Learning, Memory, and Cognition: Animal Perspectives

28

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28.1 Cognition: Definition

Cognition is the integrating process that utilizes many different forms of memory, creates internal representations of the experienced world and provides a reference for expecting the future of the animal's own actions. It thus allows the animal to decide between different options in reference to the expected outcome of its potential actions. All these processes occur as intrinsic operations of the nervous system, and provide an implicit form of knowledge for controlling behavior. None of these processes need to – and certainly will not – become explicit within the nervous systems of many animal species (in particular invertebrates and lower vertebrates), but such processes must be assumed to also exist in these animal species. It is the goal of comparative animal cognition to relate the complexity of the nervous system to the level of internal processing.

Neural integration processes are manifold and span a large range of possibilities all of which can be viewed from an evolutionary perspective as adaptations to the specific demands posed by the environment to the particular species. At one extreme one can find organisms dominated by their inherited information (**phylogenetic memory**) developing only minimal experience-based adaptation. At the other extreme, phylogenetic memory merely provides a broad framework, and **experience-based memory** dominates. Phylogenetic memory controls behavior in rather tight stimulus-response connections requiring little if any internal processing other than sensory coding and generation of motor programs. The factors determining the specific combination and weights of inherited and experience-dependent memories in an individual are not yet well understood. A short individual lifetime, few environmental changes during a lifetime, and highly specialized living conditions will favor the dominance of inherited information; a longer individual lifetime, less adaptation to particular environmental niches and rapid environmental changes relative to the lifespan reduce the value of phylogenetic memory and increase the role of **individual learning**. Social living style also seems important. Here the species' genome must equip the individuals for acting under much more variable environmental conditions because of the society's longer lifetime, and because the communicative processes within the society demand a larger range of cognitive processes.

The complexity and size of the nervous system may be related to the dominance of inherited or experience-dependent memories, in the sense that individual learning demands a larger nervous system having greater complexity. However, the primary parameter determining the size of the nervous system is body size, and secondary parameters like richness of the sensory world, abundance of motor patterns and cognitive capacities, are difficult to relate to brain size, because such parameters cannot be adequately measured and thus a comparison based on them is practically impossible between animals adapted to different environments. Nevertheless, it appears obvious that animals differ with respect to their sensory, motor, and cognitive capacities. Individual learning within the

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species-specific sensory and motor domains will lead to more flexible behavior, and thus to more advanced cognitive functions. Predicting the future will therefore be less constrained, and more options will enrich the animal's present state.

Cognitive components of behavior are characterized by the following faculties: (i) rich and cross-linked forms of sensory and motor processing; (ii) flexibility and experience-dependent plasticity in choice performance; and (iii) long-term (on the timescale of the respective animal's lifespan) adaptation of behavioral routines. These three features allow the creation of novel behavior through different forms of learning and memory processing. Among them, we can cite: (i) rule learning and causal reasoning; (ii) observatory learning during communication, imitation, and navigation, and (iii) recognition of individuals in a society and self-recognition. All these characteristics are based on implicit forms of knowledge and do not require any explicit (or conscious) processing. However, internal processing at the level of working memory (or representation) as an indication of rudimentary forms of explicit processing may exist in invertebrates and lower vertebrates within the context of observatory learning and social communication.

28.2 Innate and Learned Behavior

Innate and learned behaviors are intimately connected leading to the concept of preparedness for learning. Mice associate nausea induced by injection of LiCl or radioactive irradiation with novel taste and smell but not with light or sound. Song birds are prepared to learn the species-specific song, and only some species may be more open to aberrant songs. The idea that anything can be learned if associativity rules are followed as put forward by Pavlov (1849–1936) and the behaviorists like B.F. Skinner (1904–1990) is not substantiated, and many examples have been described for species-specific constraints in learning.

Often similar behaviors are performed by closely related species, but in one species it involves learning, in the other it is solely controlled innately. The two species of braconid wasps *Cotesia glomerata* and *Cotesia flavipes* are stem-boring parasitoids. While *C. flavipes* exhibits innate preference for its host's odors – the larvae of *Pieris brassica* (Lepidoptera) – the closely-related *C. glomerata* learns the varying odor profiles of its *Pieris* host larvae, which depend on the plants it feeds on. No other differences in behavior between these two species were found, indicating that experience-dependent adjustment and innate stereotypy are two close strategies and are not related to any great differences between the neural systems involved. It will be interesting to search for structures in the brain that differ in these two species and may be related to these two strategies.

A particularly close connection between innate and learned behavior is **imprinting** (see Chap. 25), the programmed forms of learning described in great detail by ethologists like Konrad Lorenz (1903–1989) for birds, but fast and stable learning early on in ontogeny is a phenomenon in all animal species. Slave-making ants have colonies in which two species of social insects coexist, one of which parasitizes on the other. Slave-making ants invade colonies of other ant species and transport the pupae back to their own nest. Adults emerging from these pupae react and work for the slave-making species as if it were its own species. The basis for this phenomenon may be olfactory imprinting by which the slave ants learn to recognize the slave-makers as members of their own species.

The mechanistic basis of olfactory imprinting has been studied in the fruit fly *Drosophila melanogaster*. Synaptogenesis in the antennal lobe, the primary olfactory neuropile in the insect brain (see Chap. 13), starts in late pupae and continues during the first days of adult life, at the same time as the behavioral response to odors matures. The antennal lobe is made up of functional units, the glomeruli. The glomeruli DM6, DM2, and V display specific growth patterns between days 1 and 12 of adult life. The modifications associated with olfactory imprinting take place at the critical age. Exposure to benzaldehyde at days 2–5 of adult life, but not at 8–11, causes behavioral adaptation as well as structural changes in DM2 and V glomeruli.

These examples show that (i) animals often exhibit innate preferences for signals allowing to rapidly and efficiently detect biologically relevant stimuli in their first encounters with them; (ii) such preferences can but may not always be modified by the animals' experience. It is still unknown how these preferences are hardwired in the naïve nervous system, but since they have been selected through the species' evolutionary history and thus belong to its phylogenetic memory it must be assumed that they are programmed by developmental processes.

Table 28.1 Categories of learning

Learning – descriptive categories	Relation of the stimuli	Evaluation of stimuli	What is learned
Nonassociative learning			
Habituation	Stimulus repetition	No evaluation	Stimulus has no meaning
Sensitization	Strong stimulus	Causes attention	General arousal
Associative learning			
Classical (Pavlovian) conditioning	Neutral stimulus CS co-occurs with meaningful stimulus	US is a reinforcer	Association of CS with US
Operant or instrumental learning	Own actions lead to reinforcement	US is a reinforcer	Hierarchy of associations
High-level learning (observation, navigation, play, learning by insight)	Directed attention in the course of self-produced behavior	Internal rather than external evaluation	Association between stimuli and behavior
Imprinting	Stimuli occurring during active behavior	Developmental preparedness	Stimuli and developmental program

28.3 Learning: Elemental Forms of Associative Learning

Learning is the capacity to change behavior as the result of individual experience in such a way that the new behavior is better adapted to the changed conditions of the environment. Learning can be grouped into three broad categories: simple nonassociative learning like habituation and sensitization, associative learning including classical conditioning and instrumental (operant) learning, and higher forms of associative learning characterized by the lack of an obvious external reinforcing stimulus and by directed attention of the animal to the outcome of self-generated behavior as in observatory learning and learning during playing (Table 28.1).

28.3.1 Nonassociative Learning

Stimulus repetition without any consequences leads to a stimulus-specific decrease of stimulus-induced responses (habituation), a lower sensitivity to the stimulus and less attention. **Habituation** is characterized by stimulus specificity, spontaneous recovery and dishabituation, a phenomenon that results from strong, sensitizing stimuli. These properties exclude the possibilities that habituation is based on sensory adaptation or motor fatigue. **Sensitization** results from a strong and unexpected stimulus that induces a state of general arousal, higher sensory sensitivity, and alerted motor responses. Repetition of sensitizing stimuli leads to fast habituation, and single stimulations may induce only short-lasting arousal. Sensitizing stimuli often carry an aversive innate meaning relating these stimuli to unconditioned stimuli in associative learning (see below).

The cellular and neural correlates of nonassociative learning are covered in Chap. 26. Eric Kandel and his coworkers conceptualized a cellular alphabet of neural plasticity leading to a hierarchy of brain mechanisms of learning and memory formation [10].

28.3.2 Classical Conditioning

Associative connections between stimuli, events, and actions are the source of information that animals use to extract causal relations in the environment. Figure 28.1 gives examples of basic paradigms of classical conditioning and Table 28.2 lists additional paradigms.

A hungry honeybee responds to the stimulation of the sucrose receptors on the antennae by an extension of its proboscis (tongue) and sucks the sucrose solution. This stimulus arouses the animal, induces directed searching responses, releases an innate response (the proboscis extension response, which represents the unconditioned responses, UR), and acts as an **unconditioned rewarding stimulus** (US) for **neutral stimuli** (CSs) like odors experienced shortly before the US. These CSs can either precede the US which leads to an association with the US (denoted as CS+), or they follow the US at an interval (backward pairing), or are not paired with the US at all. In these cases they are not associated with the US, thus called CS–. The probability of a group of animals to extend their probosces during the CS+ in expectation of the US (**conditioned responses**, CR) increases with the number of forward pairing trials (CS+/US acquisition Fig. 28.1a) and does not change for backward pairing of

US/CS (or may decrease over trials if CS– is first responded to due to generalization, see Fig. 28.1d). Pavlov called the first form of conditioning **excitatory learning**, the latter one **inhibitory learning**. No change of behavior occurs if the animals experience stimulations of the CS alone or the US alone, but multiple exposures to the CS alone may retard acquisition of this CS in later forward-pairing trials (CS+/US). Conditioned animals lose their CR to the CS+ if the CS is presented multiple times without the US, an indication of extinction learning (Fig. 28.1a, right graph). This form of inhibitory learning can depend on the context conditions in which the animal experiences the loss of predictive power of the CS for US. It is, therefore, concluded that the memory of the CS-US connection is not lost but rather a new memory is formed, namely that now the CS predicts the absence of the UC. This conclusion is supported by the finding that at a later time the CS will partially gain its predictive power for the US (spontaneous recovery after extinction learning, Fig. 28.1a, right graph). In classical conditioning, typically the establishment of a CS-CR connection does not require any particular behavior of the animal. In an omission paradigm (Fig. 28.1b) the animal is rewarded when it does **not** respond to the CS but not rewarded when it responds. Still honeybees under these conditions learn equally well indicating that an operant component is not involved. Often learning is not directly reflected in a behavioral change and can be uncovered only later when animals are exposed to forward-pairing trials. In honeybees backward pairing of US and CS in a first phase of conditioning will lead to lower acquisition to the same CS in a second phase (Fig. 28.1c). The acquisition function to forward pairing of the same CS with the US is depressed as compared to an acquisition function without or with a lower number of such preexposures. This form of learning (latent learning) appears to involve associations of the stimuli with those emanating from the context, because the resistance to acquisition effect can be context dependent, indicating that stimulus associations are established without the contribution of an US. Inhibitory learning of CS– in a first phase of differential conditioning is also seen when the CS– becomes the CS+ in a second phase (**reversal conditioning**, Fig. 28.1d). Acquisition in the second phase is retarded. The reinforcing property of the US can also be transferred to a CS (**second-order conditioning**, Fig. 28.1e). CS1 is forward paired with US in a first phase. In a second phase a novel CS (CS2) is forward paired with CS1 (CS2/CS1 pairing). CS2 is learned (rise of CR probability to CS2) and responses to CS1

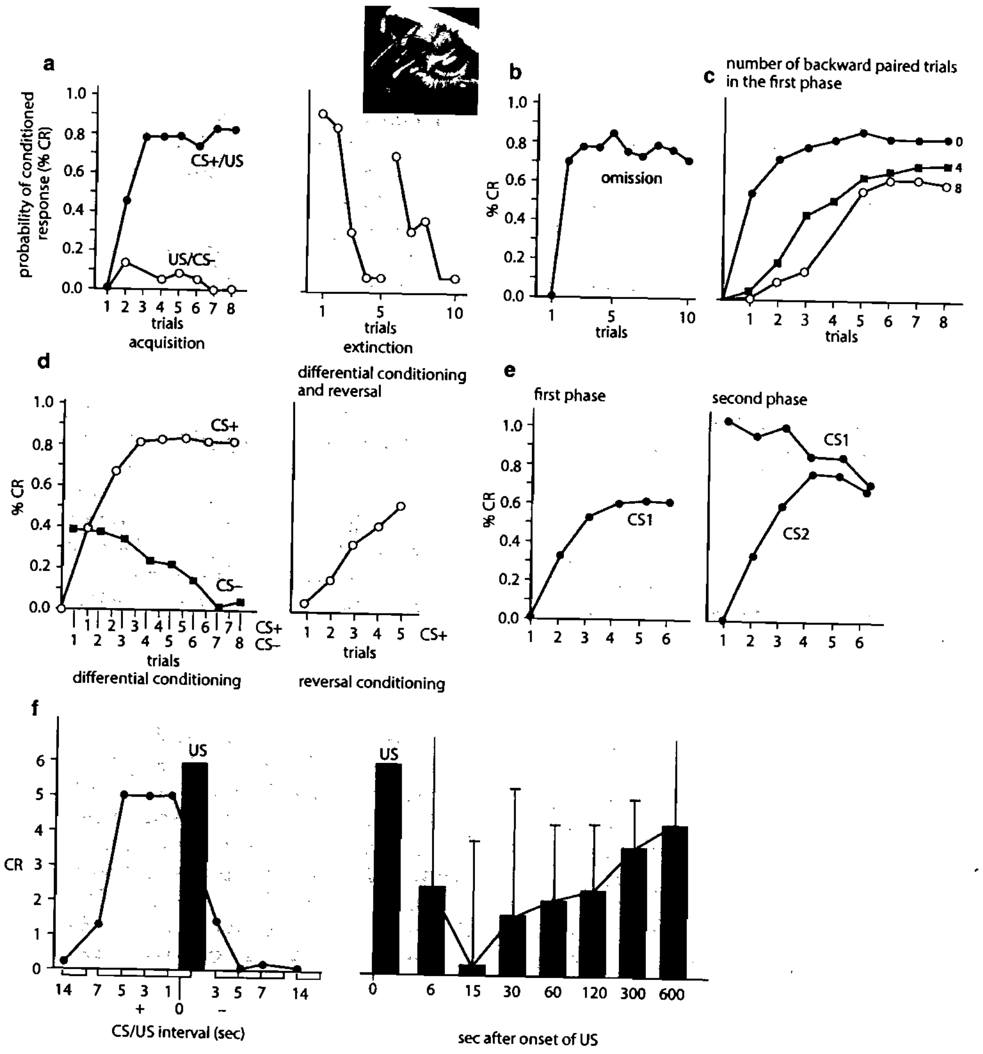


Fig. 28.1 Elemental forms of classical conditioning exemplified for odor reward conditioning in honey bees. (**a**) The inset shows how a bee is harnessed in a tube. The hungry bee extends its proboscis (tongue) reflexively when its antennae taste sucrose, the unconditioned stimulus, US. Odors received by the olfactory receptors on the antennae serve as conditioned stimuli, CS. The *left graph* shows how the probability of the conditioned responses in a group of animals (proboscis extension response, PER) increases with the number of forward pairing trials (CS/US). Backward paired trials (US/CS) do not lead to conditioned PER. The *right graph* gives the result of an extinction experiment. Repeated exposures to the CS without the US leads to reduction of PER probability. After an interruption of 1–2 h the conditioned PER recovers partially, an effect known as spontaneous recovery from extinction. (**b**) Classical conditioning can be distinguished from operant conditioning by an omission procedure. The US is only given if the animal did not show the conditioned response (omission). This omission acquisition function of the PER shows pure classical conditioning, because acquisition is not reduced (compare with **a**). (**c**) If animals experience unpaired CS und US presentations, subsequent acquisition to paired CS/US trials is retarded. The *upper curve* (0 unpaired trials) provides the control group (normal acquisition after no exposure to unpaired trials). The *other two curves* show that retardation of acquisition depends on the number of previously experienced unpaired trials. (**d**) Differential conditioning involves two CSs, CS+ is forward-paired with US, CS– is backward-paired. Conditioned PER rises for the CS+. CS– is initially responded to more strongly because of generalization between CS+ and CS–. Further CS– unpaired trials lead to a reduction of PER to CS–. In a second phase CS– becomes the CS+. Now acquisition is retarded because of the unpaired trials in the first phase. (**e**) Second-order conditioning. CS1 is forwards paired with US in the first phase. In the second phase a new odor (CS2) is forward-paired with CS1 (first CS2 then CS1). The reinforcing capacity of CS1 which it gained in the first phase is transmitted to CS2. Concurrently the conditioned PER is reduced for CS1. (**f**) The effect of CS/US interval. The *left graph* shows how conditioned PER depends on the interval between CS and US (*gray* vertical bar extending from 0 to 2 s on the interval scale). The CS is presented for 2 s either before (*left side*: +) or after US (*right side*: –). Optimal conditioning is found for forward-pairing. The *right graph* shows the effect of backward-pairing. Since PER is zero to the CS when it follows the US, the hidden inhibitory component of backward-pairing was uncovered by exposing the animal in a second phase to forward-pairing to the same CS. The inhibitory backward-pairing effect is strongest for a UC–CS interval of 15 s

Table 28.2 A selection of associative learning paradigms

Paradigm	Phase 1	Phase 2	Test
1. Sensory preconditioning	A/B	A/US	B tested
2. Differential conditioning	A/US	B–	A and B tested
3. Inhibitory conditioning	A–	A/US	A tested
4. Second-order conditioning	A/US	B/A	B tested
5. Within compound association	A/X, B/Y	A/US	A and B tested
6. Blocking	A/US	A+B/US	B tested
7. Massed and spaced trials on acquisition and retention			

A, *B*, *X*, *Y* denote neutral stimuli, *US* reinforcer; the sign/indicates paired presentation of the stimuli, *A*– or *B*– presentation of the respective stimulus alone, *A*+*B* both stimuli are presented simultaneously, *A tested* or *B tested* means that the respective stimuli are presented without the reinforcer in order to evaluate what the animal has learned about A and B extinguish. A crucial parameter in classical conditioning is the contiguity between CS and US. Figure 28.1f shows how excitatory and inhibitory learning depend on the timing of the CS with the US. A preceding CS (CS+) gains its predictive power for the US most effectively for short intervals before the onset of US. Excitatory learning is reflected directly in the probability of CR induced by CS+. Inhibitory learning is often not directly reflected in a behavioral change. In that case it needs to be uncovered in a second phase of conditioning, e.g., a forward pairing of the same CS+ with US (as shown in Fig. 28.1c). Stronger inhibitory learning will lead to stronger resistance to acquisition in the second phase. The timing of US and CS− in inhibitory learning can be different from that of excitatory learning. In the honeybee optimal intervals between US and CS− lie between 5 and 25 s after US onset.

Pavlov's terms excitatory and inhibitory conditioning do not refer to the strength or probability of behavior controlled by learning but to the connections developed between CS and US. If the US is an aversive stimulus, excitatory conditioning will lead to less CR, and inhibitory learning to more CR. It is an interesting but unresolved question how excitatory and inhibitory conditioning in reward and punishment learning are related. Does inhibitory reward learning resemble aspects of excitatory punishment learning? In other words, does backward conditioning to an aversive stimulus induce some rewarding potential ("release from punishment") of the CS?

The paradigms of classical conditioning emphasize the importance of CS-US contiguity, however the latent learning phenomenon (Fig. 28.1c) indicates already that this cannot be the only parameter controlling learning. Other paradigms strengthen this conclusion. In **sensory preconditioning** (Table 28.2) two CSs (CS1 and CS2) are first presented together without any US. In a second training phase, one of them (CS1) is paired with the US. In the test phase, CS2 is tested alone and it is found that also CS2 induced CR although CS2 was never paired with the US. In blocking experiments (Table 28.2) a first training phase consists of CS1-US pairings. In the second training phase, CS2 is added, so that the compound CS1CS2 is paired with the US. Surprisingly, it is found that CS2 is less well or not at all learned although it is paired with the US. Learning of CS2 is somehow blocked by the experience of CS1-US pairing in the first phase. These and other paradigms of classical conditioning document the limitations of a simple contiguity effect and call for other explanations. These will be described below.

The rules of **associative learning** have been worked out in great detail by Pavlov and the American behaviorists. These rules are of heuristic value if applied with adequate care and if one considers the restriction that species-specific constraints and environmental conditions may lead to exceptions. In particular, they provide a frame for the design of experiments aiming to extract the crucial components in associative behavioral change. Rules of learning emphasize the role of the contiguity of events (their temporal relations) and their contingencies (the probabilities of co-occurrence of events). Because contiguity and contingency of events are more important than sensory modality or the motor pattern involved, forms of learning can be compared across species, environmental conditions, sensory modalities, and behavioral acts. In the course of learning, neutral environmental stimuli and actions of the animal lead to meaningful outcomes and thus become predictors for that outcome. When a hungry animal finds food, the own actions and the signals associated with this meaningful outcome are stored for future behavior. The meaningful component plays a decisive role because it surprises the animal, it has an innate or learned value with respect to the need of the animal, and it has the potential to reinforce the stimuli and actions with its value. Such a meaningful stimulus can either be (i) an external stimulus (in classical conditioning it is called the unconditioned stimulus, US, with the value of acting as a reward or a punishment), (ii) a successful or failing action (as in instrumental learning, see below), or (iii) an internally generated value function as in observatory representation related to meaning and value (see below).

The most powerful rule of associative learning has been formalized by Rescorla and Wagner [21] (see Box 28.1). Many phenomena of learning are well captured by this concept called the **delta rule**, which states that animals learn when an event is not expected and therefore surprises the animal. The rule defines whether and how much is learned depending on how surprising the association of CS and US is, and surprise is quantified by the difference between expected and actual event. The theory also states that all CSs involved in a learning trial compete for the limited capacity of this difference (**capacity of attention**). A number of learning phenomena are well captured by the theory (Box 28.1). **Expectation** and **surprise** are concepts of a cognitive interpretation for these simple forms of associative learning, and although the authors did not relate their theory to cognitive concepts the success of the theory also lies in the cognitive dimension of its key parameter, expectation.

Box 28.1 The Delta Rule of Classical Conditioning

Rescorla and Wagner [21] realized that the simple co-occurrence of CS and US in associative learning does not capture the results found in several conditioning experiments. They argued associative learning occurs not because two events co-occur but because that co-occurrence is unanticipated on the basis of current associative strength. The Rescorla-Wagner model attempts to capture that idea in a more formal way.

The Rescorla-Wagner model is based on the assumption that an associative change in each stimulus depends not only on its own state (how well it can be learned, how often it had been associated with the reinforcer) but also on the states of other stimuli concurrently present. Take the associative strength for a stimulus X to be V_X and for a stimulus A to be V_A. Then, the associative strength to the compound stimulus (V_{AX}) will be

$$V_{AX} = V_A + V_X$$

On a learning trial in which a compound stimulus (AX) is followed by US, the changes in associative strength (ΔV) for A and X are:

$$\Delta V_A = [\alpha_A \beta_1](\lambda_1 - V_{AX})$$

and

$$\Delta V_X = [\alpha_X \beta_1](\lambda_1 - V_{AX})$$

λ_1 is the maximum conditioning that US_1 can produce, and therefore represents the limit of learning. The α and β are rate parameters dependent, respectively, on the CS and US. These parameters are viewed as having fixed values based on the physical properties of the particular CS and US. On any given trial the current associative strength V_{AX} is compared with λ and the difference is treated like an error to be corrected. This happens by producing a change in associative strength (ΔV) accordingly. Consequently, this is an error correction model.

This model predicts a number of previously unknown results particularly in blocking and conditioned inhibition experiments. In a blocking experiment one stimulus A has been paired with the US, then the compound stimulus AX is paired with US. Little or nothing is learned by the stimulus X. The model describes the effect as follows: A pairing with the US makes X ineffective to US pairing because the first conditioning of A results in V_A being close to λ; then on an AX trial V_{AX} is close to λ because V_X is zero, resulting in an error term ($\lambda - V_{AX}$) that is close to zero; hence ΔV_X is close to zero and there is little resulting change in V_X.

The neural substrates of associations as established in classical conditioning are thought to be related to a rule of neural plasticity as formulated by Hebb in 1949 [11], and which can be summarized by the catchy sentence: "Wire together what fires together" (see Chap. 25). Indeed phenomena like associative LTP and the molecular properties of coincidence detectors such as the NMDA receptor or the adenylyl cyclase and other proteins (see Chap. 26) illustrate molecular mechanisms of associative plasticity in the nervous system. However, there are several problems with these ideas: (1) The timing of CS and US in both excitatory and inhibitory conditioning (usually several to many seconds) are very different from the timing of spikes in spike timing plasticity (usually in the range of a few ms). The discrepancy becomes even more drastic in learning phenomena like nausea-induced learning in which the interval between CS and US can be hours. (2) Latent learning, sensory preconditioning and blocking indicate that contiguity of stimuli is not the only and possibly not even the decisive parameter in associative learning. Rather properties like expectation, deviation from expectation (error signal), and attention need to be considered for which individual molecular and cellular properties are not sufficient but network properties need to be considered.

28.3.3 Instrumental or Operant Conditioning

As opposed to classical conditioning, instrumental or operant conditioning requires an active involvement of the animal. A spontaneously generated behavior leads to an event (a value signal V). For example, a hungry animal searches for food (it produces actions A) in a particular sensory environment (S) and finding it induces a rewarding signal (V). Under these conditions the animal learns the relations between its own actions A, the external

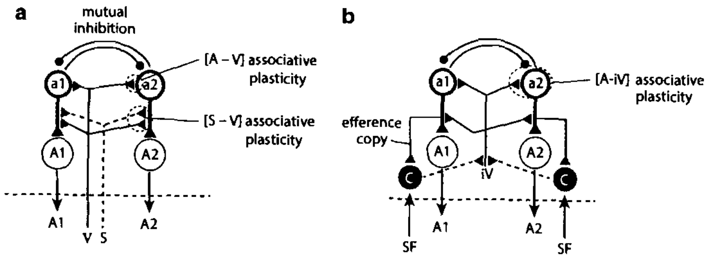

a
mutual inhibition
a1
a2
[A – V] associative plasticity
[S – V] associative plasticity
A1
A2
A1
V
S
A2
b
a1
a2
[A-iV] associative plasticity
efference copy
A1
A2
iV
C
C
A1
A2
SF
SF

Fig. 28.2 Conceptual model of neural operations potentially underlying operant learning. Two motor patterns (actions A1 and A2) are spontaneously generated by pattern generators (a1, a2), whose execution is mutually exclusive by reciprocal inhibition. (**a**) In the case of operant learning with an external value signal either action A1 or A2 leads to a desirable (or avoided) effect as signaled by reward or punishment (*red line*: value signal V). The neural correlate of V strengthens or weakens the respective motor patterns by associatively altering their corresponding neural activities a1 or a2. These associative alterations may also depend on the sensory signals S (*dotted line*) connected with the conditions under which the value signal occurs. The two forms of associations (sensory–value association [S–V]) and (action–outcome association [A–V]) can be related to classical and operant conditioning effects, respectively (see text). (**b**) In the case of operant learning without an external value signal, the sensory feedback SF resulting from the execution of motor pattern A1 or A2 is compared with the corollary discharge (*brown lines*) of the respective motor patterns a1 or a2 (C: comparator). A mismatch leads to an error signal (*blue dotted line*) that activates an internal value system (iV, *red line*) leading to associative alterations in the activation of a1 or a2

conditions signaling the outcome (S) and the evaluating stimulus (V). Thus, there are three associations to be formed: that between action A and stimulus (S) [A–S], the action-value association [A–V], and the stimulus-value association [S–V]. Figure 28.2a presents a conceptual model of neural operations potentially underlying **operant learning**. Two motor patterns (actions A1 and A2) are spontaneously generated by pattern generators (see Chap. 23) a1, a2, whose execution is made mutually exclusive by reciprocal inhibition. Action A1 or A2 lead to a desirable (or avoided) effect as signaled by reward or punishment (value signal V). The neural correlate of V strengthens or weakens the respective motor pattern by associatively altering their corresponding neural activities a1 or a2. These associative alterations may also depend on the sensory signals S connected with the conditions under which the value signal occurs. The three associations ([A–S], [S–V], [A–V]) are partly independent, because the same [A–V] association can be formed for different S, or different actions can lead to the same outcome. [S–V] associations are of the Pavlovian kind (**classical conditioning**) and appear to be established independently and in different neurons than the other two associations: [A–V] associations are related to **goal-directed behavior** (or operant behavior in a strict sense); [A–S] associations are thought to lead to **habit formation**, the development of stereotypical motor patterns under particular stimulus conditions. Behavioral test procedures allow to at least partially separate between these three forms of learning. For example, if the animal is exposed to highly variable contingencies between own actions and outcome [A–V] associations are down-graded and habit formation [A–S] becomes the dominant behavior adaptation. In the extreme case when own actions are fully independent of the occurrence of the value signal animals become passive and produce no actions any more, a situation called **learned helplessness**.

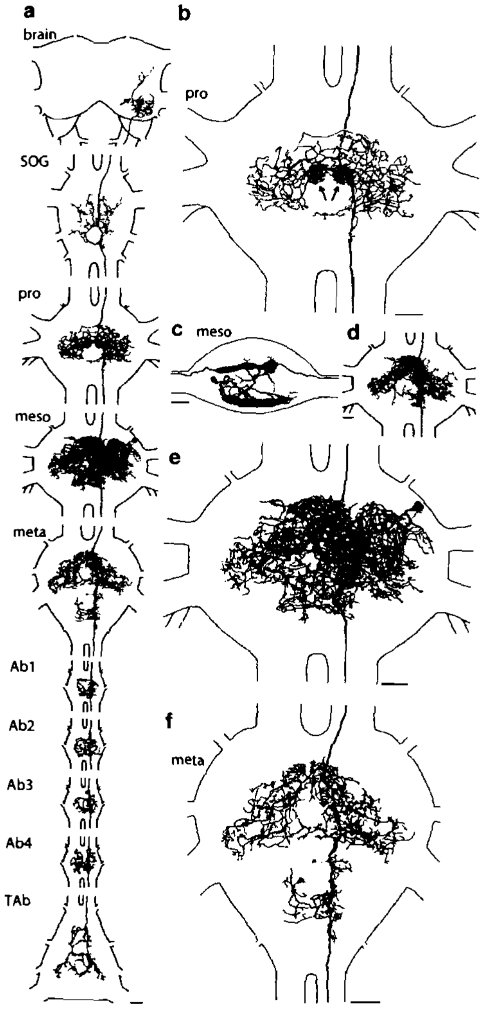
Different brain regions are involved in habitual [A–S] and goal directed [A–V] learning in mammals. [A–S] learning can be mediated at many locations within the nervous system, including the spinal cord, the basal ganglia and the striatum, whereas goal directed [A–V] learning is mediated by cortical structures such as the prelimbic area and the insular cortex, and by neurons in the basal ganglia. In fast sequences of operant learning trials (seconds), neurons of the

prefrontal cortex and the caudate nucleus (a structure of the basal ganglia in the mammalian brain) code outcome-reward relations in their sustained activity: correct responses in the last trial lead to lasting activity, wrong responses to reduced activity. This finding indicates that the network of neurons involved in operant learning stores the neural correlates of outcome-reward relations for some extended time. This might have two reasons: to keep a transient memory trace for the next decisions to be made and to facilitate long-lasting storage of the memory trace in stable altered synaptic strengths which requires protein synthesis (see Chap. 26).

Studies on operant learning in *Aplysia* and *Drosophila* allow tracing some of these associations to particular identified neurons and cellular pathways. The motor neuron B52 in the feeding pattern generator of *Aplysia* receives input from both mechanosensory neurons (representing the CS) and the value-representing dopamine neurons. The dopamine neurons also synapse onto presynaptic terminals of the mechanosensory neurons upstream to B52. Coincident activity of dopamine neurons and B52 leads to [A–V] associations of operant behavior by enhancing the excitability of B52 (threshold for spiking is reduced and input resistance enhanced). Coincident activity of dopamine neurons and mechanosensory neurons strengthens their presynaptic activity (classical conditioning, [S–V] association). Interestingly, when [S–V] associations are induced alone B52 excitability is reduced indicating a (as yet unknown) link between classical and operant conditioning in this circuit. In *Drosophila*, operant learning (e.g., a stationary flying fly in an arena in which the animal controls the appearance of stimuli by its behavior and is heated up when is steers towards a particular stimulus) involves both classical [S–V] and operant [A–V] conditioning. The first one develops fast, the latter slowly. The transition from the fast to the slow learning effect requires the mushroom body. The cellular pathways underlying the two forms of plasticity differ. Classical conditioning requires the rutabaga gene-related adenylyl cyclase, operant conditioning a protein kinase C-dependent pathway (see Chap. 26).

Some forms of operant learning lead to improvement of motor performance just by the repetition of motor program without an obvious evaluating signal. In many animal species movements are not perfect when performed the first time. Running, swimming, flying, singing, and other forms of communication may become better, faster, and less energy consuming with practice. New motor patterns in manipulating objects (e.g., pollinating insects extracting nectar and pollen from flowers, birds building a nest and using tools, or mammals preparing food for ingestion) improve with exercise. If the execution of a motor pattern is disturbed (for example, by injury to a limb) changes of the movement pattern can adjust for the damage. The concepts accounting for these forms of learning (Fig. 28.2b) assume the comparison between a sensory feedback (SF) resulting from the execution of movement A1, A2 (the outcome) and a neural template (an **efference copy**) of the neural program initiating the movement. The efference copy is also called a **corollary discharge**, because it accompanies the neural activity leading to the motor pattern and runs in parallel to it (see Chap. 23). The comparison between efference copy and sensory feedback in a neural comparator (C) leads to an error signal (*blue line* in Fig. 28.2b) that activates an internal neural value system leading to associative alterations in the activation of a1 or a2. The corollary discharge can be considered as a neural correlate of expectation, a pattern of activity that precedes conditions in the external world. Thus, on a formal ground the neural operation of comparison between corollary discharge and sensory feedback is equivalent to the deviation from expectation ΔV_A as derived in the delta rule in classical conditioning (see Box 28.1), and ΔV_A can be considered to be equivalent to a neural error signal.

The corollary discharge (efference copy) was postulated already by Helmholtz (1821–1894) and has been conceptualized to be forwarded from the motor system to the sensory system providing inhibitory input to the incoming sensory signals. However, it has been difficult to identify such neural pathways. A single multisegmental interneuron (Fig. 28.3, corollary discharge interneuron CDI) was found in the cricket which provides presynaptic inhibition to auditory afferents and postsynaptic inhibition to auditory interneurons when the animal produces its own song but not when it hears songs from other animals. When the animal sings without sound (fictive song) CDI is excited and inhibits the coding of played songs. The authors [19] managed to stimulate CDI intracellularly, resulting in inhibited auditory encoding. They also found that excitation of CDI is specific for self-generated songs and not for other motor patterns, demonstrating that CDI is both necessary and sufficient for the blocking of sensory input expected to be received from own song production. It will be interesting to see whether a mismatch between the expected song pattern and the received song produces an error signal that may be used to fine-tune own song production, e.g., after some disturbance of the song production by the wings.



The concept of an **error signal** driving associative learning has also a strong impact on neural studies of learning related plasticity in the nervous system. The dopamine neurons of the ventral tegmentum of the mammalian brain, for example, change their response properties to the CS according to a modified delta rule [22]. A similar effect was found in an identified neuron in the honeybee brain [9]. This neuron known as VUMmx1 (ventral unpaired median neuron 1 in the maxillary neuromere) codes for the reinforcing property of the US sucrose in olfactory learning, and thus appears to have similar properties as the dopamine neurons in the mammalian brain. As Fig. 28.4 shows, VUMmx1 changes its response properties in the course of learning as do the dopamine neurons in primates (Fig. 28.5). During differential conditioning VUMmx1 develops responses to the CS+ and stops responding to CS−. If now the US is given after the CS+ one finds no responses to the US anymore, but a US after CS− is well responded to. Thus, an expected US (after CS+) is ineffective, whereas an unexpected US (after CS−) is highly effective. The delta rule and the concept of comparison between corollary discharge and sensory feedback postulate that learning occurs only if $\Delta V_A > 0$. In classical conditioning these properties were related to blocking and second-order conditioning (see Box 28.1 and Table 28.2). In operant conditioning no learning occurs when the error signal is zero. It is conceivable that the acquired responses of the value neurons (the activity of dopamine neurons or of VUMmx1) implement the neural error signal and act as neural reinforcement. However, it has not yet been proven that the neural error signals resulting from a mismatch between the corollary discharge and the sensory feedback really drive the internal value system.

Fig. 28.3 Morphology of a single, multisegmental interneuron responsible for pre- and postsynaptic inhibition of auditory neurons in the singing cricket (*Gryllus bimaculatus*) representing a corollary discharge neuron (CDI). (**a**) A whole-mount staining of the CDI in the CNS of an adult male cricket in ventral view. The soma and dendrites are located in the mesothoracic ganglion, and two axons project throughout the whole CNS with extensive varicose arborizations that are bilateral in every ganglion except the brain. The *arrow* in brain indicates the anterior branch of CDI. (**b**) Axonal arborizations in the prothoracic ganglion; *arrows* indicate overlap with the auditory neuropils. (**c**) Lateral view of CDI in mesothoracic ganglion. The soma is positioned medially near the dorsolateral edge of the ganglion. From the soma the primary neurite extends in a loop toward the middle of the ganglion and gives off a widespread bilateral array of smooth branches typical of insect dendrites. Two axons originate centrally in the ganglion and extend both anteriorly and posteriorly. (**d**) Ventral axonal arborizations in the mesothoracic ganglion. (**e**) Dendritic (dorsal) and axonal (ventral) arborizations of CDI in the mesothoracic ganglion. (**f**) Axonal arborizations of CDI in the metathoracic ganglion have a similar morphology to those in the mesothoracic ganglion. Abbreviations: *SOG* subesophageal ganglion, *Pro* prothoracic ganglion, *Meso* mesothoracic ganglion, *Meta* metathoracic ganglion, *Ab1 to Ab4* abdominal ganglia 1–4, *TAb* terminal abdominal ganglion. Scale bars: 100 μm (After [19] with permission from AAAS)

28.4 Nonelemental Forms of Associative Learning

28.4.1 Definition and Standard Paradigms

Nonelemental forms of learning were developed to reach a more detailed analysis of learning. Here, the associative strength of a stimulus, event, or action is

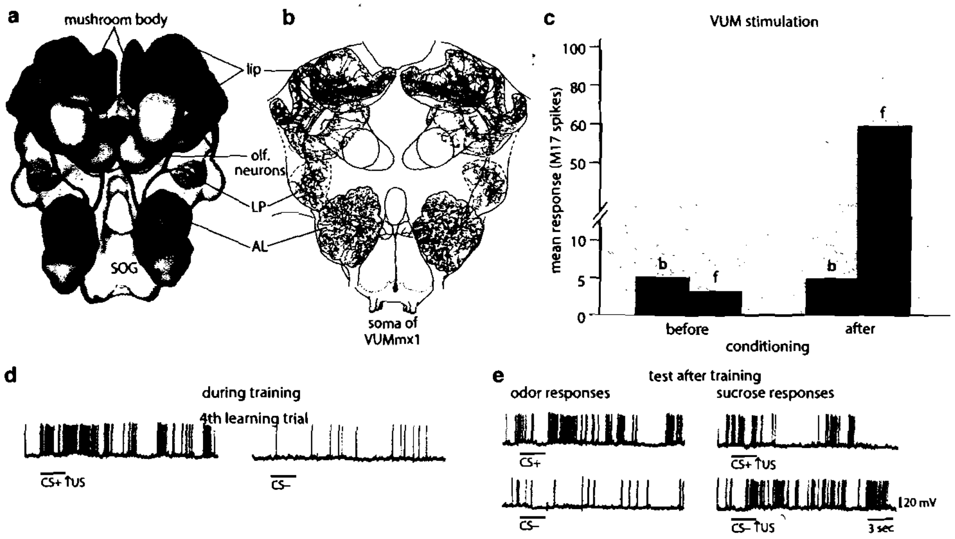


Fig. 28.4 Properties of a single identified neuron (*VUMmx1*, ventral unpaired median neuron 1 of the maxillary neuromere) in the bee brain that represents the reward in olfactory learning. (**a**) The honeybee brain. The olfactory neuropils are marked in *blue*, the antennal lobe (*AL*), the lip region of the mushroom body, the lateral protocerebrum (*LP*). The tracts of olfactory interneurons (*olf. neurons*) connect the AL with the lip and the lateral protocerebrum. (**b**) The VUMmx1. Dendritic branches converging with the olfactory neuropils are marked in *blue*. The soma of VUMmx1 is located in the ventral midline of the subesophageal ganglion (*SOG*). (**c**) Intracellular stimulation of the VUMmx1 replaces the sucrose reward in olfactory conditioning. Before conditioning, the low level of potentials in a muscle involved in the extension of the proboscis (ordinate) indicates that the animals did not respond to the odor. After conditioning, the responses are high in animals experiencing forward pairing of odor and VUMmx1 excitation f but did not change after backward-pairing b. (**d**) VUMmx1 learns about the CS. In differential conditioning the response increases for CS+ and decreases for CS−. Note that a CS+ trial includes the stimulation with US (sucrose) to which VUMmx1 shows a strong response. (**e**) Tests after differential conditioning show an enhanced response to CS+ and a reduced response to CS−. If an expected US follows CS+ the US response is blocked, whereas an unexpected US after CS− is strongly responded to (After [9] with permission from Macmillan Publishers Ltd.: [Nature], © (1993) and [17], © (2001), with permission from Elsevier)

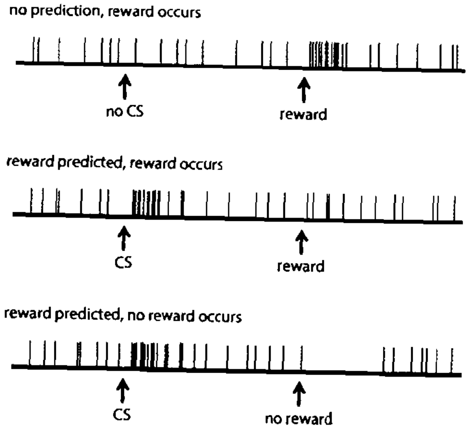


Fig. 28.5 The reward system in the mammalian brain. Recordings from dopamine neurons of the ventral tegmentum during reward learning in a monkey [23]. *Top*: Before learning, a drop of appetitive fruit juice occurs in the absence of prediction – hence a positive error in the prediction of reward. The dopamine neuron is activated by this unpredicted occurrence of juice. *Middle*: After learning, the conditioned stimulus predicts reward, and the reward occurs according to the prediction – hence no error in the prediction of reward is seen. The dopamine neuron is activated by the reward-predicting stimulus but fails to be activated by the predicted reward. *Bottom*: After learning, the conditioned stimulus predicts a reward, but the reward fails to occur because of a mistake in the behavioral response of the monkey. The activity of the dopamine neuron is depressed exactly at the time when the reward would have occurred. The depression occurs more than 1 s after the conditioned stimulus without any intervening stimuli, revealing an internal representation of the time of the predicted reward. Each panel shows the time histogram and raster of impulses from the same neuron *CS* conditioned reward-predicting stimulus

ambiguous and therefore cannot predict obvious ways of solving a problem. For example: Stimulus A is rewarded as often as not rewarded, but it is rewarded whenever it is presented together with a different stimulus B, whereas it is nonrewarded when presented together with a third stimulus C (AB+ vs. AC–, + indicating reward, – no reward). The animal cannot rely on the pure associative strength of A, but must include the context B or C.

Standard paradigms for nonelemental learning include: negative patterning (A+, B+, AB–), biconditional discrimination (AB+, CD+, AC–, BD–), and feature-neutral discrimination (B+, AC+, C–, AB–). In all of these, each stimulus appears rewarded as often as not. In **negative patterning** the animal learns to respond to the single stimuli A and B but not to their compound AB. This problem does not admit elemental solutions, since the animals learn that AB has to be different from the linear sum of A and B. In **biconditional discrimination**, the animal learns to respond to the compounds AB and CD and not to the compounds AC and BD. Each element A, B, C, or D, appears rewarded as often as not such that it is impossible to rely on the associative strength of a given stimulus to solve the task. In **feature-neutral discrimination**, the animal learns to respond to B and to the compound AC but not to C and the compound AB. In this case, each element is again ambiguous such that the animal learns the predictive value of the compounds AB and AC, independent of their composing elements. Other less formalized paradigms are contextual learning and rule learning (see below). The more formalized problems appear to be closer to neural interpretations, and have been assigned to cortical and hippocampal circuits in mammals as opposed to elemental forms of associative learning which may not require these circuits.

Two behavioral theories have been proposed for explaining negative patterning and biconditional discrimination: the **configural theory**, which proposes that a compound AB creates an entity different from its components ($AB = X \neq A + B$), and the **unique-cue theory**, which proposes that a compound is processed as the sum of its components plus a stimulus (u) that is unique to the joint presentation of the elements in the mixture ($AB = A + B + u$). In the latter case, the unique cue supports an inhibitory strength assigned to the compound.

Free-flying honeybees and fixed bees conditioned to olfactory stimuli with sucrose reward (see Fig. 28.1) solve a biconditional discrimination (AB+, CD+, AC–, BD–) and negative patterning task (A+, B+, AB–). Thus, bees base their discrimination on separate neural processing of the compound AB. It is argued that a high-order integration center of the insect brain, the mushroom body (see Chap. 13) is involved. The data are in line with the unique cue theory, and it is concluded that the unique cue is created by convergent neural pathways in the mushroom body. Lobsters placed in an aquarium learn to avoid an olfactory stimulus delivered in water with a mechanosensory disturbance. When they are trained to an olfactory compound AX lobsters stop searching AX but still search when presented A alone, X alone, or a novel odor Y. Similarly, a novel compound AY does not inhibit searching behavior. This result is consistent with learning the compound AX as an entity different from its components A and X.

28.4.2 Selective Attention, Discrimination, and Generalization

Animals attend to stimuli depending on their motivations and needs. Hungry animals are more sensitive to food-related stimuli, sexually motivated animals to sexual stimuli coming from a potential partner, frightened animals to stimuli that signal protection and shelter. Selective attention consists in the ability to focus perceptually on a particular stimulus and to ignore nonrelevant stimuli. It implies that the representation of the stimulus has been filtered or modified, presumably so that it can be processed or responded to more efficiently. Ethologists illustrate selective attention with "search images" (innate or learned perceptual mechanisms that promote the behavior in question), sensory physiologists point out that selective attention leads to higher sensitivity and more accuracy in perceiving attended stimuli, and learning theorists notice that selective attention can be induced and modified by particular procedures of training. We are dealing here with the latter. **Discriminative learning** is the traditional approach. The animal gradually learns to attend a discriminative stimulus. For example, a rabbit is trained in an eye blink paradigm to respond to a sound of 1,200 Hz (Fig. 28.6a). In one situation (T1) only the 1,200 Hz pulse appears shortly before the air puff against the eye (absolute training), in a different situation (T1-T2) a sound of 2,400 Hz (T2) is intermixed with T1 and is not followed by an air puff (differential training), in a third situation (T1-L) a light bulb is switched on which is also not followed by an air puff (differential training with another modality). Sound discrimination is best after differential training, but the light stimulus leads also to better sound discrimination. The attention-inducing effect of a stimulus of other modality can be very strong (Fig. 28.6b). A pigeon learns to peck an illumined key when a sound S+ of the frequency 1,000 Hz appears (upper curve: frequency discrimination is very low). If the illumination of the key is switched on and off from time to time without the sound but food pellets appear only when both the sound rings and the key light is on, sound frequency discrimination is much better (lower function). A discriminative signal of the same modality can also shift stimulus discrimination. Figure 28.6c shows the result of training a horse to a circle of 60 mm diameter (S+) who had to discriminate it from circles with smaller or larger diameters. The generalization profile for different diameters of circles was rather symmetrical. When the same horse was exposed to differential training with a 38-mm circle, the generalization function was quite asymmetrical shifting best discrimination to even larger circles than S+. These experiments document that animals generalize less after differential conditioning, probably because excitatory and inhibitory learning interact (see above). Furthermore, generalization decreases when the animal is more attentive to the stimulus.

Attention also changes in long series of training as indicated in a rather paradoxical but well-documented phenomenon, **overtraining reversal effect**. In such a situation animals are trained to, e.g., dual choice discrimination (S1+, S2–); then the schedule is reversed (S1–, S2+). Animals are found to be more prepared to reversal after longer training. It is argued that overtraining leads to a loss of attention, and the reversal makes the animals attentive again by the surprise effect. This interpretation postulates that the animal develops an expectation about the outcome of their (trained) behavior. Evidence for this interpretation comes from experiments in which two stimulus conditions were trained, one (S1) associated with a particular reward (dry food), another one (S2) with water. When the animals were made either thirsty or hungry and exposed to both S1 and S2 they chose S2 when thirsty and S1 when hungry (differential outcome effects).

Do insects have selective attention? *Drosophila* flying stationary in a circular arena switch their visual tracking between two vertical bars thus demonstrating selection of two possible targets. Local field potentials recorded in the central brain (possibly originating in the mushroom bodies) show that activity in the 20–30 Hz range increases as a response to selecting a bar. The local field potentials increase with the novelty and the salience of the stimuli, are anticipatory and are reduced when the fly is in a sleep-like state. These results suggest that selective attention underlies visual tracking in flies. Honeybees discriminate colors and patterns depending on the kind of training (absolute, differential). Overtraining leads to better reversal learning as it does in mammals. Honeybees learn different stimulus-reward associations for different contexts indicating that they pay attention to context-relevant stimuli. However, the effects of attention-inducing stimuli on discrimination learning and generalization as well as differential outcome effects were not systematically tested in any invertebrate yet.

28.4.3 Rule Learning, Rational Reasoning, and Insight

28.4.3.1 Delayed Matching to Sample

Rules need to be extracted from multiple exposures to a perceptual and/or a performance task when single exposures do not provide the information about the underlying rule.

A rather simple problem for rule-learning is **delayed matching to sample or non-sample (DMTS, DMTNS)**. In such a problem the animal has to choose (or to not choose) the target which resembles the one it was exposed to just before. Successful extraction of the rule implies that the animal performs correctly to novel stimuli. Imagine a honeybee is trained to fly into a maze in which she has to make a decision to enter one or the other of two arms that are arranged like a Y (therefore this arrangement is called a Y-maze). The bee learns to choose the visual targets (colors, patterns) at the end of each arm depending on what it has seen when entering the maze. DMTS and DMTNS tasks are well learned by the bee under such conditions, and the bee transfers the rule to a novel task. For example, if she had learned to fly to the blue target when blue was seen at the entrance, and to the yellow target when yellow was seen, the bee transfers this rule to a novel visual task: if she is exposed for the first time to two patterns of vertical or horizontal stripes she will apply the same rule. She even transfers the rule from learned visual targets to an olfactory task [8]. In mammals it was found that extended delays between the signals to be compared in DMTS and DMTNS requires the hippocampus. A more complicated problem is **transitive inference**. In this problem, animals have to learn a transitivity rule, i.e., if A>B and B>C, then A>C. Preference for A over C in this context can be explained by two strategies: either a form of deductive reasoning in which the experimental subjects construct and manipulate a unitary and linear representation of the implicit hierarchy A>B>C; or a form of associative responding as a function of reinforced and not reinforced experiences, in which case animals choose among stimuli based on their associative strength. The latter explanation can be ruled out by careful experimental design, e.g., by training an animal to five different visual stimuli A, B, C, D, and E in a multiple discrimination task A+ vs. B–, B+ vs. C–, C+ vs. D–, D+ vs. E–. Such training involves overlapping of adjacent premise pairs (A>B, B>C, C>D, D>E), which underlie a linear hierarchy A>B>C>D>E. After training, animals are tested with B vs. D, a nonadjacent pair of stimuli that was never explicitly trained. In theory, B and D have equivalent associative strengths because they were associated with reinforcement or absence of it equally often. Thus, if the choice of the animal is guided by the stimulus' associative strength, it should choose randomly between B and D. If, however, it applies a transitivity rule, it should prefer B over D. Many mammals extract the transitivity rule, honeybees appear not to learn it.

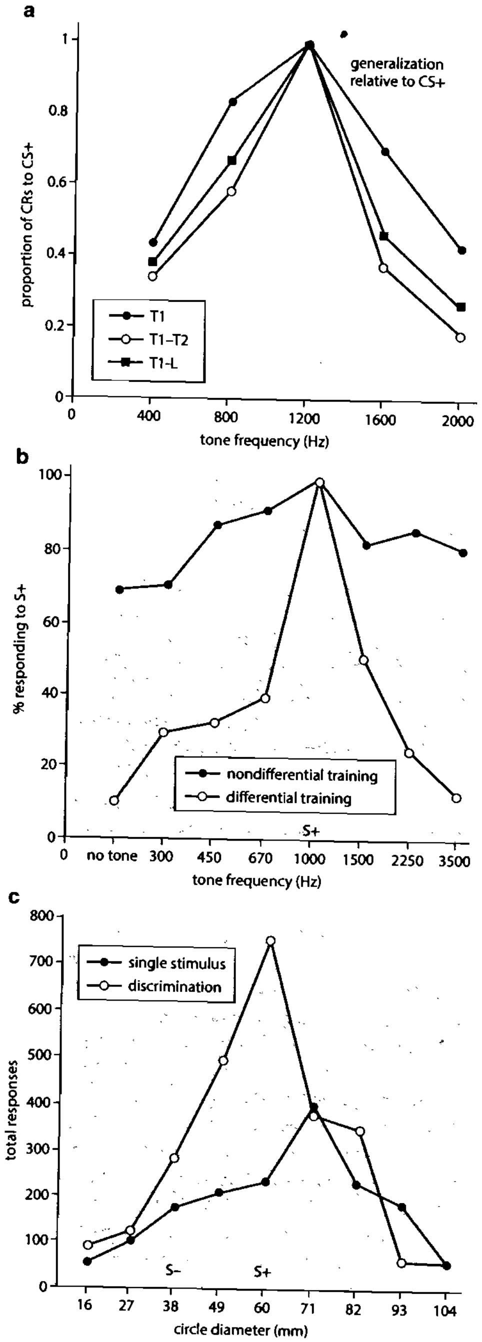


Fig. 28.6 **Discrimination and generalization.** (**a**) The eyeblink response of rabbits was trained to a tone of a frequency of 1,200 Hz either alone (*T1*, absolute training) or differentially to two tones, T1 (CS+: 1,200 Hz) forward-paired, T2 (CS–: 2,400 Hz) backward-paired, or to a tone T1 (CS+: 1,200 Hz) forward-paired and a light stimulus (CS–: L) backward-paired. Notice that the generalization gradient is narrower after differential conditioning even if CS– is of a different modality. (**b**) Differential conditioning leads to sharp generalization functions. Pigeons were trained to peck a key when a tone of 1,000 Hz was presented. In the case of absolute training, pigeons generalized to tones of all frequencies tested, after differential training, the generalization gradient becomes sharp and centered around the trained tone of 1,000 Hz. (**c**) Differential operant conditioning can lead to a peak shift of generalization. Initially a horse was rewarded for pressing a bar in a 60-mm-diameter circle after 60 s. Testing different circles of different diameters (abscissa) shows a symmetrical generalization function centering around the trained stimulus (*open circles*, single stimulus). Afterwards a CS– of 38 mm diameter was introduced and again different diameters were tested (*filled circles*, discrimination). The generalization function shifts to larger diameters (After [14], © (2008), with permission from Elsevier)

28.4.3.2 Occasion Setting

The so-called **occasion setting** problem requires also the extraction of a rule although nonelemental forms of associations may be sufficient. In this problem, a given stimulus, the occasion setter, informs the animal about the task. This basic form of conditional learning admits different variants depending on the number of occasion setters and discriminations involved, which have received different names. An example involving two occasion setters is the so-called **transwitching problem**. In this problem, an animal is trained differentially with two stimuli, A and B, and with two different occasion setters C1 and C2. With C1 stimulus A is rewarded while stimulus B is not (A+ vs. B–), with C2 it is the opposite (A– vs. B+). Focusing on the elements alone does not allow solving the problem as each element (A, B) appears equally as rewarded and nonrewarded. Each occasion setter (C1, C2) is also rewarded and nonrewarded, depending on its occurrence with A or B. Animals have therefore to learn that C1 and C2 define the valid contingency. The transwitching problem is considered a form of contextual learning because the occasion setters C1 and C2 can be viewed as contexts determining the appropriateness of each choice. Note that biconditional discrimination (AB+, CD+, BC–, AD-see above) is also a transwitching problem, and thus an occasion setting problem, if one considers A and C as occasion setters for B and D (i.e., given A, B+ vs. D–, and given C, B– vs. D+). All of these problems are forms of conditional learning in which a stimulus can have different associates depending on the conditions in which it is presented.

28.4.3.3 Categorization

When animals categorize objects, they apply both the rule of similarity and of difference. Some objects are treated as belonging to the same category, and others to a different category. Pigeons learn hundreds of pictures of natural objects and categorize them differently (houses, humans, flowers, cars, etc). When exposed to new exemplars they group them accordingly. Honeybees can extract the feature as symmetrical vs. asymmetrical from multiple instances and transfer this categorization to new exemplars. Both pigeons and honeybees learn a reversal of their behavior to the category much faster than establishing the rule at the very first instance.

In all these experiments it is crucial to control that some low-level feature (e.g., overall brightness or color, overall spatial frequency distribution, a common particular key feature) may not explain the behavioral categorization effect. Even so, it is not clear what it means that animals categorize objects. Do they create an abstract concept of a category as humans do, e.g., that of symmetry, of houses, of trees? Since little is known about the neural correlates of such concepts, the question cannot yet be answered. Possibly there is one exception – the concept of number.

28.4.3.4 Counting

Can animals *count*? One of the difficulties in answering this question lies in the enormous variety of behaviors that can be controlled by numerical attributes of stimuli. An organism may be trained to select the larger (or the smaller) of two arrays of items, with the experimenter controlling the non-numerical attributes of the stimuli (e.g., area or density), so that only the number of items in the array can reliably predict reinforcement. The concept of number is abstract and should allow the animal to transfer across different sensory modalities and across different test procedures. True counting requires the presence of cardinality, the one-to-one assignment of a numerical tag to an array, and the presence of ordinality, the ability to order these numerical tags. Furthermore, the animal needs to be able to transfer to new numbers. For example, a rat trained to press a lever twice after two light flashes and four times after four light flashes ought to be able to spontaneously press a lever three times after three light flashes with no additional training. This strict definition of counting has been met in very few experiments. Rats were trained to press the right lever when two sounds were presented and to press the left lever when four sounds were presented. The non-numerical features of the stimuli – such as the duration of each sound, the interval between sounds, and the total duration of the sound sequence – was controlled so that a reliable discrimination could be based only on the number of the sounds in a sequence. After rats learned this discrimination, the sounds were replaced by light flashes. The rats followed the previously learned rule. In several cases the transfer between items has been well documented, e.g., in ravens, a gray parrot, monkeys, and apes. The chimpanzee Ai was found to be able to perform a three-unit ordering task which included different behaviors depending on whether a higher or a lower algebraic number (up to three) was expected. It thus seems clear that primates and birds can think in at least simple terms about how many objects they perceive. Thinking about numbers in animals may seem to be a matter that would seldom have been useful enough in the past for natural selection to have favored it. Yet when it becomes important to think in this way in order to get food, ravens and few other birds, as well as rats, monkeys, and apes learn to do so, apparently employing a general ability to learn simple concepts.

A less strict definition of counting includes the capacity of animals to judge about the approximate number of items (numerosity) and the sequential experience of items in navigation (precounting). Discrimination between numbers of items up to seven is well documented in birds and mammals, but less well in insects. Sequentially experienced signals have numerical attributes, and animals may use this for navigation (see below). Bees trained to fly in a tunnel experienced up to four visual signals at varying distances. The feeding place was located at a constant relative position with respect to the sequential signals. In a test situation bees searched accurately between the first and second signal if trained to such a relative position, less accurately between the second and third position when trained to that position, and behaved randomly when trained to the position between the third and fourth position. This result indicates that bees might be capable of some form of precounting up to a number of three.

28.4.3.5 Causal Reasoning

Do animals understand that their actions lead to particular consequences? Causal reasoning in the strict sense has been considered as a key cognitive faculty that divides humans from animals. Animals accordingly have been thought to approximate causal learning by associative processes. It has been difficult to ask whether animals understand that their actions cause an outcome rather than just learning about the correlation between stimuli, actions, and outcome. Figure 28.7 describes a series of experiments showing that rats have a much deeper understanding of the causal nature of their actions. One group of rats observed that presentations of a light (L) was followed by a tone (T) and by food (F). In an operant conditioning paradigm they then learned to expect food after pressing a lever that causes a tone. Another group of animals learned that food is predicted by a noisy tone N indicating a direct cause of N for food. If animals of group one caused the appearance of the tone T (intervening situation) they searched less for food than animals of group 2 after they caused N. Obviously, causing the tone by their own action led to a different expectation of the outcome in the first group than causing the tone in the second group. The kind of "thought" about the physical world which the animal may have implicitly applied could be: "I did not cause the tone, therefore the light must be predictive, and thus I expect food" (for the observing situation). For the intervening situation it could be: "I caused the tone, therefore there should be no light, and thus I do not

expect food". Obviously the rats derived predictions of the outcomes of interventions after passive observational learning. These competences cannot be explained by associative theories and require the assumption that rats are capable of causal reasoning [3].

28.4.3.6 Insight

Selecting and constructing **tools** is frequently seen in animals ranging from rather stereotypical and innately programmed behavior (as e.g., in weaver ants that use their larvae for knitting together bent leaves to construct a nest) to highly flexible and learned behavior (such as tool use in primates). Animals manipulate material giving the impression that they have an insight into the physical conditions of the world. Ravens spontaneously pull a string with a piece of meat at its end upwards by stepwise catching the string with the pick, lifting it, and stepping on the string with one leg (Fig. 28.8b). The most compelling evidence for the understanding of causal properties of physical objects comes from corvids. A New Caledonian crow spontaneously bent a piece of ineffective straight wire into an effective hook tool for retrieving food (Fig. 28.8a) [2].

28.4.3.7 Individual Recognition and Self-Recognition

A cognitive component of **self** may be related to individuality as recognized by others and by the animal itself. Cricket males perform rivalry songs, defend their territories, and fight against each other. Winners and losers appear to learn to recognize each other on an individual basis. The yellow-black patterns of the faces and the abdomen of the paper wasp *Polistes fuscatus* vary considerably, making it possible that individual animals in these small colonies might recognize each other. Altering these facial and/or abdominal color patterns induces aggression against such animals, irrespective of whether their patterns were made to signal higher or lower ranking, arguing that this altered aggressiveness indicates individual recognition [24].

Queens of small ant colonies (*Formica fusca*) are individually recognized by their offspring [6], but how about the workers of insect societies? Insect societies are highly structured in groups of animals performing particular behavior (brood care, cleaning, defense, foraging). Members of some of these groups may differ in body morphology (e.g., soldier ants) and stay with the group for their entire life, other group assignments are age dependent and highly adaptive to the colony needs (as is the case in a honeybee colony). Stable or temporal group membership is mutually recognized most likely by odor profiles. E.O. Wilson states on the final page of "The Insect Societies" (1971): "The insect societies are, for the most part, impersonal. The small, relatively primitive colonies of bumble bees and Polistes wasps are based on dominance hierarchies, and individuals appear to recognize one another to a limited extent. In other kinds of social insects, however, personalized relationships play little or no role. The sheer size of the colonies and the short life of the members make it inefficient, if not impossible, to establish individual bonds." However, the sheer unlimited capacity of

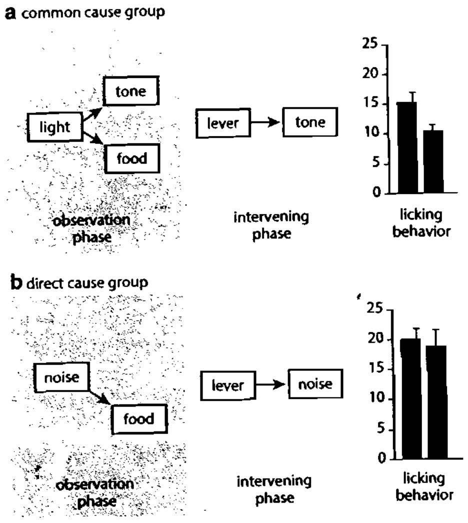


Fig. 28.7 Causal reasoning in rats. (a) *Top*: Group one experienced L (light) as a predictor of T (tone) and F (food). In group two a noisy tone N predicted F (observing situation). *Bottom*: Later, in an intervening situation animals of group one could elicit T and those of group 2 could elicit N by pressing a bar (*arrow* to T and N). If the animals had learned the logic relations between light (L), tone (T) and food (F) (group one) or between noise (N) and food (F) (group two) the two groups should behave differently in an intervening situation because eliciting T alone by animals of group one should not lead them to expect F. (b) Experimental results. Mean licking behavior was used to measure expected food rewards. Animals of group one expect the food significantly less often than those of group two (Modified from [3] with permission from AAAS)

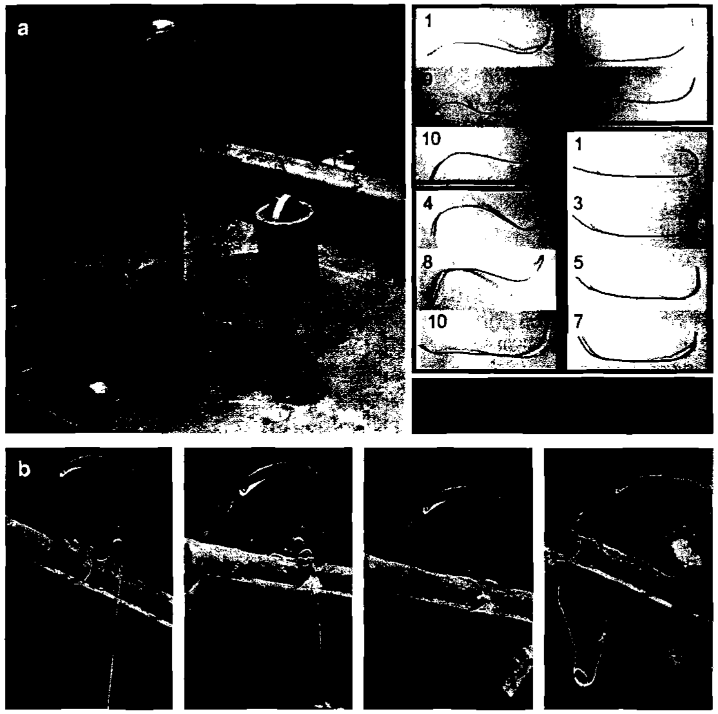


Fig. 28.8 Two examples of insight in birds. (a) The Caledonian crow bends a wire to a hook such that it can be used to pull up a container with food deposited in a transparent container. The hooks produced by four different birds are shown on the *right side* (After [2] © (2009), National Academy of Sciences, U.S.A., with permission). **(b)** A raven pulls up a piece of meat hanging on a string. The behavior is not learned but performed at once after the bird has inspected the situation from the distance. Pulling procedure requires sequences of catching the string with the beak, pulling it up, and stepping on it (After [12], with permission)

insects to discriminate odors (see Chap. 13) provides the potential for discrimination of a very large number of group constellations, potentially even to the level of individual recognition.

Does an animal know about itself? **Self recognition** in animals involves at least four different levels: intentionality, individual recognition in a social context, response to a mirror image of the own body, and episodic-like memory. Operant learning includes an intentional component: self-generated behavior creates an expectation via a parallel pathway (efference copy) which allows the distinction between self-produced causal events and environmental events (intentional aspect of behavior). One may even assume that the internal representation of actions (efference copy) developed in evolution for self–nonself discrimination. The identification of the nervous system with its body is probably the most basic component of this distinction. Thus, any animal can be considered as an agent that causes things to happen and recognize these things as caused by itself. Operant behavior is, furthermore, goal directed. The self-generated causes will eventually be more favorable to the animal than the environmental causes. At this level of argumentation any animal will experience "self" as different from "nonself". Such a body-self could be considered to indicate a low level of cognition.

Feeling **pain** may be taken as an indication of body-self experience. Do invertebrates experience pain, a form of self-recognition that includes an emotional and a warning component that points to the future (see Chap. 21)? Locusts and crabs cast off body appendages when attacked. Do they experience different forms of sensory input when they perform these actions themselves or when the same appendages are removed? When honeybees lose their stinger the abdomen is damaged so much that the animal will die. It has been observed that alarm pheromone, which usually triggers an attack flight, induces stress analgesia via an opioid system in the honeybee, potentially indicating that a preparatory response of the nervous system leads to a reduction of the strong sensory input from

the body distraction. Opioids, which are usually associated with stress-induced analgesia, have been found in other invertebrates such as crickets and the praying mantis, thus suggesting that their presence may serve to counteract the effect of nociceptive stimuli as in vertebrates.

A common test of self-recognition uses a mirror. Octopus react aggressively to both the own mirror image and a conspecific making it unlikely that they recognize themselves (but they may well be recognized by others as an individual). Primates and some birds pass the mirror test. A magpie spontaneously tries to clean a white paint mark on its head when detecting its mirror image [20]. Based on the different evolutionary history of the bird and primate brain, it is argued that the neural mechanisms of self-recognition in these two groups of animals are convergent traits. Practically nothing is known about their neural basis.

Humans remember episodes of the past, recollect them consciously, and relate them to their own memory in space and time (**episodic** or **autobiographic memory** also called **autonoetic consciousness**). Operant learning provides continuous information about the self-induced causes and distinguishes them from environmental causes (see above). This allows the animal to test whether its expectations about the physics of the world are met, a form of exploring the world. Because the relevant conditions of the world change with the changing requirements of the own body, the distinction between self-related memory and memory about environmental conditions is highly important. It allows to store the own needs and desires together with the actions leading to their satisfaction, which is, in essence, an episodic memory. Since we do not know the conscious state of the animal, such memories have been called episodic-like. Episodic-like memory provides the strongest hint of self-recognition in animals because they include the experience that "I can control the world by my actions". It is this cognitive "I" which defines the self much more than own body recognition in the mirror test.

28.4.4 Learning by Observation

28.4.4.1 What Is Observation?

Animals improve their perceptual and motor performances and develop new behaviors by observation. Imprinting and many forms of social learning (imitation, acoustic and visual communication, traditions) are based on observation without obvious external reinforcing stimuli rather than on associative learning. How do animals know when and what to learn? Most likely several neural mechanisms are involved given the large range and conditions under which observation learning occurs. A rather low-level mechanism has been mentioned already above in the context of improvement of motor performance by an error signal. It is possible that in a way akin to motor learning (see above, Fig. 28.2b), an internal value coding pathway is generated. In this case, observation learning could function mechanistically in a way similar to associative learning, if the conditions under which it happens activate an internal value system. In imprinting, this could be just the innate program of a sign stimulus. The emotions involved in the social context could form such a value system. In other conditions, e.g., exploration in space, tool manipulation, and play, selective attention could be the source for the activation of a value system – however, little is known about the neural mechanisms. The apparent lack of an obvious external value signal may also result from the replacement of a primary reinforcing stimulus by a learned (second-order) reinforcing stimulus. For example, the positive feeling of social coherence could result from primary rewarding signals (feeding, care taking) in the context of social embedding. Learning in the social context may then be second-order associative conditioning.

These arguments support the notion that the mechanisms of observation learning are of associative nature. Although multiple observations indicate an activation of modulatory systems under conditions of enhanced and directed attention as it happens during exploration, social communication, and playful tool manipulation, it cannot be excluded that observation learning may also involve nonassociative mechanisms possibly based on the sheer sequence of events.

28.4.4.2 Navigation

Animals and humans know where they are and where they are going next. The question is, how do they know and what does "knowing" actually mean? In migrating animals (insects, fish, turtles, birds, mammals) long-distance vectors are innately determined. Learning the route may play a role in cases of multiple migrations of the same individual but is not a requirement for successful migration. Median-range navigation involves multiple starts and returns from and to a central point, e.g., a nesting site. Learning is an essential strategy under these conditions. We humans experience our ability to orient and navigate in space and time as a set of functions to which we can relate our attention separately and specifically. We identify an object, take a bearing, and approach it when we sense it from a distance. When planning a route we retrieve from memory a sequence of views, and coordinate our navigational task accordingly. Our introspection of a mental map is experienced as a type of frame for localizing ourselves and the geometric relations of objects. This mental map corresponds to some degree to the physical map that results from measurements of distances and angles or from a bird's-eye view [25]. At the same time we have the ability to communicate locations, how to reach them, and what to expect from them.

Obviously, navigation involves multiple perceptual and computational mechanisms at peripheral and central levels of neural integration. Objects are identified, picture memories (not only in the visual domain) and their sequences are formed, motor performances along traveled routes are learned relative to the own body (**egocentric navigation**) and to the spatial relations to and between objects (**allocentric navigation**). All of these multiple cognitive faculties may be partially integrated into a coherent spatial representation, a cognitive (or mental) map. Studies in humans and animals tell us that cognitive maps are not the only possible reference system – for example, path integration or picture memories may be used instead or in addition.

Path integration (Fig. 28.9a) requires the computation of the rotatory and translatory components of movement. Body rotation can be measured with respect to external information (e.g., sun compass, far distant cues) or to internal information (kinestetics, e.g., by vestibular system, movements of body parts, see Chap. 16). The translatory component requires an odometer (distance measure) that may gain its information visually (as in flying insects by visual flow) or from some form of step counting (as shown in ants). The neural mechanisms of path integration are unknown. In mammals, modeling studies suggest that the path integrator resides in the entorhinal cortex integrating the signals from spatially tuned principle cells (grid cells) and that of head direction cells, which then is communicated to the hippocampus forming the properties of the place cells [5, 16] (Fig. 28.10). Head direction cells, grid cells, and place cells provide the animal with information about its location relative to local and further distant landmarks. Place cells in particular code not only spatial relations but also local cues like the odor and the sequence of experiences made along the way towards the location. Spatial coding in the hippocampus resides in multiple spatial representations (neural maps) and is highly dynamic. Spatial coding changes (is remapped) when the geometry of the environment changes. These properties make it likely that the multiple and adaptive neural maps in the hippocampus provide the substrate of a cognitive map (see below).

Path integration allows the animal to return to the point of origin along a straight path. The precision of the inbound path decreases with the length of curved outbound path because of error accumulation in the integration process. Path integration is an egocentric mechanism as long as the animal does not learn anything about the spatial relations of the objects experienced during inbound and outbound movements. If it does (this is the case, e.g., in the honeybee and most likely in other animals), then it is a component of an allocentric mechanism.

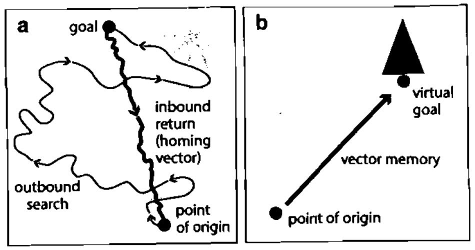
Goal-directed vectors (Fig. 28.9b): Animals steer towards goals without access to any signals emanating from the goal. This is evident in migratory movements, but occurs also in close range navigation. In that case, vector information relative to a compass (Sun, Moon, stars, Earth magnetic field, steady winds, far distant cues) and an odometer is derived from former learning (e.g., the straight return path in path integration, or in the case of the honeybee the vector communicated in the waggle dance). Vectors provide sufficient information for reaching a goal but also for communicating goals among individuals if the angular and distance components are related to commonly agreed references. The honeybees' waggle dance is such a case. Frequently used routes along memorized vectors lead to learning about the spatial relations of the landmarks along the route, and thus convert an initially egocentric navigation into an allocentric one.

Picture memories (Fig. 28.9c): Animals learn the visual appearance of the environment around a particularly important location (e.g., the nest) often when viewing from a rather stable vantage point. This behavior is particularly well known in insects. The simple model as shown in Fig. 28.9c assumes a retinotopically stable visual memory and a search strategy that minimizes the angular deviations between the memory and the actually experienced image. Although the mechanisms assumed in this heuristic model do certainly not apply to navigating animals they still propose a minimal concept of navigation according to picture memories. Animals may store several to many picture memories, and thus may navigate from one vantage point to the next.

Cognitive map (Fig. 28.9d): Animals are particularly attentive to landmark features when exploring the environment. It is this situation of observatory learning that may allow to determine and memorize spatial relations between objects in a general sense. It is possible that particularly salient features of the landscape (like boarder lines between areas, slope of the landscape, panorama, rivers etc. which are usually referred to as **gradients**) may establish a geometrically organized but spatially coarse "gradient map". Such a gradient map could include islands of fine-grain picture memories such that animals traveling according combined maps have a patchwork of information about where they are and where to go next.

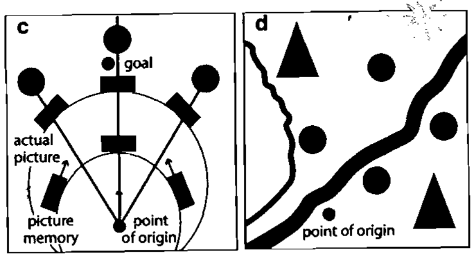
Evidence that animals form cognitive maps comes from the following observations: (i) Tolman who coined the term cognitive map observed that animals (rats, mice) chose the shortest distance to a desired place if they had explored the area (e.g., a maze) before. Since these seminal studies **novel shortcuts** became the signature for a map structure of spatial memory. (ii) When animals are not yet fully trained in a maze they may hesitate at the choice points and perform movements in the direction of the intended goal. (iii) When animals are trained in a complex maze with multiple routes to the goal and one path is blocked they tend to decide for the nearest and shortest open path. (iv) Rats swimming in a milky water learn the location of a safe platform under water with respect to the geometry of the surrounding marks (Morris' water maze). All these behaviors require a functioning hippocampus.

In mammals the hippocampus (together with the entorhinal cortex) communicates with the prefrontal cortex (Fig. 28.10). Functional imaging studies in humans support the view that the hippocampus complex represents locations (grid and place cells), computes shortcuts by path integration together with neurons coding head direction and yet unknown signals from an odometer (the neural distance measuring device), and supports the learning of places from particular views. Action-based representations have been linked to the dorsal striatum, and observer-independent cognitive maps appear to depend critically on retrospinal cortex together with the hippocampus. The essential role of the hippocampus for navigation is also known in fish, reptiles, and birds, and the volume



path integration

vector memory



picture memory and sequential matching

cognitive map

Fig. 28.9 Mechanisms of navigation. (**a**) In path integration animals are able to return to the point of origin (e.g., a nest) along a straight path after reaching the return point (goal) along curved movement. The rotatory component of their movements may be measured relative to a far distance source (e.g., the sun), and the translatory movement by some form of an odometer (distance measure). If the animals do not relate its outbound and inbound movements to the geometry of landmarks but to body centred measures path integration is an egocentric form of navigation. (**b**) A vector memory provides the animal with the possibility to reach a distant goal without access to stimuli emanating from the goal (virtual goal). The directional component may be read from a compass (e.g., sun compass), the distance component from an odometer. Both components may be innate as in the case of migration over very long distances or learned (for navigation in the close surrounding). (**c**) A picture memory allows the animal to localize itself relative to the geometry of landmarks as seen from a vantage point (point of origin). Finding this vantage point may involve sequential matching procedures in which the deviation of the actually experienced view from the picture memory is used to reduce the deviation which will bring the animal closer and closer to the vantage point by trial and error. (**d**) The memory structure of a cognitive map relates to the geometry of landmarks relative to a compass system. Such a cognitive map could either be a complete representation of the spatial relations of local landmarks or it could store predominantly those relations between long ranging landmarks (gradient map) into which local view based memories are embedded. In the first case an animal will be able to reach the point of origin from any location within the map, in the latter case the gradient map would be used first to reach an estimated location and then to create a homeward flight by multiple matching procedures of multiple picture memories

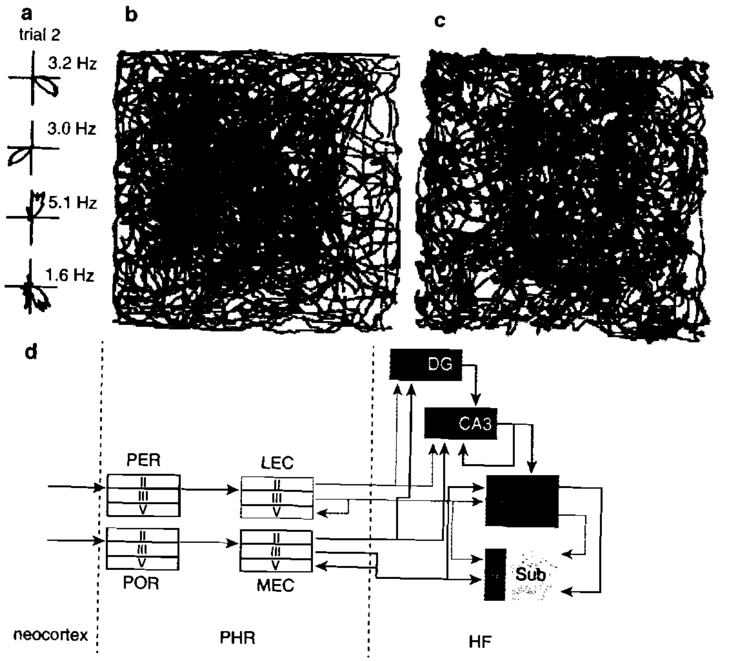


Fig. 28.10 Examples of head-direction cells, a place cell, and a grid cell recorded from a rat hippocampus. **(a)** Response characteristics of four head-direction cells. The polar plot describes the neural activity of the respective cell when the animal is looking into the direction indicated by the angular orientation of the *blue line*. The strength of the neural response is given by the deviation from the center (After [15] with permission from AAAS). **(b)** Place cell. The *gray lines* give the running path (trajectory) of a rat exploring a square environment. The *red color* marks the location when the place cell is firing. The population of place cells with different spatial firing properties defines the location of the animal. **(c)** A grid cell is characterized by multiple firing locations arranged in a hexagonal pattern. Grid cells differ with respect to the spatial separation and size of the subfields. **(d)** Circuitry of the hippocampus. The neocortex is connected to the hippocampus mainly via two pathways through the parahippocampal cortex (*PHR*). One projects through the perirhinal cortex (*PER*) and the lateral entorhinal cortex (*LEC*); the other projects through the postrhinal cortex (*POR*) and the medial entorhinal cortex (*MEC*). Cells that carry information about the position of the animal, such as grid cells, head-direction cells, and boarder cells (not shown in the upper diagram) are found in the MEC but not in the LEC. MEC and LEC project to the same regions in the hippocampus, both via direct projections to each hippocampal subfield and via the indirect trisynaptic circuit through dentate gyrus (*DG*) and CA3. Place cells are pyramidal cells of the hippocampal formation (*HF*) (After [5], © (2010), with permission from Elsevier)

of the hippocampus does not only increase in London taxi drivers but also in pigeons with more navigational experience.

Nothing is known about the neural substrate of navigation in any insect. The multisensory convergence in the mushroom body of insects makes it likely that this integration center is involved in navigation. In addition, the central complex may well be involved because it contains neural nets that code the sun compass-related polarization pattern of the sky and the movement of the animal relative to objects [13, 18].

28.5 Working Memory: Planning and Decision Making

28.5.1 Working Memory: A Definition

Learning leads to a change in behavior. The information necessary to control new and better adapted behavior resides in the nervous system at many levels and is used to control behavior in the future. The entirety of all neural changes induced by learning represents a **memory trace**. Three different components of the memory trace are to be distinguished: consolidation, retrieval, and execution. Learning does not produce the final memory trace immediately. Time- and event-dependent processes form the trace, and are conceptualized as **consolidation processes**. Short-term memory is transformed into mid-term and long-term memory, and the molecular, cellular, neural, and systems-related processes are one of the most intensively studied questions in neuroscience today (see Chap. 26). Stable memory traces need to be moved from a silent into an activated state by **retrieval processes**. Internal conditions of the animal, external cues, and a neural search process (see below) shift a silent memory into an active memory. The **expression** of the active memory may undergo *selection processes* before its content is expressed. Animals need to decide between different options as they reside in memory, and the decision process requires access to the expected outcomes. The expected outcomes are stored in memory, too, and only when the respective memory contents are retrieved they will be accessible to selection processes. This network of interactions between retrieval, selection, and execution is conceptualized in a particular form of memory – working memory.

The concept of **working memory** has been derived from psychological studies in humans, particularly children, which examined the interference of two or more tasks to be performed simultaneously [7]. For example, a subject may be asked to do a simple arithmetic (counting backwards) and at the same time keeping an item in memory. It was found that the capacity of working memory is limited, grows with age of the children, and can be assigned to subcomponents (called the phonological loop, the visuospatial sketchpad, and the episodic buffer) which all interact and converge with a central executive [1]. In animal studies, working memory is often related to a particular form of short-term memory as it is tested in delayed matching to sample or delayed matching to nonsample tasks (DMTS, DMTNS, see above). The memory span is also limited, depends heavily on the task, is sensitive to interference from distracting signals, and depends on the hippocampus. If the DMTS and DMTNS task requires the application of a rule learned in multiple trails, animals have to recruit the memory for the rule and decide whether the rule applies or not.

A basic form of working memory was already mentioned in the model of operant learning (Fig. 28.2b). The comparator C receives input both from the efference copy (which can be considered as the readout of a memory trace) and the sensory feedback accompanying the execution of the action SF. In this elementary form, a decision has to be made on the basis of the match/mismatch between efference copy and SF. Under more complex conditions the animal will find itself exposed to internal body conditions (S1 in Fig. 28.11) and environmental signals that retrieve multiple memory traces which lead to different outcomes if applied (S2, S3 in Fig. 28.11). These signals together will retrieve from stable reference memory several potentially relevant memories (e.g., sensory memories, motor performance memories, value memories) that are shifted into working memory and constitute the active conditions of working memory. The central executive processes receiving such input from working memory will produce the respective patterns of corollary discharge representing the expected outcome of the potential motor patterns. Multiple rounds between working memory and central executive are thought to lead to a decision process that finally will initiate actions.

The conceptual model in Fig. 28.11 does not require any conscious recollection but captures the processing of implicit knowledge as it is available to any nervous system that needs to decide between different behaviors. Any motor command produces an expectation of its outcome (the corollary discharge or efference copy) which is available to the working memory for internal processing leading to an evaluation of whether the expected outcome is desirable on the basis of former experience and body conditions. As all forms of memory, working memory is a process of global neural nets rather than a localized function in any specialized area. In the mammalian brain the striatum, premotor cortex, and inferior parietal cortex will be more involved in the evaluation of potential motor performances, the hippocampus more in those of spatial and sequential navigation tasks, the dopamine system of the ventral tegmentum more on that of the expected reward.

The decision-making process involves components which are well studied in cortical sensory systems. Lower signal-to-noise ratios (equivalent to less strong neural representations, e.g., of a memory readout) are outcompeted by neural activations with higher signal-to-noise ratio. The basic mechanism of neural nets to settle in well-defined representations is mutual inhibition as experienced in visual illusion flip images. Thus, decisions between options that can switch indicate rivalling neural processes. Decision between more

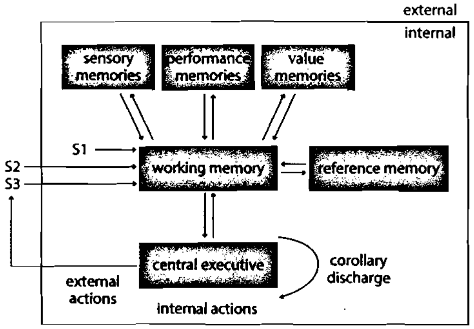


Fig. 28.11 Conceptual model of processes underlying working memory as it may apply to implicit knowledge of any nervous system that needs to decide between several behaviors. Working memory receives sensory input from body signals (*S1*) and external signals (*S2, S3*). Using these signals it retrieves from stable reference memory relevant memory contents and transfers it into an active state. These active memory contents may belong to sensory memory, performance memory, value memory, or others. Each of these multiple memories are related to particular behaviors that are executed centrally (central executive) leading to the activation of internal actions as represented by their corollary discharge or efference copy. The reciprocal interaction between working memory and central executive will lead to a decision between competing outcomes and finally execute external actions

close neural representations requires longer processing time, as well as decision between more options. A major yet open question relates to those neural mechanisms which connect and orchestrate the multiple parallel processes characterizing working memory function. One proposal is that synchronous spiking activity may be the requirement and the signature for neural decision processes.

28.6 Animal Thinking: The Basics

Studies in animal behavior and its neural basis developed into a science by rejecting anthropomorphic terminology and strictly applying descriptive terms. Behavioral processes not directly measurable were either ignored or not accepted as topics for scientific endeavor, as e.g., memory, spontaneity, and creativity of the brain. Behaviorism and ethology, although differing in many respects, developed rather similar strategies in understanding behavior as reflection of input/output properties. As a consequence, spontaneity and creativity of the nervous system was not in the focus of mainstream comparative behavioral biology and neuroscience for most of the last century. In the wake of the cognitive revolution, the conceptual move from black box attitudes to the recognition of the brain as a creative system, research on animal cognition has begun to ask what kind of knowledge animals use to find their way around, how they make decisions between options, and how they represent the social relationships of others around them.

Nervous systems vary in size and architecture, and thus animals come with different adaptations to similar problems. It is sometimes assumed that "simple" nervous systems like those of arthropods and mollusks solve the problems by radically different mechanisms relying on innate routines and elementary forms of associative learning. However, constructing a great divide between simple and advanced nervous systems will lead us astray because the basic logical structure of the processes underlying spontaneity, decision making, planning, and communication are more or less the same. It is a more productive position to envisage the differences in quantitative terms rather than qualitative terms providing us with a wealth of "model systems" to elucidate the essence of the basic processes.

Thinking about the basic design of a brain that subserves cognitive functions, one recognizes a structure of essential modules and their interconnectivity (Fig. 28.12). This architecture of modules appears to be shared by a large range of animal species and may even apply to the worm-like creature at the basis of the evolutionary divide between protostomes and deuterostomes, these two largest evolutionary streams of bilateral animals with a centralized nervous system [4]. Although there are multiples of each of the modules depicted in Fig. 28.11 (multiple perceptual systems, multiple belief-generating systems, multiple desire-generating systems, multiple action-planning systems, multiple motor control systems), the basic idea put forward in this scheme is that perceptual systems feed to three downstream systems arranged both serially and in parallel that converge on the action planning system. Thus, perceptual systems can reach the action-planning systems directly, and, in addition, the desire- and belief-generating systems receiving the same perceptual information will act in parallel onto action-planning, as well.

Given the similarity in the basic design of nervous systems we may ask: Are animals aware of themselves, of what they are doing, of what they are expecting, and what they intend? This question touches on an epistemological problem, and we would have to ask what is meant by "**awareness**". Certainly we do not mean human awareness, as it is accessible to us by introspection. We certainly do also not imply that all animal species with their enormously different nervous systems have the same kind of "animal awareness". This means that terms like self-awareness, expectation, planning, creativity, and even learning and memory have different meanings for different animals. However, judging from all that we know so far, the difference relates to the level of complexity and not to fundamental differences. It will be the goal of future comparative studies to understand how quantitative differences in the structure and operation of nervous systems lead to the large range of animal cognition around us.

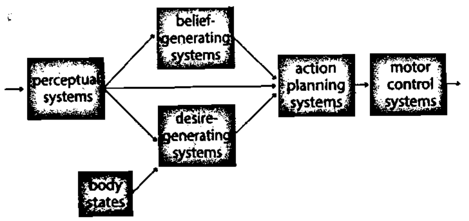


Fig. 28.12 The cognitive structure of brains composed of modules for perception, desire, and memory stores (belief-generating systems). Action planning can either be generated by direct inputs from the perceptual systems or result from processes that are generated in parallel pathways weighting the perceptual inputs with respect to expected outcomes (belief-generating systems) and the motivational conditions of the animals body (desire-generating systems). These modules can either be rather basic (as in more simple nervous systems) or highly complex, but in any case the basic structure particularly with respect to direct and indirect pathways and necessity of operations between the models may apply to any nervous system (After [4] with permission from Oxford University Press)

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