolation to form memories. For example, the **amygdyla** a small region is specifically responsible for integrating more traumatic events (in humans such as post-traumatic stress disorder. In animals the amygdyla is likely to associations regarding attempted predation attempts against an animal. Besides such small but potently acting brain regions like the amygydala, food hoarding is a highly complex cognitive task. During the process of caching visual information from nearby landmarks is stored. The sun-compass orientation mechanisms might also be used (see Chapter 12). Olfaction may also be used (Sherry and Duff 1996).
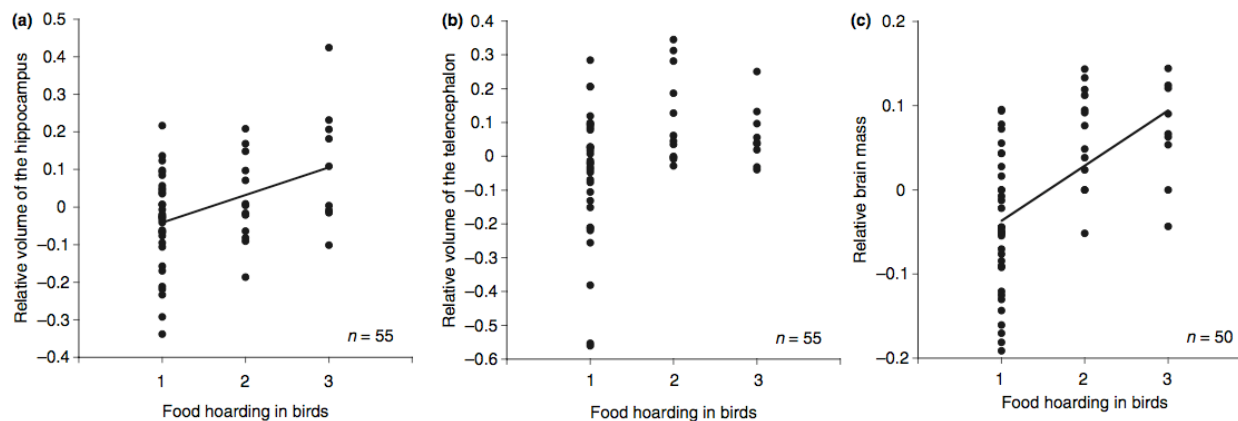

Figure 17.4. Relationship between food hoarding and (a) volume of hippocampus relative to volume of the telencephalon. (b) volume of the telencephalon relative to body size and (c) brain mass relative to body size, all data based on the raw species data. Lines are phylogenetically corrected linear regression lines and presented only if the corresponding phylogenetic associations were significant (from Garamszegi and Eens 2004).

If specialization to food hoarding selects for the enlargement of different neural structures responsible for the learning, and the sensory and motor control of this behavior, Garamszegi and Eens (2004) hypothesized that it also selects for large brains. Although the relative size of the hippocampus is small, simultaneous neural specializations to food hoarding may occur in other regions of the brain with significant volumetric importance. Therefore, if food hoarding is a cognitively complex task involving elaboration of a variety of brain regions, the total brain volume should vary with the specialization of this behavior. As Garamszegi and Eens (2004) predicted, the size of the hippocampus was associated with the level of specialization in food-hoarding behavior and the size of the brain increased in a correlated fashion (Fig. 17.4).

Plasticity in hippocampal volume

Experiments on caching environments where birds are given or deprived of caching opportunities shows that neuronal growth also results from experience. Clayton and Krebs (1994) used a simple set-up in which marsh tits were provided with the opportunity to either stash seeds in holes drilled in branches, or seeds were finely ground so they could feed, but not stash seeds. The neuronal growth in the hippocampus was rapid in Group 1, which experienced an environment conducive to hoarding seeds from the age of independence (e.g., by trial 8=24 d exposure the exhibited enlarged hippocampi) (Fig. 17.5). Those birds that only experienced the ability to cache after trial 8 showed a reduced

Figure 17.5. Development of food-storing behavior, memory-based retrieval and the hippocampus in hand-raised marsh tits. (a) The number of seeds (Mean ± SE) stored by three groups of marsh tits during a 20-min storing trial (Group 1 – exposed to food storing at 35 d, the age of independence (e.g., trial 1), Group 2 – control levels of food storing until 59 d (e.g., trial 8), and group 3 – control levels of storing throughout (e.g., seeds were finely ground so they had to eat them and could not store them). Group 1 birds rapidly increased in storing behavior between the 3rd to 4th trial (day 41-44). In Group 2, storing emerged with 2 to 3 trials of exposure to a storage environment. (b). Development of spatial memory for storage sites in Group 1 birds. The plot of cumulative numbers of seeds found as a function of cumulative number of 'visits' to potential storage sites (small holes in branches) is quite good but still less than the theoretical maximum of perfect retrieval performance (e.g., the 1:1 line, not shown). (c) Mean (± SE) of relative hippocampal volume (departure from regression of hippocampus to telencephalon volume) of experimental (Group 1, 2) and control (Group 3) birds at three time-points in the experiment. Notice that birds given caching experience show rapid increase or simple threshold effect on hippocampal volume, while deprivation of experience actual results in a cumulative attrition of hippocampal volume (from Clayton and Krebs 1995).
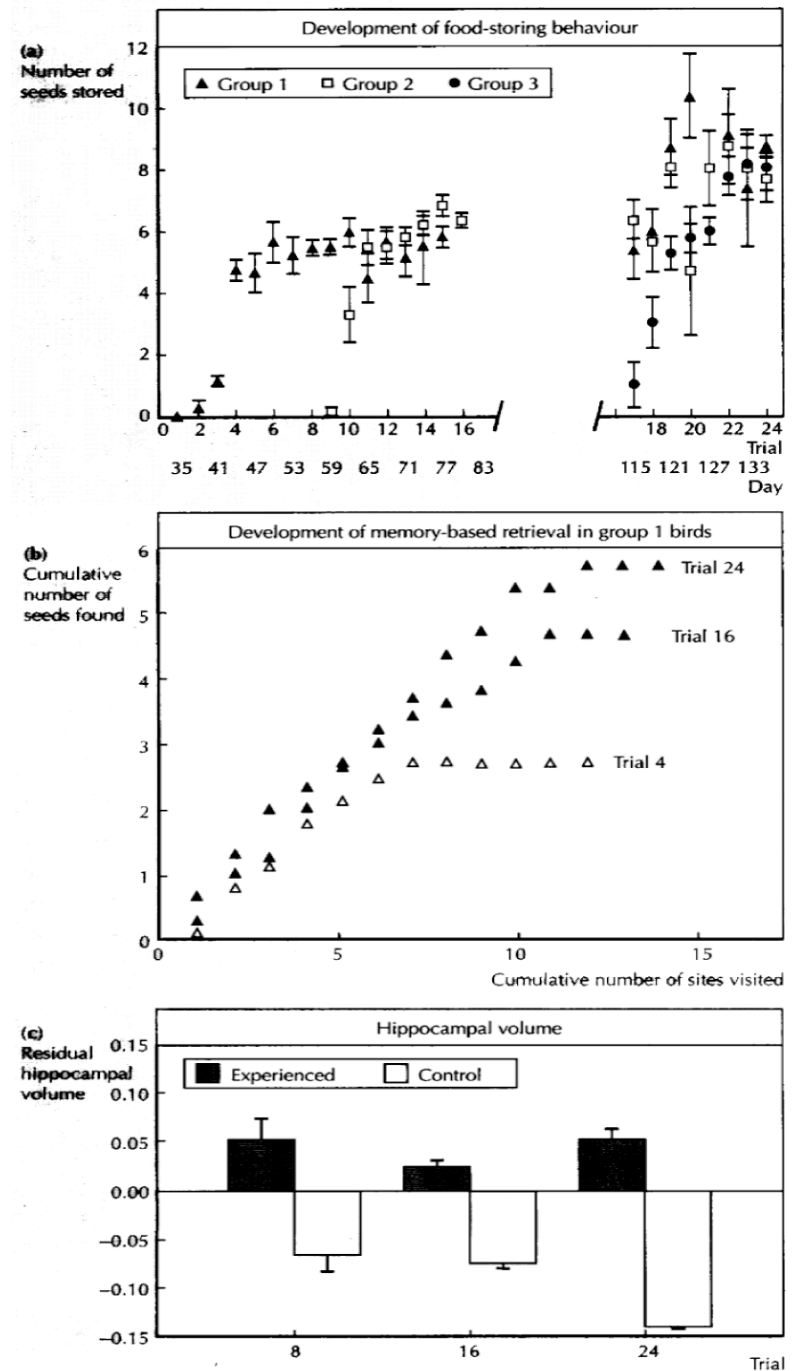
level of growth by trial 16 (= 48 d), but quickly caught up by trial 24 (=72 d). In marked contrast, birds that were deprived of a caching environment had a marked *attrition* in hippocampal volume (Fig. 17.5c).
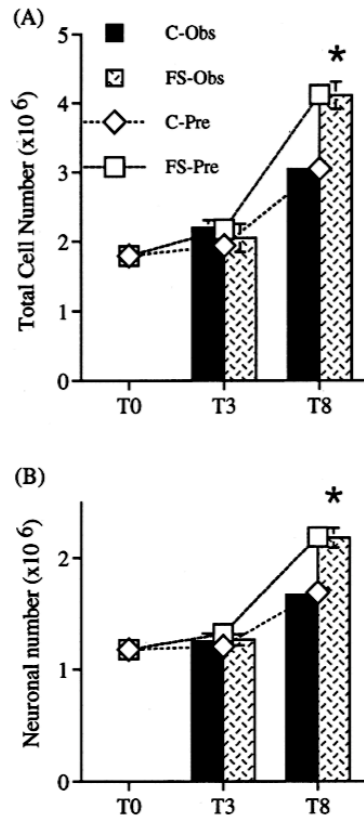

Figure 17.6. Mean observed (S.E.) and predicted (Pre.) total hippocampal cell number and (B) total hippocampal neuronal number in the food-storing (FS) and control (C) birds after three and 8 trials (T0 = pre-training group). Predicted values were derived from data on birth (cell division) and death rate (apoptosis, Fig. 17.7) of neuronal cells. Graphs show the close match between the predicted and observed total cell and neuronal numbers at T3 and T8 (from Patel et al. 1997).
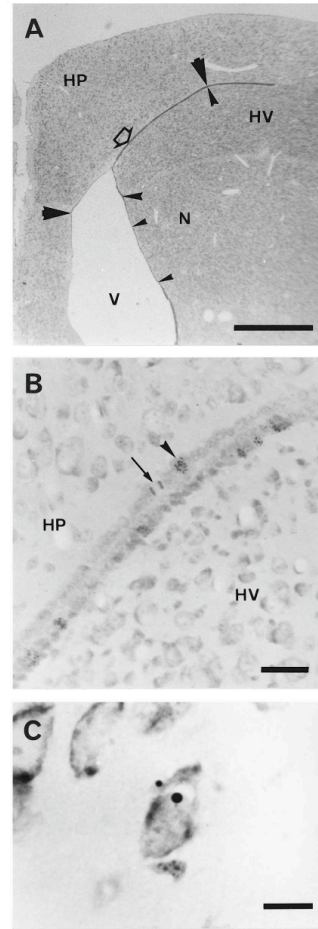
Of course a simple assay for hippocampal volume does not prove that new cell division has actually occurred. To prove neurogenesis a radiolabelled marker must be used to determine which cells were born since the onset of the environmental enrichment. Patel et al. (1997) followed up the learning environment experiments on caching with tracer studies of hippocampal region (Fig. 17.6) (e.g., of the sort used to prove neurogenesis in song nuclei in birds, Chapter 16). New cells were clearly born in the enriched caching environment group, thereby contributing to the overall increase in hippocampal volume.

Plasticity in hippocampal volume

Volumetric studies have been conducted in a range of subjects including London taxi-drivers, polygynous male voles, nest-parasitic female cowbirds, and a number of food-storing birds. In these systems the size of the hippocampus is correlated with tasks that involve an extra demand for spatial learning and memory condition. Despite the detailed studies on a number of species, the first test of which component of spatial memory is enhanced via the hippocampus has just been done. There are at least 3 constituent aspects to spatial learning and memory:

1) **memory capacity** – the number of site is remembered,
2) **memory persistence** – duration over which a site is remembered,
3) **spatial resolution** – the least distance at which remembered sites can be discriminated (analogous to perceptual resolving power with regards to IFD, see Chapter 7).

Biegler et al. (2001) compared retention times (e.g., average time that a subject remembered a location on a touch screen) between a food storer, the coal tit, *Parus ater*, vs. non-storer species the great tit, *Parus major*. This test involves a computer challenge similar to the training used in cryptic prey detection (Chapter 14). Birds were trained to peck at 1 to 4

Figure 17.7. (A) Photograph of a coronal section (left side) showing the VZ regions measured on the sides of the hippocampus (HP, between the two large arrowheads), hyperstriatum ventrale (HV, between the two medium arrowheads) and the neostriatum (N, between the two small arrowheads). The large arrowheads also mark the medial and lateral boundaries of the HP at this level. Open arrow points to the VZ; V = ventricle; Scale bar = 560 m. (B) Ventricular zone cells labeled with [3H] thymidine, 2 h after injection of the label (arrowheads). A mitotic cell in telophase (e.g, cell birth) (arrow) is shown in this photograph near a [3H] thymidine labeled cell (arrowhead), both of which are in the VZ adjacent to the HP. Other [3H] thymidine labeled cells are present in the VZ adjacent to the HV (not shown). The focus is on the mitotic cell. Scale bar = 30 m. (C) A photograph of a typical **apoptotic cell** in a Nissl stained section of the HP. Scale bar = 7.8 m. Data on birth and death rates were used to predict cell numbers (e.g., see Figure. 17.6) (from Patel et al. 1997).

white squares (2 cm × 2 cm; the ''sample'') on a computer-controlled touch screen (Fig. 17.8). The screen was touch sensitive and images disappeared after a peck was directed at them. Once all images had been pecked and after a retention interval of 1 sec, birds were presented with a square in one of these earlier locations and a second square in a new location. Correct choices were followed by delivery of a small piece of peanut as a reward; errors were followed by the onset of the intertrial interval. The intertrial interval was always 90 sec. (N.B., this positive and negative reinforcement was similar to the test of the search image hypothesis as a constraint on learning in blue jays, see Chapter 6).

Beigler et al. (2001) predicted 3 outcomes. If food-storers have greater memory capacity than non-storers, Biegler et al. (2001) hypothesized that performance should be similar when there is only 1 item to remember, but should diverge with increasing number of items. Non-storers would have worse performance when required to remember more items (e.g., a difference in slope should be present, Fig. 1A). If species differed only in the spatial resolution of memory, they should achieve similar performance levels when items are far apart, but the food storers should perform better when items are close together (Fig. 1B). If food storers only have longer-lasting memory, then species difference in performance should be similar regardless of number of number of items or proximity, but the retention interval will simply be elevated (Fig. 1C).

Coal tits performed better than great tits on a task that assessed memory persistence (Fig. 17.10) as predicted by the outcome in Figure 17.9c but not on a task that assessed memory resolution or on one that tested
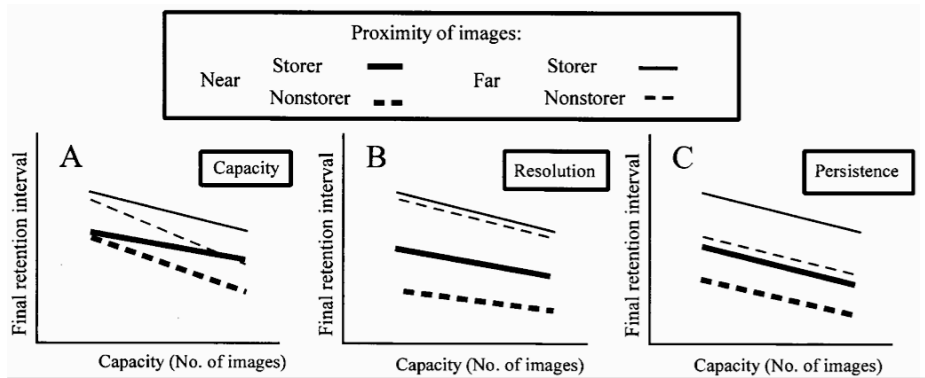

Figure 17.9. Predicted outcomes if hippocampal enlargement is associated with either memory capacity, resolution, or persistence. The storers are represented by the solid lines, the nonstorers by dashed lines. Heavy lines represent images that are near to each other and thin lines represent images that are far apart. (A) If species differ in memory capacity, performance should be similar when there is little to remember, but diverge as memory load increases. The pair of lines for each group are the predictions for the way in which performance levels should change with increasing numbers of sample images when choice images differ in proximity. (B) If species differ in spatial resolution, performance should be similar when the images are far apart, but differ when they are close together. (C) If species differ in memory persistence, the differences should be apparent from the smallest memory load and remain the same as memory load increases, regardless of proximity (from Biegler et
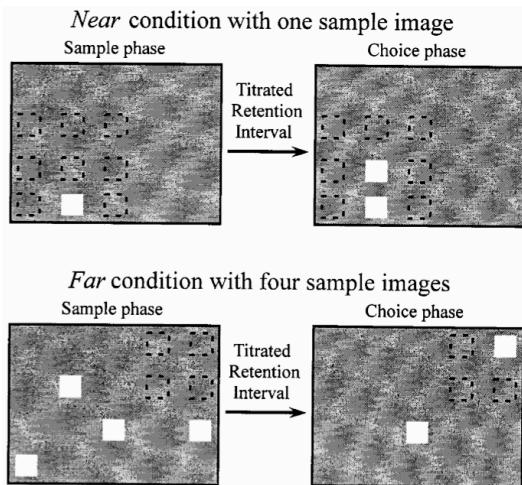

Figure 17.8. A schematic of the experimental design showing examples of the variation in the number of sample images and in the distance at which choices were presented. From 1 to 4 white squares were displayed in the sample phase. In the Choice phase of the Near condition, 1 image (and only 1, regardless of the number of sample images) was placed in 1 of the positions immediately adjacent to the target, which are marked by stippled outlines. The birds were presented only with white squares. In the Choice phase of the Far condition, there was no sample in the positions immediately adjacent to the target. The combination of 1 to 4 samples with Near and Far conditions resulted in a total of 8 different conditions (Biegler et al. 2001).

Figure 17.10. Final retention intervals (seconds) reached by the birds at the end of the experiment. Data are means and SE. The storers are represented by the filled circles, the nonstorers by the open circles. Heavy lines represent images that are near to each other and thin lines represent images that are far apart. The experimental data matches the predictions of the role of the hippocampus as enhancing persistence of spatial locations in memory (from Biegler et al. 1997).
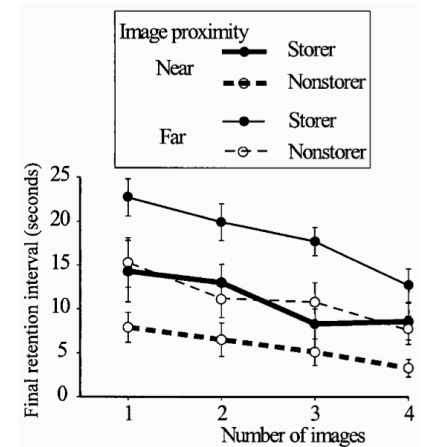
memory capacity (not shown). These results show that the advantage to the food-storing species associated with an enlarged hippocampus is one of memory persistence. They qualify their results by noting that they did not study long-term memory, only short-term spatial memory. Other aspects of memory might be recruited (e.g., memory capacity) in the case of long-term memory, but this interesting experiment requires testing by an intrepid student of animal behavior.

Behavioral syndromes and social learning: shy-bold learners

Individual differences in exploratory behavior in novel environments have been observed in most vertebrates (fish, mammals, and birds) except reptiles and amphibians. Familiarity with local environment is essential to survival. Through exploration, animals learn the location of food, retreat sites, and establish relationships with their neighbors.

Individual differences in behavioral reactions to novel situations are exhibited by mice and rats (van Oortmerssen et al. 1985, Benus et al. 1987a,b), bluegill sunfish (Clark and Ehlinger 1987), pumpkinseed fish (Wilson et al. 1993), pigs (Hessing et al. 1994), and great tits (Verbeek et al. 1994). Laboratory selection experiments have established that breeding populations of aggressive and non-aggressive mice have marked differences in social and nonsocial coping strategies. Non-aggressive mice are passive copers that are highly exploratory and adjust quickly to environmental changes. Aggressive individuals are active copers that develop routine like-behavior, spend less time on exploration, and actively try to modify changes in the environment rather than adjust to them (van Oortmerssen et al. 1985, Benus et al. 1987, 1990, 1991). Psychologists also identify behavioral differences in humans along a shy-bold continuum. Both aggressive mice and bold humans act normally in a new situation and actively explore while shy individuals, like their non-aggressive rodent counterparts, react passively and often retreat (Kagan 1991, Wilson et al. 1993).

In great tits, behaviors have been dichotomized into two categories: fast explorers and slow explorers (Verbeek et al. 1994). Fast explorers move quickly through a novel environment and visit most sites, but spend little time at any individual site. Birds in this category also display difficulty

in altering their foraging patterns when feeding sites are experimentally altered. Conversely, slow explorers spend more time at individual sites in a novel environment, but do not necessarily explore the entire observation chamber. These birds quickly adapt their foraging habit to changes in their environment. If differences in juveniles continued into adulthood, one would expect the alternative behavioral effects of each class to be manifest as distinct life history patterns. Researchers have been able to select for these traits in breeding colonies (Verbeek et al. 1994, pers. comm. C. Both). This, along with the genetic basis for aggression and other associated behaviors in mice indicates that individual behavioral differences may arise from differential selection depending on the environment (Clark and Ehlinger 1987).

These early observations on animal personalities (Sih et al. 2004) has led to an explosion of new information on the heritability of these traits, the linkage of these traits to learning styles, and the fitness consequences of shy-bold behavioral syndromes for growth, survival and reproductive success. From a practical standpoint, the personalities are scored based on a large number of behaviors that are then distilled into a summary statistic called a principle component axis. Principle component axes are the axes are simply a weighted sum of the original behavioral traits, which compartmentalize the variation in new composite measures (see Side Box 17.1). Let's just take a simple case of two traits for juvenile perch: number of prey attacks and number of times fish was in the open (Fig. 17.11), away from the retreat site during a standard trial in a laboratory experiment (Magnhagen and Staffan 2002).
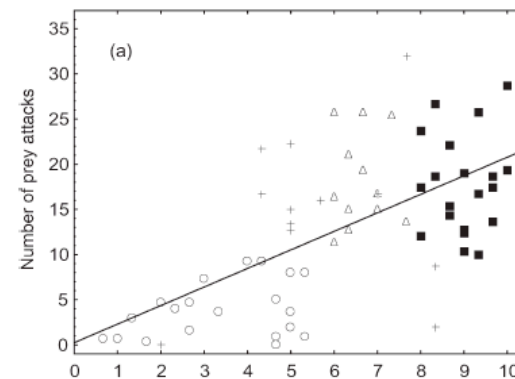

Fig. 17.11. Correlation between mean number of prey attacks and number of times juvenile perch were observed out in the open during first experiment. Bold fish (squares) are defined to be high on both scores while shy fish are defined to be low on both scores (circles), or intermediate (triangle or plus). A classic shy-bold continuum in two traits. (Magnhagen and Staffan 2002)
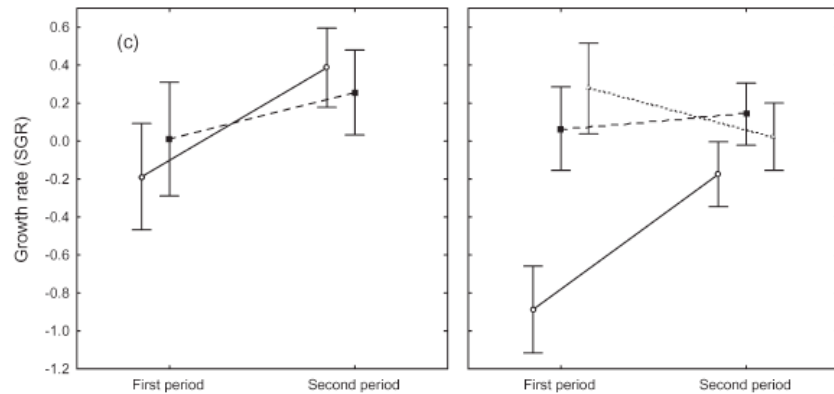
Figure 17.12. Effect of shy-bold on growth rate during two periods, when fish were housed only with the same type (left), or when housed in mixed groups (right). (from Maghagen and Staffan 2002).

One of the most interesting comparisons arises in the context of the effects of shy-bold behavior on a performance trait like growth rate in different social environments. Maghagen and Staffan (2002) compared the growth of shy and bold fish when they were housed with fish that are the same (e.g., bold with bold and shy with shy), compared to mixed schools (shy with bold). There is an immediate effect on the growth of shy fish when housed with bold fish, however, in subsequent growth periods these shy fish can achieve the same growth as bold or intermediate fish (Fig. 17.12). The change in shy fish during the second period implies some kind of learning process or acclimation is involved.

These laboratory observations in controlled social situations are salient for natural selection on learning. In a natural context, the short-term response of shy fish may result in a growth cost to their behavior, when surrounded by bold fish. However, if shy fish have a higher survival, owing to their propensity to stay in retreats, then predators will remove bold fish at a higher rate. Thus the learning polymorphism may be under some form of frequency-dependent selection arising from the balance between mortality and growth in the wild (see also Chapter 7).

In other model systems, like birds, it is possible to construct aviaries and test the differences between shy and bold individuals in the presence or absence of conspecifics. Recent evidence form the great tit, *Parus*

major, indicates that shy and bold individuals react in dramatically different ways to either feeding or anti-predator contexts.

Differences between shy-bold animals in foraging and potential anti-predator behaviors are common in laboratory studies. For example, in non-social feeding contexts, there is no difference between shy-bold great tits in their latency to escape when startled (Oers et al. 2002). However, in a social context, latency to startle is dramatically affected by both activity of companion birds, and by the behavioral predispositions of the birds (Fig. 17.13).

Besides these controlled experiments in the aviary in lab contexts, evidence is

Figure 17.13. Relation between the activity of a companion and the difference in startle latency between a nonsocial and social context (context difference) for (a) females and (b) males in the great tit, *Parus* major. Open circles and dashed line = fast explorers (FE); closed circles and solid line = slow explorers (SE). (from Oers et al. 2002).

accumulating that such animal personalities have dramatic effects on tradeoffs among components of the life history such as time to maturity versus weaning success. For example, big horn sheep females that are bold tend to mature earlier and have higher weaning success on the first bout of reproduction, which is termed the **primiparous** episode (Fig. 17.14).

Links between shy-bold and a full set of life history tradeoffs such as survival vs. reproductive success have yet to be made. Moreover, while links to frequency-dependent selection are implied by experiments in which social context affect behavior (e.g., social selection), the fact that
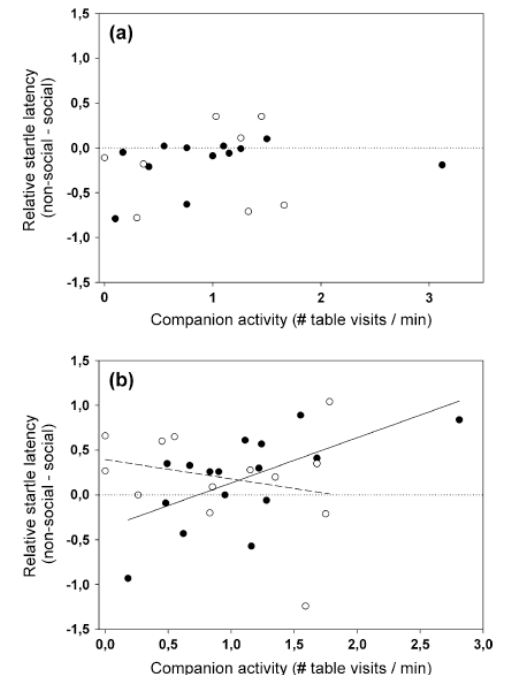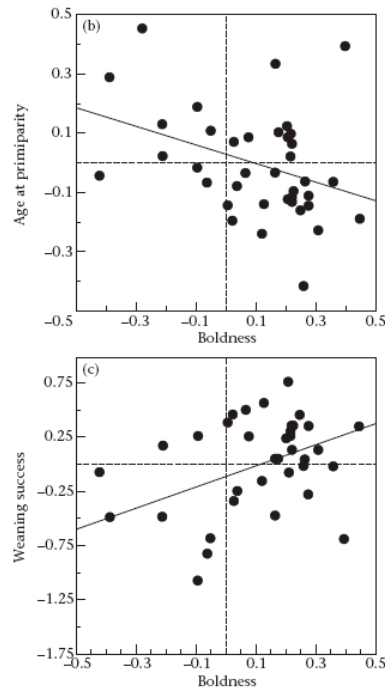
Figure 17.14. Relationships between temperament indices and life-history traits in bighorn ewes at Ram Mountain, Alberta, Canada (a) Docility and age at primiparity, standardized for density, ewe mass and boldness. (b) Boldness and weaning success standardized by ewe age (Reale et al. 2000).

the shy-bold types can alter their behavior suggests that learning can attenuate the force of frequency-dependent behavior. However, as noted in the Side Box 17.1, the heritability for some shy-bold metrics of the dumpling squid such as in threat situations remains high while that heritability in other situations is likely to be attenuated by learning or other adjustments (such as in a feeding context).

To generate fitness inferences of shy and bold personality types in nature researchers rely on long-term field pedigrees in which animals are tracked over very long time periods. The number of pedigree studies is growing (e.g., big horn sheep, soay sheep, red deer, lizards, greater reed warblers, red squirrels) and the application of pedigree data to behavioral personalities is likewise growing. For example, the red squirrel of northern Canada has a pedigree that has been followed for over the past two decades. Female aggressiveness was first scored in a simple outdoor test. A total of 71 adult females and 27 juvenile (young of the year) females were scored with three behavioral tests. The first was an open field, which is used to quantify activity, exploration and stress responses in a novel environment (Walsh & Cummins 1976; Martin & Réale 2007). The second test, mirror-image stimulation, is used to assess aggressive and sociable behaviors (Svendsen & Armitage 1973). The third behavioral test quantified the response of squirrels to handling (Carere & van Oers 2004). Immediately after transferring an individual from a trap to a handling bag, Boon et al. (2007) measured struggle rate. Several of these behavioral scores can be statistically collapsed into a few axes representing behaviors like aggression with the

technique of principal components analysis (see Side Box 17.1 for an example with the dumpling squid). The survival of progeny from a female red squirrel in the nest and overwinter was then correlated with personality types of the female.

The magnitude and direction of selection on personality types of the red squirrel changed among life history stages and across years (Fig. 17.15). Boon et al. (2007) suggest a role for balancing selection in the maintenance of personality. **Balancing selection** results from two opposing forces in which differences in the direction of selection across life history phases end up generating a fitness optimum. In the case of red squirrels, aggressive mothers are poor at getting progeny through the earliest phases of reproduction, but excellent at getting the progeny to survive overwinter. The converse is true for less aggressive mothers.
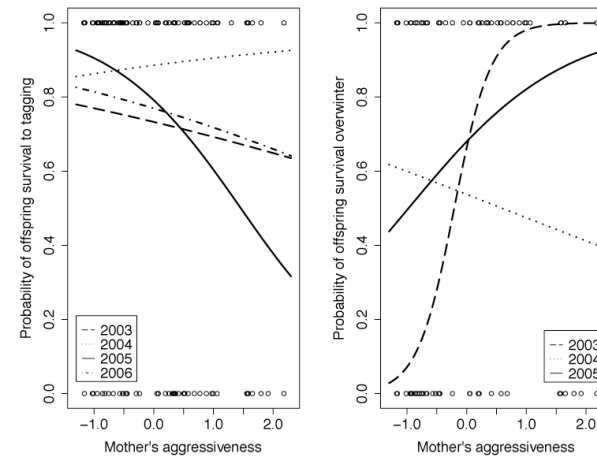

Figure 17.15. a) The survival of juvenile North American red squirrels from birth until 25–30 days of age, shortly before emergence, depends on the aggressiveness of their mother and varies by year. (b) The overwinter survival of juveniles from weaning until 1 May of the following year also depends on the mother (Boon et al. 2007).

Much work still remains to determine how heritable variation in personalities is maintained in nature. In studies in great tits (Dingmanse et al. 2004) indicate that the interaction of both parents has a dramatic impact on number of recruits (see Side Box 17.1). The study illustrates logistical difficulties of estimating fitness on learning styles in nature.

Side Box 17.1. Exploratory behavior in the wild

Measuring the fitness consequences of parental learning personalities in the wild is a daunting task. Dingmanse et al. (2004) devised a clever field aviary with a novel exploratory environment, which was lined with a double stack of holding pens (Fig. 17.16). This allowed for rapid throughput of great tits, *Parus major*, in the testing arena. They then carried out a standard pedigree analysis of fitness to calculate the fitness consequences of female exploratory behavior for the progeny (Fig. 17.17), as well as the interaction of parents (Fig. 17. 18).

First, there were striking differences in selection on exploratory behavior among years. Moreover, survival rate of the mother *versus* father differed dramatically with respect to exploratory behavior among years. Second, survival of female progeny as a function of average exploratory behavior of parents varied among years, but no patterns were observed among male progeny. Third, the most intriguing pattern, success of parents depended on the interaction of their exploratory scores. Females with a low score that nested with a low-score male had high success, as did females and males with high score. Therefore, Dingmanse et al. (2004) had evidence that assortative mating would be favored by selection, but they did not necessarily show that the birds actually mated in an assortative fashion. This behavioral predisposition of is great importance to the theories of genetic and cultural evolution with regards to learning styles in free-ranging animals.

Interpreting annual patterns of recruitment documented by Dingemanse *et al.* (2004) is less straightforward. As Dall (2004) points out, a number of questions remain. Why, in the season after the good winter, did mated pairs that matched each other's exploratory personalities produce more recruits? Indeed, either pairs mated randomly with respect to personality, if the male was a first year breeder, or exploratory tendencies were negatively correlated within pairs with older males. Future work will need to elucidate consequences of the great tit exploratory personalities across all life history stages. In particular, dispersing juveniles must also be accounted for, as it appears that pairs that mate assortatively produce fledglings in better condition and fast–fast pairs beget young that disperse further Dingmanse et al. (2003). Finally, a key issue not addressed in this work is why exploratory behavior should be so consistent within individual great tits and heritable. What is it that selects against individuals that adjust their boldness to current conditions?

Figure 17.17. The relationship between 2 fitness components and individual personality for three successive years (1999–2001) in male and female great tits, *Parus major*. (*a*) Annual adult survival as a function of their exploratory behavior. Lines represent the slopes of the relationship between adult survival and exploration score. (*b*) Number of offspring surviving to breeding (recruits) as functions of the exploratory behaviors of their parents. The dashed lines give the arithmetic mean exploration score for each sex and year combination (from Dingmanse et al. 2004).
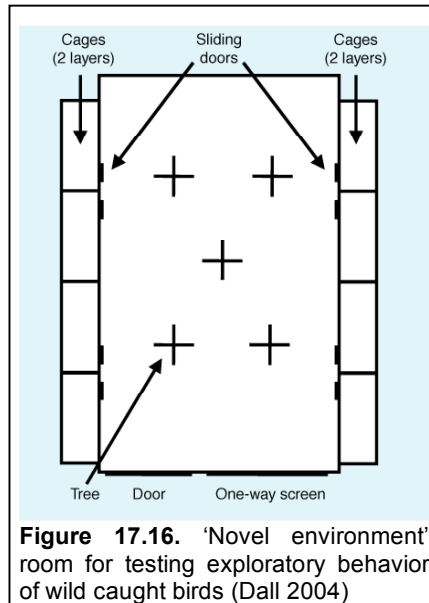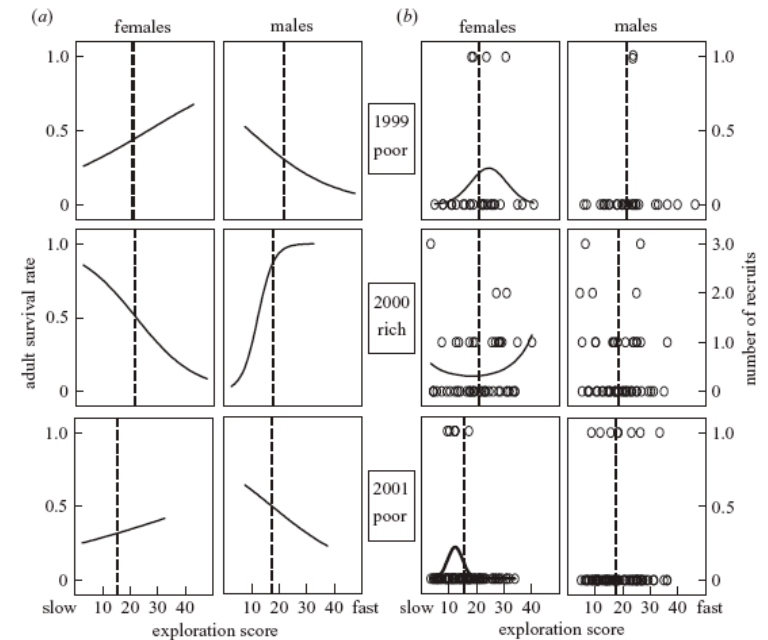

Figure 17.16. 'Novel environment' room for testing exploratory behavior of wild caught birds (Dall 2004)
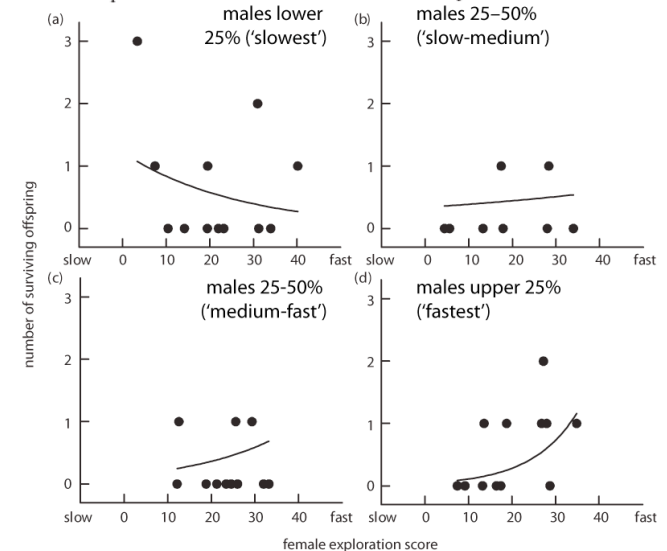

Figure 17.18. Effect of exploratory behavior of both parents on number of offspring surviving to breeding in the year 2000 (*n* = 44 pairs). Exploratory behavior of females is given on the x-axis. Male exploratory scores are divided into 4 groups of equal numbers.

The shy-bold continuum may unify continuous variation in behavioral traits, with the discrete variation of alternative strategies. As such the underlying genetics and selection may prove central in unraveling many key issues in behavioral ecology, and even issues of animal intelligence.

The role of shy-bold in dominance interactions

A step in this direction is to study the role of shy-bold personalities on the establishment of dominance hierarchies. A very interesting study on shy-bold behaviors of the great tit, *Parus major*, reveals the role of this personality continuum on the establishment of dominance interactions, which can provide an avenue by which social selection can operate.

In the great tit studies (Verbeek et al. 1994) personality types are termed fast- vs. slow-explorer, based on their exploration of a novel arena with perches (Side Box 17.2). A slow-explorer takes a long time to traverse the perches, while a fast exploring rapidly moves from one perch to a new perch and visits all stations in short order. Early studies on the establishment of dominance hierarchies in aviaries revealed that when equal mixtures of fast (4 birds) vs. slow (4 birds) explorers where set up in aviaries, they non-randomly assembled into a dominance hierarchy in which only one single fast-explorer held the dominant position, but surprisingly the other 4 slow explorers tended to hold positions 2-5, and the remaining three fast explorers held the lowest 3 positions.

Detailed behavioral observations revealed that slow explorers would not engage in the early dominance struggles, which tended to only be among fast explorers. However, after these dominance relations among fast explorers were established slow explorers would exert dominance over the losers among the fast explorers. Here, an endocrine perspective might be very instrumental. Based on work presented in chapter 6 on games, animals losing contests often experience different corticosterone profiles than winners. This social 'stress' effect may make the losers vulnerable to the alternative personalities like the slow explorers who await the outcome of dominance interactions among a group of fast explorers. Interestingly, stress and corticosterone levels *per se* dissolves some of the neural connections in the hippocampus, perhaps creating a tabula rasa of sorts that can be reshaped after a stressful event.

The development of shy-bold personality types

One of my early childhood fascinations was with the sheer intelligence of cephalopods. I would watch each episode of Jacques Cousteau with earnest in the hopes of learning more about squid, cuttlefish and the octopus. I fantasized that Jacques would capture a giant squid, which has the largest invertebrate brain in the world. The giant squid brain is only exceeded by its nemesis the sperm whale in sheer brain size. Alas no one has yet caught a giant squid, nor do we have any observations on this piece de résistance of invertebrate intelligence in action.

Nevertheless, the cephalopods have served as a remarkable model system for investigating animal intelligence. Recent studies by Sinn et al. (2007) reveal how shy-bold types are heritably transmitted across generations (Side Box 17.2) and how shy-bold types unfold in the development of personality across an individual's lifetime (Fig. 17. 19).

Most recently, Sinn et al. (2007) scored shy-bold behaviors at 5 different time points of an animal's lifespan. Squid that were 'bold' in threat tests were not necessarily 'bold' in feeding tests (Fig. 17.19), and this lack of across-context correlations was observed across their entire life span. Thus, it appears that, at least among their testing scenarios, squid have the behavioral flexibility from birth to express context-specific shy/bold behavior (Coleman & Wilson 1998; Sinn & Moltschaniwsky 2005).

Figure 17.19. Mean patterns of shy/bold scores across development, and in two different contexts (feeding and threat, see Side Box 17.2 for how scores are computed). Error bars represent SE, and the solid vertical line indicates the beginning of sexual maturity (Sinn et al. 2007).
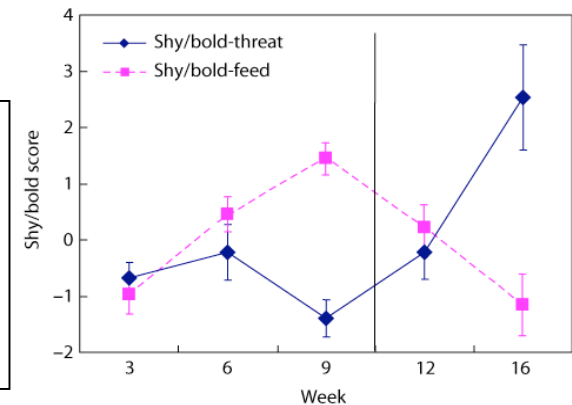
Side Box 17.2. The heritability and fitness components for animal personalities: the dumpling squid

Table 17.1. The first step is shy-bold scales is to reduce the large number of behaviors that are scored using a statistical method, which is common in behavioral analysis that is called **principal components analysis**. The first axis for dumpling squid is a linear combination of 6 traits in bold, whereas activity traits are significant for a different set of traits and reactivity are traits that are linear combinations of a third set of traits. These axes describe different components of behavior (Sinn et al. 2006).

Table 1 Principal component loadings used to generate shy–bold (PCA1), activity (PCA2) and reactivity (PCA3) scores in threat tests. Original loadings were derived from PCA analysis on a large sample ($n = 97$) of adult squid (Sinn & Moltschaniwskyj, 2005).

|	Principal component		
Behaviour	Shy–bold	Activity	Reactivity
Number of touches	**0.802**	−0.201	−0.338
First behaviour after touch	**0.864**	0.111	−0.282
Jet	**−0.638**	0.150	**0.562**
Grab	**0.845**	0.000	0.140
Arm flower posture	**0.424**	**0.683**	0.264
Log time spent moving	**−0.434**	**0.684**	0.019
Amble	−0.128	**0.569**	−0.326
Colour change	−0.032	**0.561**	−0.089
Fin swim	−0.037	**0.863**	−0.051
Log time to first bury	−0.023	−0.035	−0.171
Bury	−0.038	0.057	−0.017
Ink	−0.210	−0.140	**0.823**
Percentage variance explained in the current subjects			
Adults	40.4	18.4	11.0
Offspring	26.7	19.9	15.2
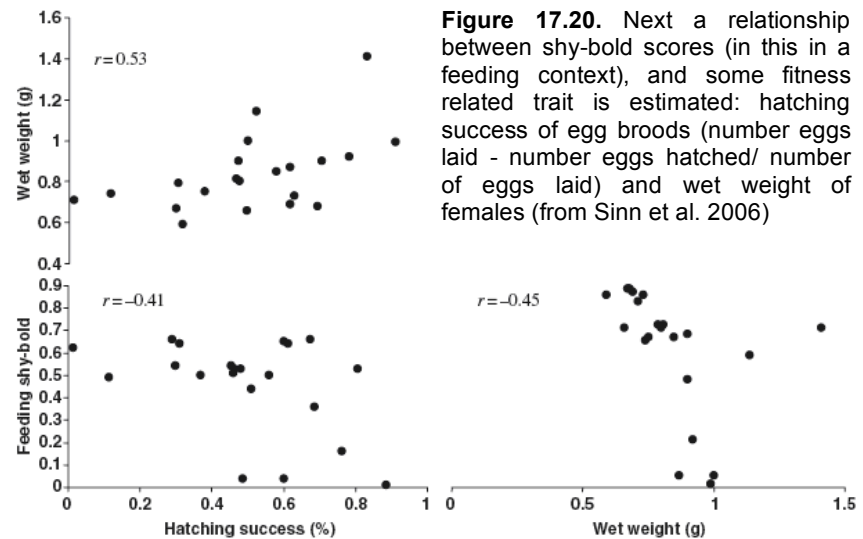
Figure 17.20. Next a relationship between shy-bold scores (in this in a feeding context), and some fitness related trait is estimated: hatching success of egg broods (number eggs laid - number eggs hatched/ number of eggs laid) and wet weight of females (from Sinn et al. 2006)

Table 2. In the final step, the most difficult correlation is estimated between parents and offspring in that such tests typically require large sample sizes or very standardized conditions across generations. Notice that in the dumpling squid example, shy-bold in the threat context is highly heritable, but not at all in the feeding context. This result is entirely consistent with an innate response in a threat context, but learned effects in a feeding context. The shy-bold analysis of perch mentioned in the text, suggests that learning in mixed groups (or conditioning of some form) modulates traits in feeding contexts. (from Sinn et al. 2006)

Table 2 Estimates of additive genetic components of variation and heritability and their associated standard errors for six squid personality traits.

	Threat			Feed		
Trait	Shy–bold	Activity	Reactivity	Shy–bold	Activity	Reactivity
Progeny only ($n = 147$)						
Mean; SD	−1.45; 0.58	0.83; 1.32	−0.33; 0.70	0.04; 0.88	5.18; 2.88	1.24; 2.75
Additive genetic	0.072 ± 0.052*	1.173 ± 0.488**	0.556 ± 0.192**	0.062 ± 0.092	0.389 ± 0.794	Φ
Residual	0.267 ± 0.049	0.567 ± 0.288	0.068 ± 0.100	0.716 ± 0.114	7.927 ± 1.166	7.565 ± 0.886
Heritability	0.213 ± 0.143	0.674 ± 0.197	0.891 ± 0.174	0.079 ± 0.117	0.047 ± 0.095	Φ

In feeding contexts, the pattern of change during development of the dumpling squid before maturity was reversed. Bolder squid were more phenotypically consistent during early juvenile periods (weeks 3-6), throughout sexual maturity (weeks 9-12), and into adulthood. The overall pattern in feeding tests was that squid that were 'bold' at week 9 remained bold through adulthood while week 9 shy individuals changed more, but in the direction of increased shyness (Fig. 21.b). The consistency of shy/bold behavior increased with age, first during juvenile life stages, and then again after sexual maturity.

Sinn et al. (2007) point out that the idea of consistent or canalized phenotypes predicts that individuals should have experiences that 'fix' their phenotypes via positive feedback loops with the environment (e.g., social environment see above), and studies on human personality types generally supports this idea (Roberts & DelVecchio 2000; Srivastava et al. 2003; Caspi et al. 2005). The results by Verbeek et al. 1994) suggest that such social feedback loops arise from interactions among conspecifics personality types. Once again hormonal studies during sexual maturity in squid and other animals should provide key insights into the structural basis of developmental plasticity in shy/bold behaviors. In the study by Sinn et al. (2007), squid categorized as intermediate shy/bold feeders (Fig. 17.21) became the largest as adults (see Fig. 17.20, Side Box 17.1).
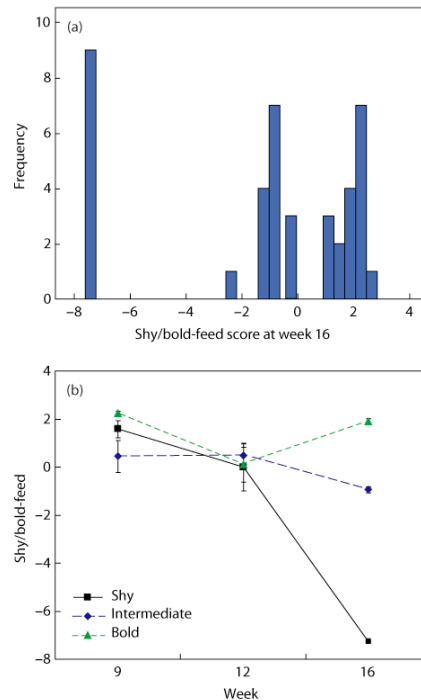

Figure 17.21. (a). The frequency distribution of shy/bold-feed scores at week 16. Squid were classified as 'shy', 'bold', or 'intermediate' based on distinct breaks in the distribution. (b). Developmental trajectories (mean±SE) of squid shy/bold 'types' (based on back-tracking from week 16 scores) in feeding tests through sexual maturity (Sinn et al. 2007).

Observational or social learning

The experiments on animal personalities clearly point to another important avenue for learning that merits attention. The role of **observational learning** has been clearly established in the animal kingdom. A classic form of observational learning was first reported in octopus in which an octopus in a separate tank watched a fellow octopus solve a puzzle of getting a lobster out of a bottle with a stopper over the entrance. There was a small hole in the stopper and the 1st octopus had to solve the puzzle by pulling on the stopper after inserting its tentacle into the hole, pull out the stopper, and gain access to the treat. The amount of time it took the "observer" octopus to solve this task was greatly reduced relative to the 1st naïve octopus indicating a capacity for observational or perhaps **imitative learning** styles.

Observational learning is not merely a property of those invertebrates endowed with an elaborate central nervous system like cephalopods, or higher vertebrates. For example, observational learning has recently been demonstrated in foraging bees, implying that cognition arising from observational learning may be widespread in the animal kingdom (Figure 17.22). For example, Worden and Papaj (2005) tested the ability of bumblebees to transfer information via observational learning. They set up an observation chamber and a chamber where either natural bumblebees or robotic bees foraged on artificial flowers. After a period of observation they released the observers to forage in a separate arena.
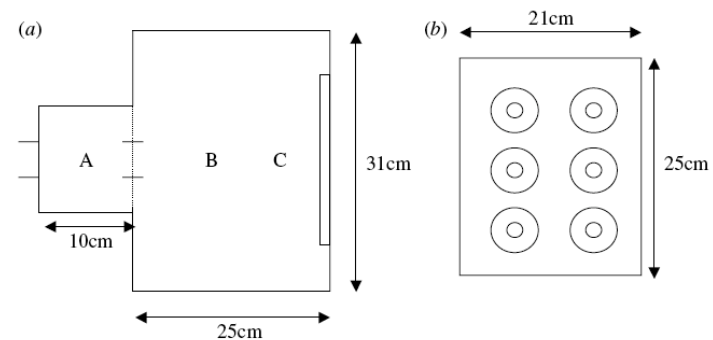

Figure 17.22. Schematic of the experimental apparatus used to assess observational learning in bumblebees. (a) The observation box (A) was attached to the modeling arena (B). The observer bee in (A) could view the foraging array (C) that was located 25 cm from the observation box. The barrier separating A from B consisted of a Plexiglas wall bordered by fine wire screening. (b) A close-up view of the foraging array showing the arrangement of the colored 'flowers'. 'Flowers' were 2.5 cm and 5.5 cm apart vertically and horizontally respectively, and consisted of colored paper rings surrounding a central wick (Warden and Papaj 2005).

The observer bumblebees exhibited a highly non-random preference for flowers that they observed foraging activity (Figure 17.23).

Figure 17.23. The proportion of landings on green flowers for bumblebees watching (a) live foraging bee models or (b) artificial models. (Warden and Papaj 2005).
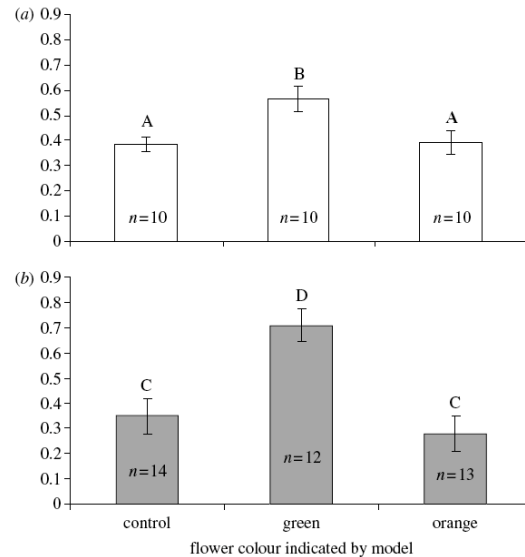
This kind of social or observational learning is so important that we will investigate imitative behaviors in Chapter 19 (Social Evolution). The possibility of positive feedback loops on learning and coping styles, as suggested by many of the new experiments on animal personalities holds great promise for understanding how animal cultures might evolve on a cultural axis. For example, as in speciation of genes where positive frequency dependent selection of mate choice can fix different combinations of genetic traits, cultural evolution and positive frequency dependent selection on learning styles can fuel a rapid fixation of one type in a given population or simply a small local neighborhood.

This tendency of learning styles to fix would be greatly amplified if one learning style were cooperative. The more reflective learning style of slow-explorers (e.g., great tits) would be the likely candidate for a coupling with cooperative behavior, given that the aggressive tendencies of fast explorers are incompatible with cooperation (see Chapter 11). These issues are of critical importance to the evolution of cooperation in the context of the cultural transmission of traits.

Study Questions for Learning and Cognition

1. Describe a short-term and a long-term change in endocrine state and the effects that each has on motivation.

2. What is the general process theory of learning? What is the principle of equipotentiality? Which of these aspects of learning theory is invalidated with the recognition of biological constraints on learning? Explain your answer with reference to the example of taste aversive conditioning and shock aversive conditioning in mice.

3. Discuss the adequacy of associative learning studies in the lab for the kinds of learning we have considered during the quarter. Your answer must include reference to at least 4 kinds of learning in a natural context.

4. Can an animal that is learning be foraging optimally? Why or why not? What are the environmental conditions that favor a learning-based foraging strategy?

5. Describe a memory constraint on foraging in bumblebees that leads to apparently risk aversive behavior.

6. What are the advantages of a bold personality type? What are the advantages of a shy personality type? Who ends up at the top of the dominance hierarchy and why? Who ends up at the bottom and why?

7. Are these generalizations in an aviary realized as fitness differences in nature? What kind of selection shapes animal personalities in natural populations?