



## Review

## The cognitive neuroscience of category learning

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**Abstract**

Recently, a multidisciplinary approach has provided new insights into the mechanisms of category learning. In this article, results from theoretical modeling, experimental psychology, clinical neuropsychology, functional neuroimaging, and single-cell studies are reviewed. Although the results are not conclusive, some general principles have emerged. Areas localized in the sensory neocortex are responsible for the perceptual representation of category exemplars, whereas lateral and anterior prefrontal structures are necessary for the encoding of category boundaries and abstract rules. The prefrontal cortex may influence categorical representation in the sensory neocortex via top-down control. The neostriatum is important in stimulus–response mapping, and the orbitofrontal cortex/ventral striatum are related to stimulus–reward associations accompanying category learning. Many category learning tasks can be performed implicitly. In conclusion, category learning paradigms provide a unique opportunity to investigate cognitive processes such as perception, memory, and attention in a systematic and interactive manner. Category learning tasks are suitable for mapping damaged brain systems in clinical populations. © 2003 Elsevier B.V. All rights reserved.

*Theme:* Neural basis of behavior*Topic:* Cognition

**Keywords:** Alzheimer's disease; Amnesia; Attention; Basal ganglia; Category learning; Executive functions; Feedback; Functional magnetic resonance imaging; Huntington's disease; Medial temporal lobe; Memory; Neuropsychology; Parkinson's disease; Perception; Positron emission tomography; Prefrontal cortex; Reward; Schizophrenia; Single cell; Striatum; Tourette syndrome

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## 1. Introduction

Living organisms have a remarkable capacity to achieve adaptive responses in diverse situations. In this respect, two basic response patterns can be distinguished: we may select a specific response for a particular object or, alternatively, the same action is performed for a number of different stimuli that share behaviorally salient features. The former case refers to identification or recognition, which requires one-to-one stimulus–response mapping, whereas the latter refers to categorization, characterized by many-to-one stimulus–response mapping (Fig. 1). For example, humans have a repertoire of behavior when encounter with dogs in general, but some actions remain specific for our own dog. General behavior is based on categorization, while selecting a specific action towards a particular object is based on recognition [92]. During perceptual categorization, unrelated components of the environment are linked up and are given salience for decision-making (value-categories) [28].

The essence of categorization is transfer to novel stimuli; after a training phase, observers are able to use category-specific responses for stimuli that they have never seen before. This abstraction process makes our behavior economical, diminishing the need of separate response

learning for each and every individual object in our environment, a doubtlessly impossible venture [48,70] (Fig. 1). However, category learning is not a unitary process [5,6]. According to the structure of training, at least three types of paradigms can be distinguished. First, subjects may learn categories by the observation of category members (exemplars). Second, corrective feedback can be provided after category-decisions, leading to a gradually improving performance from chance level to a full ability to classify novel items. Feedback is a basic form of reward, giving value to objects of our environment and related responses (consider, for example, the value-categories of Edelman [28]). Third, getting acquainted with abstract verbal rules, humans are able to achieve a remarkably good categorization performance, even without seeing any exemplar. Considering these very different approaches, one can be sure that category learning is not homogeneous at the neurobiological level, and hence the discovery of neuronal correlates is not straightforward [5,6]. To achieve this goal, the most fruitful approach is the collaboration of traditionally separate disciplines. Indeed, category learning research is one of the best examples to illustrate multidisciplinary approach in modern cognitive neuroscience. This paper attempts to review and synthesize recent data from theoretical modeling, experimental psychology, neuropsychology, functional neuroimaging, and single-cell animal studies in order to present a comprehensive picture about how categories are learned and represented in the brain. Not surprisingly, such synthesis is closely related to more general brain functions such as perception, memory, and attention. A detailed discussion of results from research on natural categories with complex perceptual and semantic properties is beyond the scope of this review, and therefore I mostly will focus on the learning of artificial categories.

Experimental psychology is an especially valuable approach, providing controlled behavioral paradigms for testing at the neurobiological level. Theoretical modeling is a natural supplement of experimental psychology, establishing hypotheses about what is going on in mind

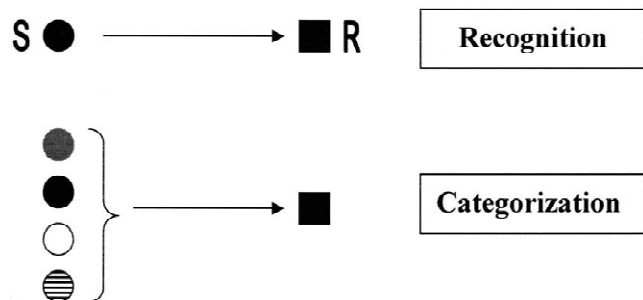


Fig. 1. During recognition, a particular stimulus /S/ is associated with a specific response /R/. During categorization, a group of similar but individually different stimuli (circles with different internal textures) is associated with a single response.

while solving a task. These two approaches can be used in populations of patients with brain damage (neuropsychology) and can be candidates of experiments using positron emission tomography (PET), functional magnetic resonance imaging (fMRI), or single-cell recordings in awake, behaving animals. First, I outline the main streams in theoretical modeling, as a starting point for the exploration of neural correlates of category learning.

## 2. Theoretical models of category learning

During the past decades, several authors tried to establish models in order to explain human performance in various category learning tasks. Despite this extensive research, there is no conclusion about the superiority of any of these approaches. Instead, it is likely that they reflect processes that work in a cooperative, supplementary or alternative way rather than in an exclusive manner. The models can be divided into four groups: (i) exemplar models, (ii) prototype models, (iii) boundary models, and (iv) cue-validity models (Table 1).

### 2.1. Exemplar models

One of the most known exemplar-based approach is Nosofsky's generalized context model (GCM) [92,93] (see also [85]). In this model, exemplars are represented as nodes in a multidimensional representational space, where dimensions are features such as color, luminance, and size (see also the multidimensional scaling (MSD) approach, Table 1 [92,93,134]). Exemplars localized closer to each other in the representational space are more similar than exemplars separated by a larger distance. Recognition and categorization are based on the similarity of a stimulus to the representations of previously seen exemplars. In recognition, similarity to a specific exemplar is computed, while in categorization a summed similarity to category exemplars is used.

An important aspect of the GCM is attentional weighting. Dimensions that are salient for the task are selectively attended, and consequently they become more dominant in determining similarity between exemplars. The GCM model has single systems for memory and attention during recognition and categorization. There are no different memory representations for individual exemplars and categories and the same attentional system is used for both task types; in recognition, selective attention is tuned to many features of individual exemplars, while in categorization, attention is directed to a restricted number of category-diagnostic features.

The original GCM does not discriminate between perceptual and decisional processes—it is not specified whether during category learning the perceptual representation of stimuli is changed or only decisional processes are altered. These are important issues, playing a central

role when one tries to apply the model for biological systems. In this respect, the prefrontal cortex may be essential for attentional and decision-making processes, while the representational space may refer to the sensory cortex where perceptual features are processed and stored [5,6,108].

### 2.2. Prototype models

Prototype models use a similar multidimensional representational space as seen in the case of exemplar models. The crucial difference between prototype and exemplar approaches is that in the prototype model categories and individual exemplars have separate representations. When observers are shown exemplars during training, they extract the central tendency or summary representation of these items, called the prototype (Fig. 2). For recognition, a stimulus is compared with individually stored exemplars, while for categorization, a stimulus is compared with the prototype in order to decide whether or not it is a member of the category [107,139–141].

There is a long-lasting argument whether exemplar or prototype models are better in explaining behavioral data [9,10,63,92,93,139–141]. Recent advances in neurobiology does not solve this problem; while neuropsychology and functional neuroimaging data indicate that different brain systems exist for recognition and categorization, some single-cell studies seem to be in favor of the single-system approach [45]. This issue will be discussed in detail.

### 2.3. Boundary models

The basic assumption of boundary models, such as the decision bound theory (DBT) and the general recognition theory (GRT), is that the representational space is divided into response regions, and observers assign different category-specific responses to these regions [3,4,80,81]. Boundary models distinguish between perceptual and decisional processes. Decisional attention alters the decision boundary, whereas perceptual attention reduces noise along the attended dimension. This approach is in parallel with current understanding of attentional systems in the brain. According to the classic view, the anterior attentional system (dorsolateral prefrontal cortex, anterior cingulate, and related basal ganglia structures) is responsible for the intentional control of selective attention, while the posterior system (posterior parietal cortex, pulvinar, and superior colliculus) mediates orientation towards environmental stimuli and enhances processing in specific perceptual channels [108,109]. A recent extension of this theory delineated the dorsal prefrontal–intraparietal circuitry as a substrate of goal-directed selection of stimuli and responses (components of executive control), whereas the inferior frontal–temporo-parietal system is believed to participate in the detection of behaviorally salient or unexpected stimuli [23]. The basic assumption of boundary

Table 1  
Models of category learning

Model	Characteristics	Key Refs.
MDS (multi-dimensional scaling)	Stimuli are points in multidimensional representational space Similarity is a monotonically decreasing function between points Similarity is modified by changing attentional demands in categorization and identification	[92,93]
GCM (generalized context model)	Categorization and identification are based on similarity to representations of previously seen exemplars Categorization: summed similarity to category exemplars Identification: similarity to a specific exemplar	[92,93]
ADM (average distance model)	Similar to the GCM Similarity decays linearly with weighted distance Distance in the representational space is taken as dissimilarity between the stimulus and category exemplars	[122]
EGCM (extended general context model)	Separation of perceptual and decision processes	[75]
ALCOVE (attention learning covering map)	Similar to the GCM Four parameters are included: discriminability of the stimuli, consistency of responding, speed of learning for exemplar–category associations and attention weights	[74]
RULEX (rule plus exception)	Observers apply one or two dimensional rules to describe categories, and memorize exceptions	[94]
PBI (probit linear model)	Categorization is based on the position of the stimulus with respect to a boundary	[4]
DBT (decision bound theory)	Time-to-time presentations of the same stimulus elicit different perceptual effects (perceptual noise) During category acquisition observers learn to divide the representational space into response regions and assign separate responses to each region Perceptual attention: reduces noise relative to the unattended dimension Decisional attention: affects decision bound	[5]
GRT (general recognition theory)	Perceptual processing is distinct from decisional processing Perceptual and decisional attention can be functionally independent (see also PBI and DBT)	[3]
COVIS (competition between verbal and implicit systems)	Explicit rules: unidimensional, linear, easy to verbalize Implicit rules (procedural learning): multidimensional, non-linear, hard to verbalize	[5]

Table 1. Continued

Model	Characteristics	Key Refs.
WPSM (weighted prototype similarity model)	Similarity between the stimulus and prototypes (central tendency in the representational space) is calculated for categorization In some versions dissimilarity is computed	[93,140]
WCVM (weighted cue validity model)	Critical values along each stimulus dimension are used to determine category membership Weighted sum over all cues is used The cue can be affected by the frequency of appearance during training	[122]

models is that decisional attention is mediated by the anterior attentional system and perceptual attention is linked to the posterior system [80,81].

Boundary models are also related to research on learning and memory. Recent theories described separate explicit (declarative) and implicit (nondeclarative) memory systems [145]. The first includes conscious and controlled processes, such as remembering a particular event, while the latter refers to automatic, non-controlled learning without conscious awareness, as in the case of acquisition of sensory and motor skills. Explicit memory is closely related to the anterior attentional system, whereas implicit processes are more independent from that [108,109]. According to the COVIS (competition between verbal and

implicit systems) model, unidimensional and linear category rules that are easy to verbalize (for example, stimuli containing green circles belong in the first category and stimuli with red circles belong in the second category) are learned by the explicit system (prefrontal cortex, anterior cingulate cortex, head of the caudate, and medial-temporal structures (hippocampal complex)), while in the case of complex rules that are hard to verbalize, the slower implicit procedural learning system takes the lead (sensory neocortex and tail of caudate) [5] (see also Section 3.5).

#### 2.4. Cue-validity models

In this approach, values from each stimulus dimension are used to determine category membership. The final output used for the determination of category membership is a weighted sum over all cues [122]. The cue can be affected by the frequency of appearance during category learning—more frequent cues have larger salience. For example, in the case of a two-dimensional representational space (color and size), particular values along these dimensions can be diagnostic for category membership (for a summary of theoretical models, see Table 1). Definitive cues are able to determine category membership in an all-or-none fashion (e.g. black stimuli belong in the first category and white stimuli belong in the second category). This unambiguous representation is excellent for higher-level rule-based category representations [5].

#### 2.5. Summary of the theoretical models

Each theoretical model suggests the existence of a representational system, in which dimensions are perceptual features. Categories can be considered as groups of individual exemplars defined by specific coordinates (feature values), central tendencies (prototypes), boundaries or definitive cues. Features are stored in sensory neocortical areas, whereas attentional modulation and decision-making is related to the fronto-striatal system [5,6].

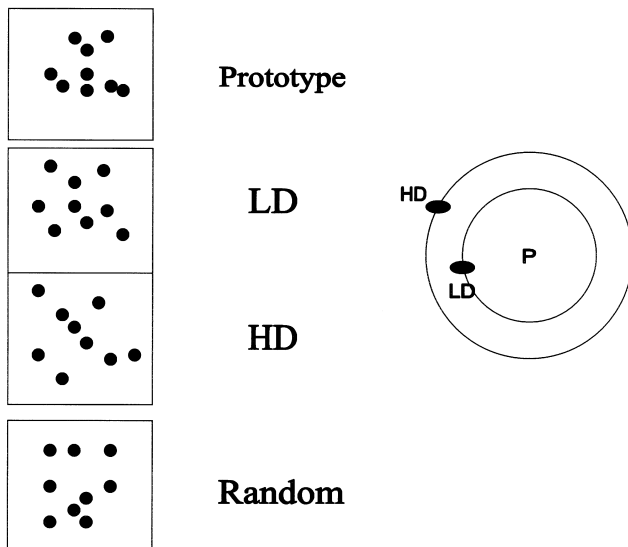


Fig. 2. The dot pattern categorization task. The basic pattern (prototype) consists of nine dots. Category exemplars are distorted versions of the prototype, whereas random patterns have a completely different structure. While the prototype (P) is localized in the center of the representational space (right side of the figure), the exemplars have a more peripheral position. Low distortions (LD) are more similar to the prototype than the high distortions (HD), and hence the LDs are closer to the prototype in the representational space.

### 3. Category learning tasks

There is a large number of category learning tasks and many of them are specifically related to different theoretical models. In this section, only those will be considered that are regularly used to explore the neurobiological mechanisms of categorization. Rarely used paradigms will be described when related brain mechanisms are discussed.

#### 3.1. The dot pattern task

The prototype stimulus consists of nine dots randomly placed in an area. Category exemplars are generated by various degrees of displacement of the dots. If the degree of displacement is high, exemplars will be less similar to the prototype (high distortions) than when the degree of displacement is smaller (low distortions) (Fig. 2) [107]. In the training phase, subjects are exposed with distortions, often without explicit instructions to learn the category. Subjects are regularly instructed to point to the dot in center of the pattern in order to distract their attention from within-category regularities. In the testing phase, new distortions, the prototype, and category-independent random dot patterns are sequentially presented, and subjects are asked to decide whether or not a stimulus is the member of the trained category. Interestingly, categorization performance is best for the prototype, followed by low and high distortions, respectively. This pattern of performance is observable despite the fact that subjects did not see the prototype in the training phase (prototype effect). In the recognition version of the test, previously memorized individual dot patterns (targets) must be selected from distracters that are low and high distortions of the target [63]. The dot pattern task is the cornerstone of prototype theories.

#### 3.2. Artificial grammar learning

This test has several versions [40,116,138,146]. In one version, subjects are presented with letter-strings, which are generated according to a specific rule that determine the order of letters. For example, strings QATA and GFBB are different exemplars, because they consist of different letters. However, they belong in the same category, because they have been generated according to the same abstract rule: the second and fourth letters are always the same. In contrast, ATAQ is very similar to QATA in its surface characteristics (letters), albeit they have been generated according to different abstract rules. Similarly to the dot pattern task, participants are not directly instructed to learn the rule—they passively view category exemplars. In the testing phase, decisions are made about new letter-strings; the task is to determine whether the new stimuli belong in the group of ‘grammatical’ items, depending on whether or not they were generated according to the rule of training phase. In different paradigms, feedback is used or

subjects are explicitly instructed to direct their attention to the underlying rule [40]. In the case of feedback learning of artificial grammar, boundary models may be preferred [3–5].

#### 3.3. Set-shifting and stimulus–reward learning

Important components of category acquisition can be assessed by using a series of visual discriminations. In these tasks, stimuli vary along a number of dimensions such as shape and color. Using feedback, subjects first learn the relevant dimension for decisions (e.g. ‘select the green stimuli’). During intradimensional (ID) shifting, new stimuli are presented but the same dimension remains relevant, that is, color must be taken into consideration for decisions. This phase of discrimination learning represents the classic criterion of categorization: generalization of knowledge for never-seen exemplars. During extradimensional (ED) shifting, the context changes and a previously irrelevant dimension must be used for decisions (e.g. shape instead of color (‘select the circles’)) [126]. Therefore, following the altered feedback, observers should override their previous strategy and shift their attention to the new dimension. This process is an essential component of the Wisconsin Card Sorting Test (WCST), which is often mentioned as a classic rule-based category learning task [126]. This is closely related to cue-validity and boundary models. In the WCST, the boundary between categories is unambiguous, and cues such as color, form, and number determine category-membership in an all-or-none fashion. Therefore, according to the COVIS model, the WCST is mediated by the explicit system that is based on easily verbalized rules [5].

Reversal learning is an ideal approach to investigate the stimulus–reward learning component of visual discriminations. In the first phase of this task, feedback is used to establish stimulus–response associations (for example, rewarding feedback is given when key A is pressed for red stimuli and key B is pressed for green stimuli) [126]. In the reversal phase of the task, the contingency changes and subjects are requested to adopt the new strategy (that is, press key A for green stimuli and press key B for red stimuli).

Gambling tasks provide a more sophisticated approach to investigate stimulus–reward patterns in category learning. The Iowa Gambling Task includes categorical decisions (selecting from different decks of cards), which are associated with different reward–punishment profiles [12]. Advantageous decisions require the avoidance of categories associated with high reward but even higher punishment (overall loss) and the preference of categories associated with smaller rewards but minimal penalties (overall gain). In the ‘Gamble’ task, the larger reward is associated with the least likely outcome in a probabilistic decision-making situation [112]. Risk-taking behavior is



characterized by the selection of larger immediate reward despite its less advantageous long-term consequences.

### 3.4. Probabilistic classification learning

In this test, subjects are asked to decide whether geometrical forms (cues) predict rain or sunshine (weather prediction task). Each cue is associated with rain and sunshine with a certain probability (Fig. 3). After each trial, including a decision about weather outcome, subjects receive a feedback. In this way, during the first 50 trials there is a gradual increase in performance. After completing the test, subjects are asked questions about the cues and other details of the test in order to evaluate their explicit knowledge [64,67]. Probabilistic classification learning is best related to boundary models. Because of the probabilistic nature of the task, category rules are hard to verbalize, and hence this task may be mediated by the implicit system of the COVIS model [5]. However, when individual exemplars must be explicitly memorized, the exemplar model may be relevant [105].

### 3.5. Rule-based and information-integration paradigms

These tasks are also motivated by the boundary models of category learning in which stimulus–response and stimulus–reward associations are important components [5]. Consider a two-dimensional representational space including the length of vertical and horizontal line-segments of stimuli (Fig. 4a). This representational space can be divided into two parts for two corresponding categories according to linear rules. In the dimensional integration condition, the length of both vertical and horizontal segments must be taken into consideration (Fig. 4b), whereas in the selective attention condition only one

dimension is relevant for categorization (Fig. 4c). Finally, the representational space can also be divided according to non-linear rules (Fig. 4d). Category rules related to linear conditions are regularly easy to verbalize, while non-linear rules are sometimes impossible to word. The first case is a rule-based mode of category learning (as seen in the case of WCST), whereas in the latter case information from many exemplars must be accumulated for categorical decisions in an implicit-procedural manner (see also the COVIS model described above) [5,37,38]. However, it must be noted that many information-integration tasks have linear category boundaries. Rule-based tasks are those in which the best possible performance can be achieved via a rule that is easy to describe verbally.

A stimulus set that was generated using similar principles is shown in Fig. 5 [52]. In this case, an ideal categorization performance can be achieved by integrating the shape of the inner element and the stimulus size (category 1: smaller circles with a square-like shape in the middle; category 2: larger circles with more circle-like shapes in the middle), and hence observers need to use two verbal rules. Consider, however, that verbal rules do not help categorize stimuli located near the boundary where stimuli show a high degree of similarity. In addition, an application of random distortion of shapes as category-irrelevant noise further increases uncertainty in category decisions.

## 4. The neuropsychology of category learning

In the following section, I review some clinical conditions in which the above described models and tasks were investigated in order to explore how different brain systems contribute to category learning.

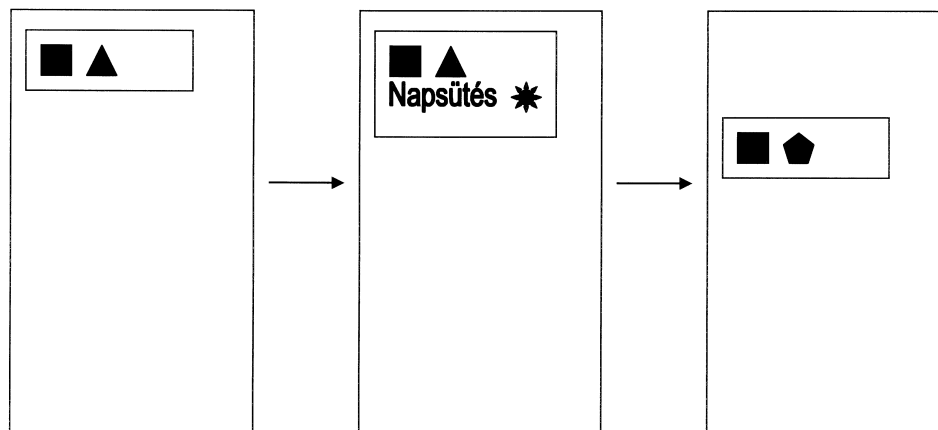


Fig. 3. The probabilistic classification learning (weather prediction) task. The subjects are presented with a stimulus (square and triangle, first frame) and are asked to decide whether the stimulus predicts sunny or rainy weather outcome. After the decision, the window moves downward and verbal (Hungarian words, Napsütés=Sunshine) and symbolic feedback appears (second frame). Then the window moves again and the next stimulus is shown (third frame) [58].

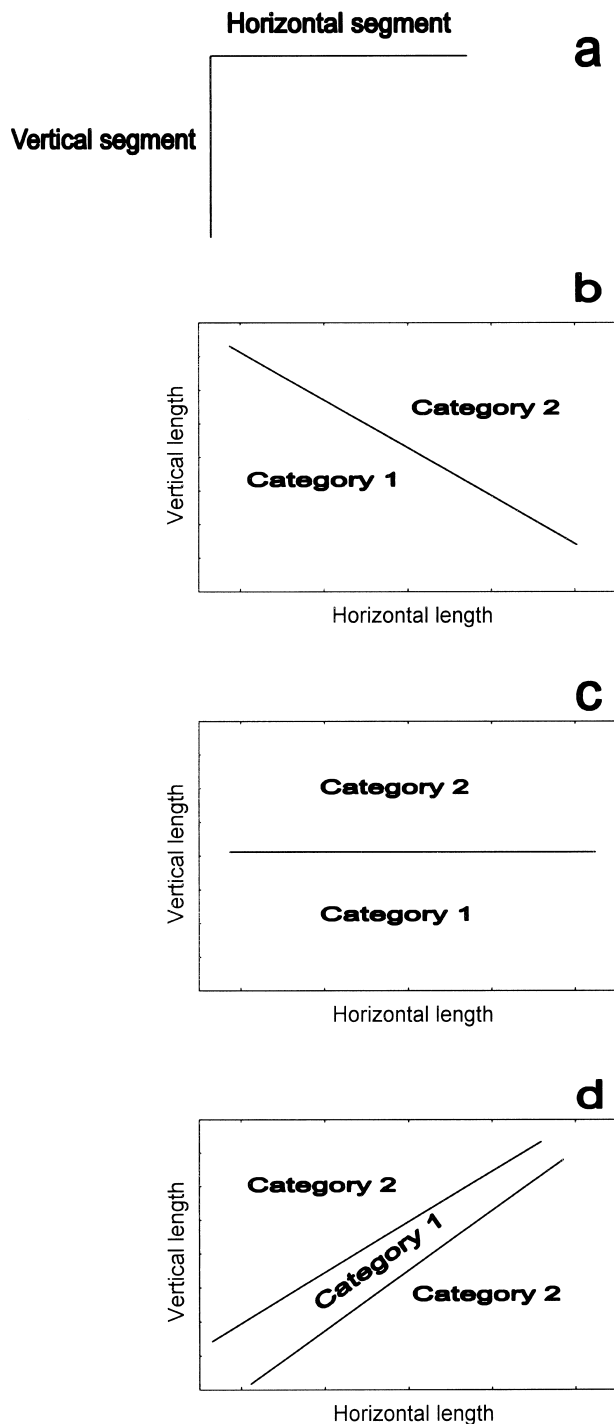


Fig. 4. (a) An example for experimental stimuli consisting of two line segments. (b) Dimensional integration condition. The two-dimensional representational space (length of the horizontal and vertical segments) is divided into two categories. The length of both segments is relevant for categorization. (c) Selective attention condition. Only the length of vertical segment is relevant for categorization. (d) Non-linear condition. The representational space is divided by non-linear rules that are difficult to word.

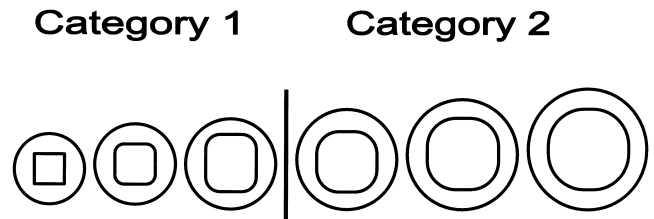


Fig. 5. Examples for experimental stimuli used for category learning tasks in patients with schizophrenia. In the representational space, each point of the initial shape (a small circle with a square in the middle) passed toward its new position (a large circle with a circle in the middle) so as to depict a continuum between these extreme configurations. The continuum was divided into multiple parts, half for the first and half for the second category. The position of each point on the lines outlining the shapes was randomized in order to introduce category-irrelevant noise. During category learning, exemplars of the two categories were presented, and then category knowledge was tested by presenting new exemplars. In different sessions, verbal rules describing the categories were provided for training or subjects were asked to retrieve such rules after the observation of exemplars in order to determine their verbal category knowledge.

#### 4.1. Separate systems for recognition and categorization? Lessons from amnesia

Two important studies conducted in patients with amnesia launched a new era in category learning research [63,67]. Following lesions to the medial temporal lobe (hippocampus, gyrus dentatus, and entorhinal cortex) or diencephalon, amnesic patients show marked deficits in explicit memory tests, affording their ability for conscious recollection of facts and events. In contrast, implicit memory is spared [145]. Knowlton and Squire reported that amnesic patients displayed intact category learning in the dot pattern task, whereas their recognition performance for particular items was severely disrupted [63]. Similarly, amnesic patients successfully improved their performance in the early (but not late) phase of the weather prediction task, contrary to the fact that they were hardly able to consciously recall details about the cues and experimental setup [64,67]. The probabilistic nature of this test may have prevented them from using explicit strategies that are not advantageous in the case of uncertain associations. After a more extensive training (100 trials), explicit mechanisms may predominate, and therefore in this late stage of the task amnesic patients display categorization deficits. However, the spared early-stage category learning was not replicated by a recent follow-up study [50], and hippocampal involvement even in early phases of the weather prediction task has been suggested [46,105]. On the other hand, however, spared implicit category learning in amnesia is supported by studies using the artificial grammar learning task [65,68], (see also [17,61,121,133]), information-integration procedures [38], and category learning of animal-like creatures [123]. Explicit category learning, requiring the retention of verbal rules, is impaired in amnesia [62] (Table 2).



Table 2  
Neuropsychology of category learning

	Dot pattern	Probabilistic classification learning	Artificial grammar	ED-shift	Reversal	MDS	Key Refs.
MTL	OK	OK (early phase)	OK	OK	OK	OK	[29,38,63–65,67,100,110]
DLPFC	OK	OK	?	↓	OK	?	[26,67,82,87,100,101,103,145]
OFC	?	?	?	OK (?)	↓	?	[12,26,82,111]
Parkinson's disease	OK	↓ (early phase)	OK	↓*	↓**	↓	[20,22,67,115,124,147,157]
Huntington's chorea	OK <sup>u</sup>	↓	?	↓	↓**	↓	[37,66,76,155]
Tourette syndrome	OK <sup>u</sup>	↓	?	?***	?	?	[58]
Alzheimer's disease	OK <sup>#</sup>	OK	?	↓ <sup>##</sup>	↓ <sup>##</sup>	?	[30,53,55]
Schizophrenia	OK	OK <sup>###</sup>	OK	↓	↓ <sup>####</sup>	?	[31,47,54,56,103,158]

DLPFC, dorsolateral prefrontal cortex lesion; ED-shift, extradimensional shift; MDS, multidimensional stimuli; MTL, medial temporal lobe lesion, OFC, orbitofrontal cortex lesion.

<sup>u</sup>Unpublished observations. \*ED-shift deficits are often non-perseverative and more severe when competing information is present. \*\*Reversal learning dysfunction is pronounced in later stages of the disease. \*\*\*Executive dysfunctions are regularly not severe in Tourette syndrome. <sup>#</sup>The selective deficit of prototype learning is present in some patients; performance is impaired in later stages of the disease. <sup>##</sup>The dysfunction is not specific and present in later stages of the disease. <sup>###</sup>Typical antipsychotic medications induce impairment in this test, probably by blocking dopamine receptors in the basal ganglia.

<sup>####</sup>Only a subgroup of patients displays deficits.

These data, particularly those from the dot pattern task, suggest that recognition and categorization are mediated by separate systems in the brain; recognition (exemplar learning) is related to the explicit medial temporal/diencephalic system, whereas categorization (prototype learning) is mediated by the implicit memory system, possibly localized in the neocortex. A serious critic of this hypothesis was published by Nosofsky and Zaki [95,96], who claimed that the dissociation observed in amnesic patients could be explained within the framework of a single exemplar-based system. They showed that the collection of weak memories for exemplars (as may happen in amnesia) is sufficient to perform successfully in the categorization task but not in the recognition task, due to the different attentional and decision criteria of these procedures. This critic can be disproved by data from patient EP who had virtually no explicit memory, and therefore even weak exemplar-traces could be excluded [69,144]. However, the study of Palmeri and Flanery [102] raised a more difficult challenge for researchers using the dot pattern task. These authors showed that prototype learning is possible without a separate training procedure, because subjects are able to learn on-line during the testing phase by using their short-term working memory, and thereby discovering category-specific regularities of the dot patterns. This question will be discussed later in more details (for a cautionary note on the models of memory and decisions, see [35]).

#### 4.2. Category learning in Alzheimer's disease

An important cornerstone of a wider relevance of the above-described findings is to replicate them in different

patient populations. The early stages of Alzheimer's disease are highly similar to selective amnesia due to massive neurodegenerative processes in the medial temporal lobe; patients are unable to consciously remember facts and events. In later stages of the disease, however, neuronal loss extends to the neocortex, resulting in more generalized cognitive impairments [15,129]. Consistently with this clinical pattern, we found impaired recognition of dot patterns (a possible marker for medial temporal lobe pathology), while categorization was not grossly impaired in patients with Alzheimer's disease [53]. However, our patients displayed a selective categorization deficit for prototype stimuli with preserved performances for distortions. In a follow-up study, we investigated the relationship between clinical stages and categorization/recognition performances [55]. Results revealed that recognition dysfunctions were present even in the earlier phases of the disorder when categorization was preserved. However, in more progressive phases when neuronal loss probably extended to the sensory neocortex, categorization was also severely impaired. Concerning the probabilistic classification learning task, Alzheimer's patients show preserved performances similarly to that seen in amnesia [30] (Table 2). Taken together, these results may support the view that separate neuronal systems exist for categorization and recognition, bearing in mind that the role of on-line learning of dot patterns during testing needs further clarification.

#### 4.3. The other side of the coin: basal ganglia disorders

Parkinson's disease and Huntington's chorea are de-

generative disorders of the basal ganglia [114,129]. These diseases are traditionally considered as disorders of the motor system, accompanied by the slowness of movements, cogwheel rigidity and tremor (Parkinson's disease) or abnormal involuntary movements (Huntington's chorea). However, other impairments can also be observed in basal ganglia disorders, including dysfunctions in motor skill learning and higher cognitive functions, such as planning and problem solving [114]. It is of particular interest that Parkinson's patients show substantial deficits in the early phase of the probabilistic classification learning task with intact remembering for cues and training events—exactly the reverse of that seen in amnesia and Alzheimer's disease [30,67]. These findings have been confirmed in other patients with basal ganglia disorders (Huntington's chorea [66], Tourette syndrome [58] (which is characterized by sudden, non-rhythmic muscle contractions, called tics), and focal lesion to the neostriatum [57]) and with different methods (information-integration paradigms) [37,79] (see also [7]) (Table 2). In two populations (Parkinson's disease and Tourette syndrome), the category learning deficit was related to the severity of motor symptoms [58,67]. Dot pattern categorization and artificial grammar learning are spared in Parkinson's disease [119].

These data indicate that implicit category learning is not a unitary construct. While probabilistic stimulus–response associations are mediated by the neostriatal system, prototype learning and artificial grammar learning seem to be independent from that, possibly related to the intact functioning of sensory neocortex.

#### 4.4. Executive functions and stimulus–reward associations in category learning

The WCST is perhaps the most widely used category learning test. In this task, subjects sort cards to one of the four categories with an identical category-relevant feature (for example, sorting according to color). Feedback is provided to ascertain the relevant feature. After a number of successful decisions, the sorting strategy changes (e.g. from color to shape), and participants must shift to the new dimension. Both set-shifting and reversal learning are essential parts of the WCST [126]. It has been demonstrated that patients with lesions to the prefrontal cortex fail to shift to the new sorting strategy (perseveration) [87]. Using an animal model, Dias et al. [26] showed that lesions to the dorsolateral prefrontal cortex (DLPFC) impair ED-shifting, whereas lesions to the orbitofrontal cortex (OFC) disrupt reversal learning. The authors concluded that the DLPFC is responsible for a higher-level regulation of attentional bias towards behaviorally relevant dimensions, whereas 'affective' aspects of stimulus–reward associations take place in the OFC. This is consistent with data from patients with cerebral lesions [100,101,103,111] (but see [82]) (Table 2).

Findings related to the role of DLPFC in ED-shifting shed light to more general issues of executive functions. One of the most important aspects of executive functions is selective attention, which is an indispensable part of exemplar, boundary, and cue-validity models of category learning. A second domain is working memory (active maintenance of relevant information in short-term memory), which may be important in on-line learning of dot pattern categories. Finally, monitoring of performance, including response-conflict and error detection, is also crucial in many category learning situations. The essence of each component (set-shifting, selective attention, working memory, and monitoring) is a top-down control of posterior cortical and subcortical areas where perceptual properties and stimulus–response mappings are encoded [36,88,135].

Whether a prefrontal representation for top-down control is maintained or disputed largely depends on the feedback, providing a reward signal. The neurotransmitter dopamine in prefrontal cortex and basal ganglia plays a central role in this respect [99]. In the DLPFC, mesocortical dopaminergic pathways stabilize or destabilize top-down representations based on success in a task. The DLPFC is closely connected with dorsal parts of the neostriatum. In the OFC and ventral striatum, which comprise an integrated cortico-subcortical system similarly to the dorsal PFC–striatal circuitry [86], mesolimbic dopaminergic pathways mediate various aspects of reward effects [130].

In Parkinson's disease, not only skill learning and probabilistic classification learning are impaired; a severe deficit is observable in ED-shifting, revealing the pathology of dorsal striatum and PFC [86]. Interestingly, ED-shifting abnormalities are prominent when a competing response is present during the task [20,115] and seem to be specifically related to dopamine denervation in the striatum, independently of the hippocampal explicit memory system [83,124]. In contrast, reversal learning is relatively spared in early stages of the disease, probably because of the less affected OFC/ventral striatal functions [22,147]. In later stages of Parkinson's disease, however, marked dysfunctions in reward processing may appear [84]. Indeed, dopamine loss is not restricted to the neostriatum in Parkinson's disease; similar alterations are present for all dopamine targets, including the PFC, ventral (limbic) striatum, and even the retina. Data from Huntington's patients with dorsal neostriatal pathology are consistent with these findings, revealing intact performances in gambling-type tasks [155] that are found to be impaired in OFC damage [12], similarly to reversal learning [26]. Nevertheless, some patients with Parkinson's disease and Huntington's chorea do show reversal learning deficits, possibly as a consequence of more severe pathology or medication side effects [22,76,147]. Overall, these results suggest that structurally different parts of the prefrontal–basal ganglia system mediate basic stimulus–reward learning and higher level selection and shifting related to the establishment of abstract rules [57,86,148].

#### 4.5. What has schizophrenia taught us about the neuropsychology of categorization?

Schizophrenia is characterized by delusions, hallucinations, and various negative symptoms such as poverty of thinking, anhedonia, and psychomotor retardation. From a neuropsychological point of view, many patients exhibit marked abnormalities in executive functions and explicit memory [32]. Therefore, it is not surprising that schizophrenia patients are impaired in the WCST [47,158] and ED-shift task [31,103], as well as in category learning procedures where an abstract verbal rule should be extracted from multidimensional stimuli [52]. In contrast, probabilistic classification learning [54], dot pattern learning [56], and artificial grammar learning [25] performances are within the normal range (Table 2). It is notable that patients receiving conventional antipsychotic medications, which antagonize dopamine receptors and hence lead to drug-induced parkinsonism, show deficient probabilistic classification learning performances [13], an independent confirmation of that reported in Parkinson's disease patients [67,157].

Since many, but not all, schizophrenia patients display profound working memory dysfunctions, one can test the hypothesis that dot pattern prototypes can be learned on-line during the testing phase without any previous training [102]. If this type of learning is mediated by the maintenance of exemplars in working memory so as to discover

category-regularity, schizophrenia patients with deficient working memory will not learn dot pattern categories without preceding training, while participants with good working memory will do so. To test this hypothesis, we investigated patients with schizophrenia who had spared ( $n=10$ ) or impaired ( $n=10$ ) visual working memory for objects, as indicated by their performances for Vanderplas figures [143]. The two schizophrenia subgroups were matched for age, education, symptoms, and IQ. Patients were considered as having impaired working memory if their performance was 1.5 S.D. below the control mean. We found that the schizophrenia patients with spared working memory displayed intact performance without a formal training phase, whereas the patients with impaired working memory failed to do so (Fig. 6). However, in the presence of training, even the schizophrenia patients with impaired working memory exhibited normal categorization of dot patterns, suggesting that implicit learning was spared in their case. These data indicate that the dot pattern categorization task can be solved using two dissociable strategies: implicit learning during a separate training phase and on-line learning without a formal training.

#### 4.6. Summary of neuropsychological data

Patients with medial temporal lobe damage (amnesia, early Alzheimer's disease) are impaired in tasks where exemplars must be explicitly memorized; when prototypes

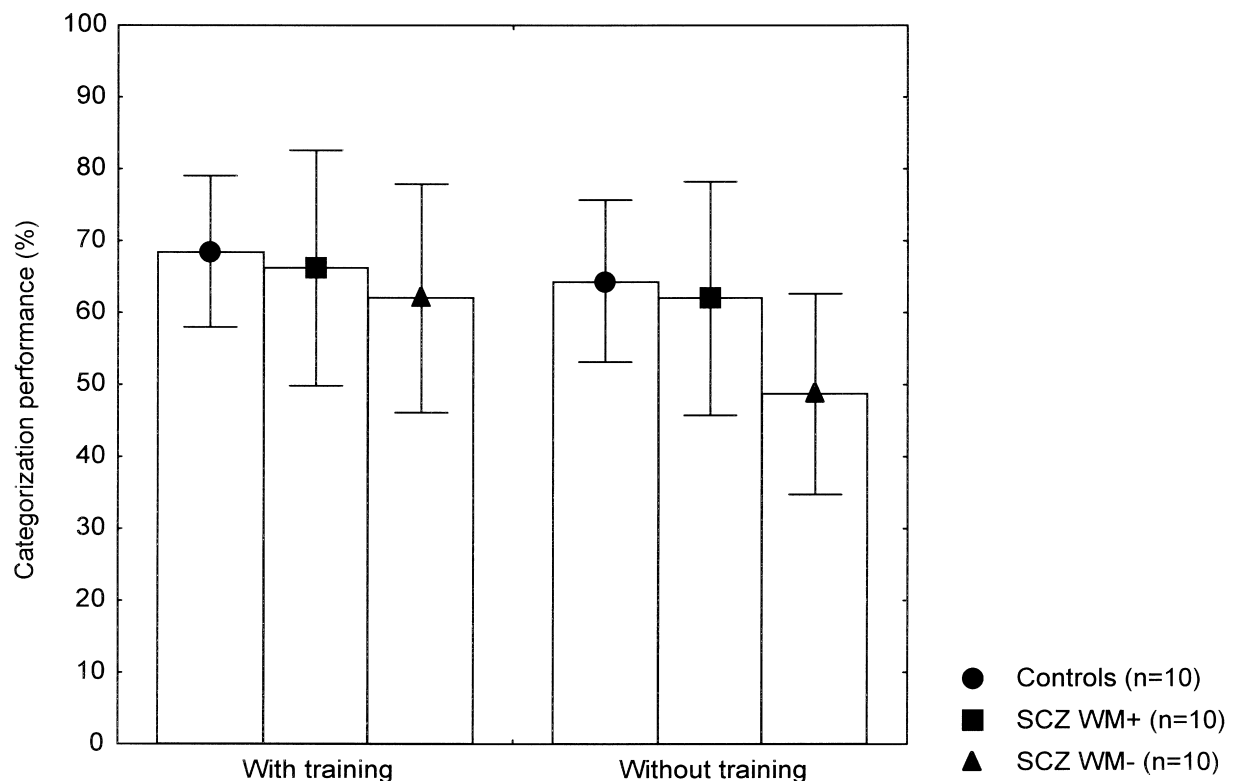


Fig. 6. Mean categorization performance in the dot pattern categorization task in the controls and in the schizophrenia patients (SCZ) with spared or impaired working memory (WM+ and WM-, respectively). When formal training was not included, the schizophrenia patients with impaired working memory performed at the chance level, while the patients with spared working memory exhibited on-line learning.

Table 3  
Relationship between models, tasks, and neuronal structures

Model	Task	Key neuronal structure
Exemplar	Probabilistic classification (paired associate)	Medial temporal lobe
Prototype	Dot pattern	Sensory neocortex
Boundary (implicit)	Probabilistic classification and artificial grammar (feedback-based) Information integration	Neostriatum
Boundary (explicit) and cue-validity	Rule-based tasks (set-shifting, Wisconsin Card Sorting Test, artificial grammar)	Lateral prefrontal cortex

Note that different versions of the same task may be related to different models and neuronal structures. For example, the paired-associate version of the probabilistic classification learning task is related to the exemplar model or the feedback-based version of the dot pattern task is related to the boundary model. The artificial grammar learning task has the most numerous versions (for details, see the text).

can be extracted or decision boundaries can be learned (probabilistic classification learning and information-integration paradigms), they show normal performances. Extensive degeneration in the sensory neocortex (severe Alzheimer's disease) leads to the loss of prototype information. As a contrast of this pattern, patients with basal ganglia disorders (Parkinson's disease, Huntington's chorea, Tourette syndrome) exhibit deficits in tasks requiring the gradual and implicit development of decision boundaries. Finally, subjects with damage to the lateral PFC are particularly impaired in the establishment of abstract rules and attentional control (Table 2). These results suggest that exemplar models may be linked to the medial temporal/diencephalic memory system, prototype models to the sensory neocortex, and cue-validity/boundary models to the fronto-striatal system (Table 3).

## 5. The functional neuroimaging of category learning

### 5.1. The dot pattern task and probabilistic classification learning

As expected from neuropsychological data, functional neuroimaging studies using the dot pattern task revealed a predominant role of the visual cortex. In two studies, Reber et al. [117,118] found that the occipital cortex (BA 17/18) showed decreased activity for category members in comparison with random dot patterns (non-members). In contrast, recognition elicited increased activity in the same areas, together with the activation of an extended PFC network, probably related to episodic memory retrieval [117]. Aizenstein et al. [1] reported a similar deactivation in the occipital cortex when category learning was implicit. In contrast, in an explicit condition when subjects were requested to focus on category-related similarities of presented items, the occipital areas displayed larger ac-

tivities for category members than for non-members (Table 4).

The relatively decreased activity for category members suggests that neuronal mechanisms similar to that found in perceptual repetition priming may be responsible for some category learning functions. Results from priming experiments indicate decreased neural responses with item repetition independently of awareness, similarly to implicit dot pattern category learning [156]. The reduction of brain responses may reflect a form of neuronal group selection, in which unnecessary cells cease producing action potentials, and only the indispensable core of neuronal assembly survives. In other words, categorization, similarly to priming, may provide a fast and economical representation for the most regular (repeating) features of the external environment. In Alzheimer's disease, priming-related deactivation is less pronounced compared with normal controls, which may explain dysfunctions in dot pattern category learning, as a consequence of less efficient selection of essential neurons during item repetition [8,59].

Rosenthal et al. [128] also investigated a simple, non-supervised form of category learning during repetitive appearance of stimuli, which consisted of a pair of vertical bright stripes. Serially presented stimuli varied by the width of the stripes. The participants were simply informed that they would see different kinds of stripes and were asked to classify them accordingly by pressing different keys. The authors found that category boundaries located near the least frequent stimuli and centered near the most frequent stimuli. The participants did not develop an explicit knowledge of the categories. It has been suggested that the establishment of categories in the absence of external supervision (feedback or abstract rule) is based on an internal self-organizing mechanism, probably related to the visual cortex. Similarly to the dot pattern task, this paradigm also reflects automatic and continuously updating processes, modified by the incoming stream of stimuli.

Table 4  
Functional neuroimaging of category learning

Task	Procedure	Key activations	Refs.
Dot patterns	Scanning during the testing phase Contrast: category members (C) vs. non-members (NC) fMRI	Occipital cortex (BA 17/18) (NC>C) R ant PFC (BA 10) (C>NC)  R inf lat PFC (BA 44/47) (C>NC)	[117]
Dot patterns	Scanning during the testing phase Categorization and recognition are investigated fMRI	Categorization: occipital cortex (BA 17/18) (NC>C) Recognition (activity for the stimulus to-be-recognized vs. distracters): R PFC (BA 6, 8), BIL BA 9, L ant PFC (BA 10), middle temporal gyrus (BA 21), occipital cortex (BA 17, 18, 19), cerebellum	[118]
Dot patterns	Scanning during the training phase Contrast: category members (C) vs. non-members (NC) Explicit condition (subjects are instructed to learn the categories) and implicit condition (subjects are asked to detect the color of stimuli) fMRI	Implicit: (NC>C) BIL SMA (BA 6), BIL sup/inf parietal cortex (BA 7, 40), R inf temporal cortex (BA 38, 41), insula, occipital cortex (BA 19) Explicit: (C>NC) BIL SMA (BA 6), BIL med PFC (BA 24, 25, 47), BA 8, occipital cortex (BA19); (NC>C) L inf PFC (BA 44), BIL inf/sup parietal cortex (BA 40, 7), R hippocampus, R thalamus	[1]
Dot patterns	Scanning during the testing phase Three conditions: categorization, recognition, discrimination based on dot number (double-subtraction) fMRI	Categorization specific: R inf PFC (BA 46, 47), BA 8, L inf PFC (BA 47), L ant PFC (BA10), L middle/sup temporal cortex (BA 21, 41), L parietal cortex (BA 19/40) Recognition specific: precuneus, occipital cortex (BA 17), L lingual gyrus (BA 18), R posterior hippocampus, cerebellum Categorization and recognition: R sup frontal cortex (BA 6, 8), R parietal cortex (BA 19, 40), R precuneus, BIL occipital cortex (BA 18), R ventral occipito-temporal cortex (BA 37)	[120]
Dot pattern	Learning two categories with feedback Scanning during stable phase of performance Reference: position discrimination and fixation PET	Categorization>position discrimination: L orbitofrontal cortex, L ant mid frontal gyrus, BIL mid frontal gyrus, L dorsal intraparietal sulcus, ant neostriatum (at lower threshold)	[153]
Checkerboard categories	Prototypes and exemplars of colored checkerboard patterns Exemplars are generated by changing the color Learning two categories using feedback Reference: detection of a stimulus, pressing a button	Categorization>reference: R PFC (BA 9, 46), BIL inf PFC (BA 45, 47), BIL inferior parietal cortex (BA 7), BIL middle occipital areas (BA 18), anterior cingulate (BA 32); L BA 7 and BIL BA 18 showed increasing activity across learning	[132]

Table 4. Continued

Task	Procedure	Key activations	Refs.
Probabilistic classification learning	Feedback-based and paired-associate versions are compared Reference: sensory-motor task with no learning component or counting stimuli	Activation of a widely distributed network (ant PFC (BA 10), occipital cortex, R n. caudatus) The n. caudatus is activated and the MTL is deactivated in the feedback task; the inverse in the paired associate task; Negative correlation between n. caudatus and MTL activity The MTL was initially active in the feedback condition and gradually become deactivated in parallel with increased activity in the n. caudatus	[104,105]
Artificial grammar learning	Training: observation of grammatical letter strings (one at a time), which comprise the members of a category During fMRI scanning: decisions about new stimuli (grammatical vs. non-grammatical) or recognition of individual letter strings	Grammatical (category members)>non-grammatical: L sup occipital cortex (BA 19), R fusiform gyrus (BA 37) Grammatical judgments>recognition: L angular gyrus (BA 39); deactivation: L inf PFC (BA 47) and R anterior cingulate (BA 32)	[138]
Artificial grammar learning	Feedback-based learning of two categories Exemplar learning within blocks, rule transfer between blocks Reference: sensory-motor control task	Category learning>reference: BIL middle/inf frontal gyrus, med PFC, BIL anterior cingulate, R posterior cingulum, L precuneus, BIL occipital cortex, cerebellum Increasing activity within blocks (exemplar learning): R PFC, R parietal–occipital cortex Increasing activity between blocks (rule learning): L PFC, R cerebellum Connectivity: decrease in R fronto-parietal, increase in L fronto-parietal and fronto-frontal connectivity during rule learning	[40]
Artificial grammar learning	Feedback-based learning of letter strings  Rule and exemplar change	Rule change: BIL ant PFC (BA 10), L sup frontal sulcus (BA 9, 10), L ventrolat PFC (BA 47) Exemplar change: L ant hippocampus	[146]
Visual discrimination learning	Intradimensional (ID)/extradimensional (ED) shift Reversal learning	ED>ID: L ant PFC (BA 10), middle frontal gyrus (L BA 8), R BA 9, R BA 46, R middle temporal cortex (BA 39) ID>ED: L lingual gyrus (BA 17), L BA 18, L inf occipital gyrus (BA 19), R middle occipital gyrus (BA 18,19), R inferior temporal cortex (BA 37), cerebellum Rev>ID: R med frontal gyrus (BA 9), L anterior cingulate (BA 24, 32), L angular gyrus (BA 39), L n. caudatus Rev>ED: L fusiform gyrus (BA 17), R sup/inf temporal gyrus (BA 20, 22)	[126]



Table 4. Continued

Task	Procedure	Key activations	Refs.
Visual discrimination learning	Reversal errors vs. correct responses	Before-shift reversal error>correct response: R ventrolat PFC, R med PFC (BA 8), R parietal cortex, BIL ventral striatum (ROI analysis)	[21]
Animal-like shapes	Learning categories by abstract rule learning vs. memorization of exemplars	Rule: R DLPFC (BA 46), BIL BA 6, BIL parietal cortex (BA 7, 19), precuneus, BIL occipital cortex (BA 18, 19), L BA 17, R thalamus, cerebellum Exemplar memory: L anterior cingulate (BA 32), R BA 18/19, L BA 17/18 cerebellum	[142]

ant, anterior; BA, Brodmann area; BIL, bilateral; DLPFC, dorsolateral prefrontal cortex; inf, inferior; L, left; lat, lateral; med, medial; MTL, medial temporal lobe; PFC, prefrontal cortex; R, right; sup, superior.

A recent study directly compared brain circuitry for categorization and recognition [120]. In this study, a categorization-specific network emerged, including the lateral and polar PFC, superior and middle temporal cortex, and parietal areas. Interestingly, activities in the orbitofrontal cortex and striatum were also found [153], although in this latter study subjects performed a feedback-driven categorization of dot patterns. Neostriatal activity is a typical finding in the probabilistic classification learning task [104,105]. In a seminal paper, Poldrack et al. [105] compared feedback-based and paired-associate learning using the weather prediction task. Besides an extensive fronto-parieto-occipital network, the neostriatum was significantly activated in the feedback-based version. In contrast, in the paired-associated task, in which subjects were requested to explicitly memorize stimulus–weather outcomes, the activity was prominent in the medial temporal lobe. Intriguingly, in the feedback-version, the medial temporal lobe also showed an initial response, but then gradually became deactivated in parallel with an increased signal in the neostriatum (Table 4). This study provided compelling evidence for a time-dependent interaction of competitive explicit and implicit memory systems in the brain (see also [90,106]). In modeling terms, paired-associate learning may refer to the exemplar approach, in which particular stimuli are explicitly memorized as members of a category. In contrast, the feedback-based version can be better interpreted in the framework of boundary models [5,92,93] (Table 3).

In many respects, these imaging findings are consistent with neuropsychological data. First, the absence of prolonged medial temporal lobe activity is consistent with the findings that patients with amnesia are able to learn these tasks [63,67]. Second, a repeated observation of neostriatal blood flow changes in the probabilistic classification learning task is in accordance with clinical data indicating impaired learning in patients with basal ganglia disorders [57,58,66,67]. However, the extensive prefrontal–parietal activation is an unexpected result, because patients with known pathologies affecting these large-scale neocortical

networks displayed intact performances [30,54–56,67,144]. When considering this controversy, it is advantageous to bear in mind that the functional significance of this large-scale activation is unknown. It is possible that prefrontal–parietal signals reflect cognitive monitoring processes that are not indispensable for category learning. For example, in the dot pattern task, Reber et al. found increased fronto-polar activity (BA 10) for category members relative to non-members [117], which was not reported in a subsequent study [118]. It is possible that subjects in the two studies applied different strategies, a more conscious and reflective in the first, and more automatic in the second. Application of functional neuroimaging methods in patients with cerebral lesions or inducing reversible functional ‘lesions’ in healthy participants with transcranial magnetic stimulation may elucidate this issue.

### 5.2. Rule application and exemplar representation

Categories can be built up by accumulating information with the observation of exemplars and by the direct acquisition of abstract rules determining category-membership. Smith et al. [142] investigated the question of learning by the observation of exemplars and by abstract rules, using categories of animal-like shapes. They found a spatially extended activation in the case of rule learning, including the DLPFC and various parietal and occipital loci. Exemplar learning was accompanied by a less extensive activation, centered in the visual cortex.

In the artificial grammar learning task, exemplar-specific learning can be observed as increased performances within an experimental block when the same items are presented with corrective feedback. Rule learning results in higher performances even at the beginning of new blocks when previously unseen exemplars are exposed with the same abstract rule. Exemplar learning is mediated by the right lateral PFC, whereas rule learning is housed in the left lateral PFC [40]. Strange et al. [146] reported that changes in rules were accompanied by activations in the fronto-

polar cortex (BA 10), whereas novel exemplars activated the left anterior hippocampus.

Skosnik et al. [138] investigated implicit mechanisms in the artificial grammar learning and found extensive activation in the visual cortex. Interestingly, the lateral PFC and anterior cingulate cortex showed deactivation (Table 4). These data suggest that the acquisition of abstract rules relies on the PFC, whereas a substantial part of exemplar information is encoded in the sensory neocortex. The medial temporal lobe (including the hippocampus) may be responsible for the explicit encoding and retrieval of exemplar-level information, integration of contextual characteristics, and novelty detection [145].

### 5.3. Set-shifting and reversal learning

Functional neuroimaging data from set-shifting paradigms and reversal learning nicely supplement the neuropsychological findings [126]. ED-shift elicits responses in the DLPFC, while ID-shift (which is basically an exemplar shift) leads to increased blood flow in visual areas, consistently with the above findings of exemplar-level representation. In contrast, probabilistic reversal learning increases blood flow in the medial and inferior PFC and basal ganglia, including the ventral striatum [21] (Table 4). Activations found in reversal learning tasks include brain areas participating in the processing of reward, showing a similarity with studies using gambling tasks [12,130]. The unusual orbitofrontal and neostriatal activity demonstrated by Vogles et al. [153] in the dot pattern category learning task can be explained by the application of feedback, a simple reward mechanism. In the light of functional neuroimaging results, it is not surprising that complex tasks such as the WCST activate widely distributed brain areas, including both dorsal and ventral parts of the PFC, inferior parietal and temporal cortex, occipito-temporal areas, and the cerebellum [14,71,89,91].

Recently, the role of dopamine in reward signaling attracted distinguished attention [130]. Probabilistic classification learning [67,157] and reversal learning [22,147] results from Parkinson's patients, where dopaminergic deficiency in the basal ganglia is present, fits well with these data. A recent PET study using  $^{11}\text{C}$  raclopride (a ligand for dopamine D2 receptors) demonstrated changes in striatal extracellular dopamine concentration during a rewarded effortful task [113]. Antipsychotic medication, leading to Parkinsonian symptoms and probabilistic classification learning deficits in schizophrenia patients, blocks the dopamine D2 receptors [13]. The more exact role of dopamine and other neurotransmitter systems in category learning, as well as the question of possible dissociation between stimulus–reward and stimulus–response learning merit further investigation.

### 5.4. Functional neuroimaging evidence for category learning subsystems: relevance for real-life categories

The functional neuroimaging data are in accordance with neuropsychological findings, suggesting that different theoretical models and their related tasks refer to category learning subsystems with distinct functional properties and neuronal substrates. These subsystems comprise the sensory neocortex (prototype and similarity representation), basal ganglia (decision boundaries guided by stimulus–response learning and reward), medial temporal lobe (explicit exemplar learning), and the lateral PFC (abstract rules and attention) (Table 3).

Based on research focusing on artificial categories, it is plausible to suppose that features setting up real-life categories are represented in the sensory neocortex. This hypothesis is supported by neuropsychological studies, demonstrating that patients with lesions to the sensory neocortex show selective recognition and naming dysfunctions for particular categories such as animals and tools [16]. Consistently with these neuropsychological findings, functional neuroimaging studies indicated category-specific activations for faces [51], places [34], body parts [27], known people, animals, and tools [18,24] in the ventral occipito-temporal visual cortex and adjacent areas. However, others suggest that the ventral occipito-temporal cortex does not consist of strictly category-specific modules [49] and category-related neuronal activity is affected by task constraints and prior experience [43,44]. It is likely that complex knowledge about real-life categories is stored in a modality-specific, distributed, but interactive network in which specialized regions exist for the processing of stimulus features such as color, form, size, motion, and functional attributes [11,150]. This cortical network is analogous to the multidimensional representational space of the MDS and GCM, which is a basic part of most theoretical models. The system is affected by attentional and decisional factors, and specific behavioral responses are associated with particular configurations of features. These associations are strengthened by reward signals as a fundamental basis of category learning. Recently, Van Turennout et al. [151] demonstrated that repeated object naming led to reduction in neuronal activity in the ventral occipito-temporal cortex, whereas the activity of basal ganglia structures increased. The practice-related decrease in the activity of sensory cortex may be similar to that found in prototype learning tasks (repeated exposure with category exemplars) [117,118], whereas increased basal ganglia activity may refer to a strengthened stimulus–response mapping. Interestingly, in a speeded categorization task, images containing animals elicited smaller fMRI signals in the occipito-temporal cortex than non-animal stimuli [39]. These data suggest that the cortico-striatal connections become essential during training with particular natural categories and in the case of speeded

decision-making (see also [2]). The functional interaction between visual areas, basal ganglia, and PFC will be further discussed in relation to single-cell studies.

## 6. Single-cell studies on category learning

This is a relatively new area in category learning research. Results from single-cell studies raise new questions, and in many points they seem to fail to support general conclusions from neuropsychology and functional neuroimaging. However, these studies investigated cellular responses from a single cortical area, providing no information about the specialization and functional interaction of separate brain structures. This shortcoming must be taken into consideration when we interpret results from single-cell studies.

### 6.1. Exemplar and category representation in the visual cortex

In 1977, Rolls et al. [127] conducted a pioneering experiment on the cellular mechanisms of recognition and categorization. The authors recorded responses of single cells in the inferior temporal (IT) cortex of monkeys, a cortical region now known to participate in visual object recognition [78] (see also Section 5.4 about the representation of real-world categories in the ventral occipito-temporal cortex). The IT cells were found to be responsive for complex shapes. Association of these visual stimuli with reward or an aversive taste did not affect the magnitude of the neuronal responses either during learning or after the training phase, suggesting that simple categories are not stored in the visual cortex. These results support the general recognition theory, assuming that perceptual and decisional processes are separated in the brain [5,6].

More than 20 years later, Vogels [152] directly explored the question of category representation in the visual cortex. Monkeys were trained in a tree–non-tree categorization task. Only approximately 25% of recorded cells in IT cortex showed some degree of category-selectivity, but many neurons were selective for a limited set of exemplars within a category or responded to exemplars of more than one category. Data analysis with a Kohonen self-organizing map indicated that broadly tuned neurons that responded to both categories but preferred one particular category were essential for categorization [149]. In computational terms, it means that one more processing layer in addition to the IT network is sufficient for categorization. A candidate for such additional stage of information processing may be the neostriatum, where many IT neurons converge to circumscribed rod-like structures, a possible integrative region for exemplar-level information [19]. Recent electrophysiological data from Parkinson's disease patients also suggest that the neostriatum may be

indeed essential for extracting and integrating category-relevant information [2]. Another possible convergence zone is the PFC, as suggested by the studies of Freedman et al. [41,42] (see later).

In another study, artificial objects were used to investigate categorical representation in the IT cortex [98]. Stimuli were parameterized complex shapes that were divided into categories by linear, quadratic, and arbitrary borders. The neurons' selectivity was influenced by parametric similarity of the stimuli and not by category boundaries. After category learning, no evidence was found for increased selectivity for stimuli from a single category or decreased responsiveness for stimuli belonging in different categories. Altogether, these studies suggest that the IT cortex participates in exemplar-level representation, but neuronal correlates of prototypes or decision boundaries are not found in this area. Category learning does not change neuronal representations of similarity in IT cortex, and hence 'response spaces' for category-level decisions may be localized elsewhere in the brain.

However, different conclusions can be drawn from another single-cell study, also targeting the IT cortex [136,137]. Participants learned to categorize line drawings of faces and fishes. Some stimulus dimensions (e.g. the degree of eye separation and eye height for faces) were relevant (diagnostic) for categorization, whereas others did not affect category-membership. Behavioral data indicated that category learning altered the similarity representation of stimuli [137]. Interestingly, more than 70% of dimension-responsive neurons were selective for the diagnostic features, but not for the non-diagnostic dimensions [136]. The major shortcoming of these studies is that neuronal responses were obtained only after category learning, and behavioral results showed some inconsistency across species (humans and monkeys) and stimuli (faces and fishes). Nevertheless, based on these findings, the authors disprove the independence of perceptual and decisional processes. Strikingly, Lee et al. [77] reported that behavioral training in a target detection task (decision-making) changed neuronal selectivity even in the primary visual cortex (perception). Overall, the Sigala et al. [136,137] data support single-system models, assigning the same neuronal representation for individual exemplars and categories. The basic regulatory factor that distinguishes between exemplar representation (recognition of individual objects) and category representation (similar responses for individually different objects from the same category) is top-down attention to diagnostic features, which may alter the functional properties of neurons in the IT cortex [131] (Table 5).

The role of sensory neocortex in categorical representations is also supported by a study using auditory stimuli [97]. Mongolian gerbils were trained to categorize rising and falling tones. During the task, high-resolution electrocorticogram was registered in the auditory cortex. The

Table 5  
Single-cell studies of category learning

Task	Features	Key findings	Refs.
Tree, non-tree categorization task	Monkey inferior temporal cortex	~25% of neurons are category selective ~10% responded only to the exemplars of the trained category Strong within-category selectivity for a limited set of exemplars Conclusion: prototypes of ordinate categories are not represented at the single-cell level in the inferior temporal cortex	[152]
Tree, non-tree categorization task	Monkey inferior temporal cortex Kohonen self-organizing map is used for the analysis of spike data from neurons	Cells responded to exemplars from more than one category or to a restricted set of exemplars from a single category The neuronal network achieved a good categorization performance (83%) using single-cell spike counts Broadly tuned neurons that respond to both categories but prefer one are the most important Conclusion: plus one layer (striatum?) to inferior temporal cortex is sufficient for categorization	[149]
Groups of parameterized complex shapes divided into categories by linear, quadratic or arbitrary borders	Monkey inferior temporal cortex	Cells' selectivity followed parametric similarity and not category boundaries Alteration in stimulus space (within category contraction, between category expansion) was not observed Categorization did not change the representation of similarity in IT cortex 'Response spaces' for categories in other areas	[98]
Line drawings of faces and fishes	Monkey inferior temporal cortex Stimuli contained diagnostic (eye separation/height) and non-diagnostic features (mouth height, nose length) Registration after training but psychophysics (similarity ratings) before and after training	>70% of feature-selective neurons were selective for the diagnostic, but not for the non-diagnostic features Category learning reduced the distance between physical and psychophysical representations in stimulus space only for the diagnostic features in monkeys, but not in humans In humans, the physical–psychophysical difference in stimulus space was smaller, and increased after category learning for non-diagnostic features, but only for fish stimuli Conclusions: category learning changes stimulus representation; the data favors for exemplar/decision boundary models	[136,137]

Table 5. Continued

Task	Features	Key findings	Refs.
Morphed animal-like shapes	Monkey prefrontal cortex Delayed match to sample (category) task Registration after training	The two monkeys focused on different features of stimuli (tail and head) Deletion of these features did not disrupt categorization ~25% of category selective neurons decreased spiking activity when the category boundary was passed ~70% of exemplar-specific neurons also showed this effect More neurons conveyed category signal in the late sample phase, but the signal was the strongest in the delay phase Category selectivity could be modified by learning	[41,42]

spatial pattern of longer latency peaks ('marked states') of the electrocorticogram clustered when the animals successfully learned to generalize to new stimuli, a characteristic marker of category-level knowledge. Thus, these electrical responses reflected category membership and not merely the physical similarity of stimuli, being more similar for within-category tones than between-category tones [97].

## 6.2. Single-cell mechanisms of category learning in the prefrontal cortex and basal ganglia

While category representation in the IT cortex remains dubious, neurons in the PFC seem to show unambiguous category responsiveness. Freedman et al. [41,42] used morphed animal-like shapes in a delayed match to sample task. They found that the majority of PFC neurons showed sudden reductions in spiking rate when the category boundary was passed. In other words, responses of neurons in the PFC were determined by category-membership rather than physical similarity of objects. Interestingly, approximately 70% of cells that preferred particular exemplars also showed the above described category effect, suggesting that category-level and exemplar-level information can be encoded by the same neuron. The neurons identified by Freedman et al. [42,42] were plastic; category-selectivity could be modified by learning new boundaries (Table 5).

The Freedman et al. [41,42] experiments also provide information about the significance of stimulus features in categorization. Eye-movement recordings revealed that the two monkeys participating in the experiment focused on different features of the stimuli (tail or head of animal-like shapes). It is possible that these features played a central role in categorization. However, this was not the case. When the focused parts of the stimuli were deleted from the images, the categorization performances were not

severely disrupted, suggesting that the monkeys used global shape information for categorical decisions instead of isolated features [42]. This is a different strategy from that suggested by Sigala et al. [136,137] where particular stimulus features were critical for categorization (e.g. eye separation and height in the case of faces) (Table 5).

Only limited information is available regarding basal ganglia structures. Interestingly, some relevant data derive from patients with Parkinson's disease who went through deep electrode implantation before neurosurgical interventions [73]. Responses of stimulus-dependent striatal cells were affected by the attended dimensions of visual stimuli that were relevant for decision-making. This suggests that attentional weighting of category-relevant features may take place in the neostriatum. In addition, cells in the neostriatum receive converging input from many IT neurons [19], providing an excellent neuronal substrate for the integration of exemplar representations and possibly for stimulus–response mapping.

Neurons in the OFC and basal ganglia are under a marked influence of dopaminergic innervation, as a cornerstone of reward signaling in the brain [130]. OFC neurons show activity during the expectation phase and after the onset of reward. Neostriatal neurons display similar activities, together with responses related to reward-dependent movements. Finally, dopaminergic neurons in the mesencephalon respond to rewards, reward-predicting stimuli, and are sensitive for errors in reward prediction [130]. These mechanisms are important when observers assign responses to different categories and this process is rewarded by feedback, and may be impaired in basal ganglia disorders.

While these data could be envisioned from neuropsychological and imaging findings, the fact that category-selective cells exist in the human hippocampus is somewhat counterintuitive [72]. However, these cells responded to complex natural categories (faces, food and cars) with



rich contextual information contents that may be encoded by medial temporal cells.

## 7. Summary and conclusions

Although the amount of information accumulated in the research area of category learning is impressive, we are far from the final conclusions. Perhaps the most important feature of category learning is multiplicity; there are several mechanisms that are necessary for categorical representations, and these are mediated by partially overlapping brain networks. The most important issues can be summarized as follows (Table 3 and Fig. 7).

(1) Frequent events in the external environment elicit recurrent brain responses and form categories based on inter-item similarity and frequency: similar and co-occurring items belong in the same category. Perceptual priming experiments indicate that repeated exposure to similar items results in gradually reduced brain responses, which is probably due to the inhibition of superfluous neuronal activity [156]. In some category learning paradigms (e.g.

the dot pattern task), similar mechanisms may operate in an implicit manner [117,118]. This type of category learning is mediated by the *sensory neocortex*, and may be spared in some severely disabled patients with neuropsychiatric disorders [55,56]. From the theoretical models, prototype-based approaches may refer to this priming-related form of category learning.

(2) In many cases, feedback is used to assign specific responses to different groups of stimuli. The *OFC* and *basal ganglia* structures are critical in such tasks. Structures in the neostriatum may integrate multiple exemplars encoded in the sensory cortex and may establish stimulus–response associations. The ventral striatum and related limbic structures (including the nucleus accumbens and the amygdala-complex), and the *OFC* are critical for stimulus–reward associations [86,130]. If the stimulus–response associations are probabilistic or the dimensionality of stimuli is complex (and hence explicit verbal rules can hardly be used to describe category membership), category learning may take place implicitly [5]. Deficits in the dopaminergic system consistently disrupt such category learning functions, whereas damage to the medial temporal

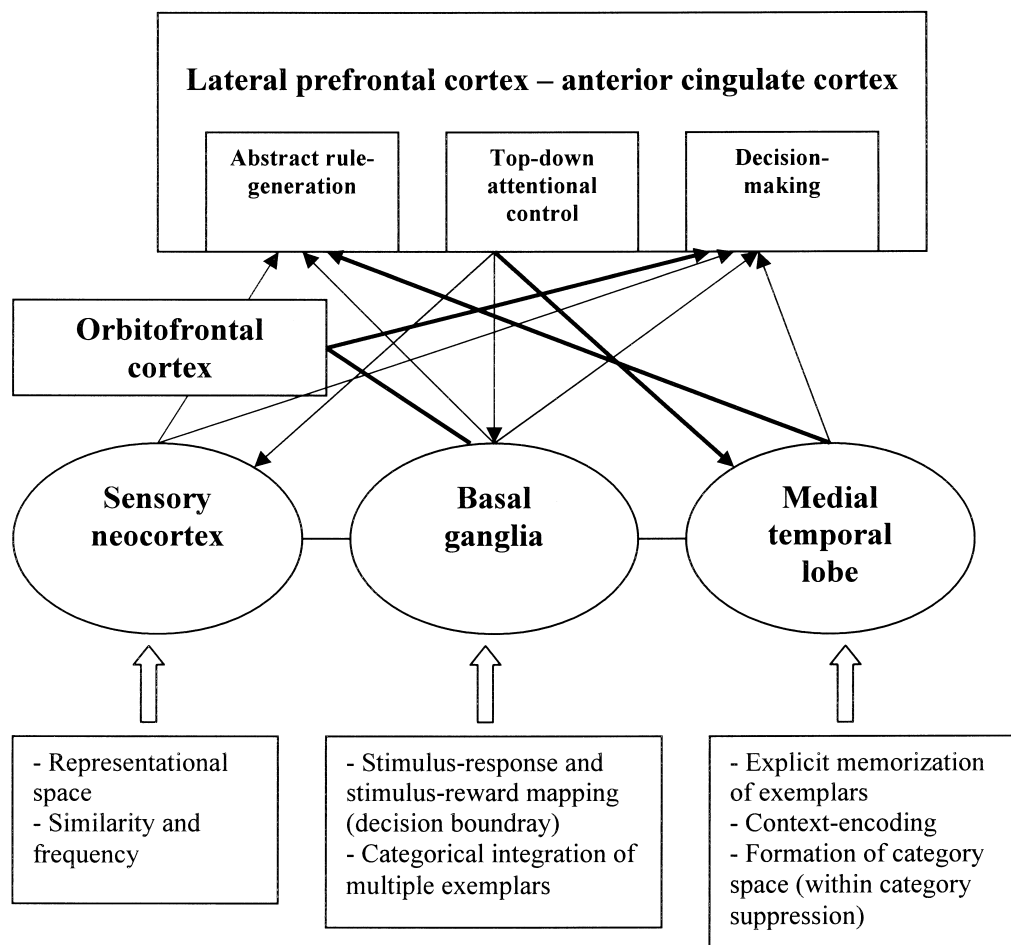


Fig. 7. An integrative model of category learning. The three category learning subsystems and the abstract rule generating, attentional, and decision-making units of the prefrontal cortex are connected (for details, see the text).



lobe or DLPFC does not have a profound adverse effect [67]. Boundary models describe many aspects of this type of category learning [3–5].

(3) *Medial temporal lobe* functions are requisites when category representation is based on the explicit memorization of few exemplars or contextual relationships must be encoded [6]. From the modeling approaches, exemplar-based frameworks are the most relevant herein. However, amnesic patients with diencephalic/medial temporal lobe lesions are capable of achieving intact performances in many category learning tasks, which probably do not require the memorization of separate exemplars [63,65,67].

(4) The *lateral* and *anterior PFC*, together with the *anterior cingulate cortex*, are important in the acquisition and shifting of abstract rules, attentional allocation, and decisional processes related to categorical judgments [5,6,108,109]. These structures carry information about rules and category membership at the single-cell level [41,42,154]. The lateral PFC may influence stimulus representation in the posterior sensory cortex via top-down control. Certain parts of the basal ganglia (dorsal striatum) are in close cooperation with the lateral PFC [86]. This system is closely related to the explicit aspect of boundary models and to cue-validity models (Table 3 and Fig. 7).

Recently, Riesenhuber and Poggio [125] offered a comprehensive model of object identification and categorization in which task-related units exist in the prefrontal cortex, receiving input from object-tuned and view-tuned units of the IT cortex. However, this model is mainly based on single-cell studies from animals and does not take into consideration human neuropsychological data, the role of explicit memory, and verbal rule generation. For example, it is evident that task-related categorization units play a central role, but severely disabled patients with very poor frontal lobe functions are still able to learn certain categories. Despite the mounting evidence, basal ganglia structures are not included in this model. In general, Riesenhuber and Poggio [125] deal with the issue how objects and categories are represented in the brain and not with the issue how new categories can be learned.

One of the most important messages of our discussion is that different types of category learning seem to be dissociable, suggesting a modular organization. The critical question is how these modules are organized into a working system. Categorical judgments are not always directed by abstract rules—in these cases priming-related mechanism (sensory neocortex), stimulus–response mapping (basal ganglia) or information about a limited number of exemplars (medial temporal lobe) are sufficient to produce a response. As shown in Fig. 7, decision-making units of the lateral PFC are independently related to the category learning subsystems. These units integrate input information and motor planning to convert sensory signals to categorical decisions, even in simple situation where abstract rules and complex attentional control are not necessary [60]. The OFC is also important in decision-

making, providing information about emotional valence and future consequences of categorical decisions [12,33].

Converging evidence from animal studies, human neuropsychology, and functional neuroimaging suggests that the parallel category learning subsystems interact during information processing, and this interaction can be competitive [105]. The subsystems are regulated by attentional mechanisms (Fig. 7), although the power of this top-down control is not equal in the case of each subsystem; the medial temporal lobe and higher-order cortical areas are more likely to be influenced than early sensory regions [108].

Although in many cases abstract rules are not optimal for categorization (see, for example, the information integration paradigms), humans tend to generate rules when conscious and flexible information processing is required. Abstract rule generation is housed in the lateral PFC receiving input from the subsystems, but these do not contribute equally to the establishment of rules; the medial temporal system, participating in explicit memory processes, seems to be particularly important in this respect [145] (Fig. 7). Nevertheless, conscious rule-based category representations are only the tip of the iceberg; categorical decisions are guided by multiple mechanisms in the brain. The critical question for further studies is how these multiple mechanisms work together and how they provide us with the complexity, flexibility, and multiplicity of real-world categories.

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