14

Memory Mechanisms

Did you know that

- learning and memory are integrally related?
- tasks testing memory mechanisms must be specially designed so that they cannot be solved without the use of memory?
- memories do not merely automatically fade through trace decay? Rather, remembering can be brought under stimulus control or instructional control.
- memory can be prospective and involve future rather than past events?
- failure to remember something is rarely due to forgetting?
- failures of memory can be caused by remembering too much?
- seemingly trivial aspects of a learning situation can help to retrieve what was learned?
- memory formation involves processes of consolidation at the levels of individual neurons, synapses between neurons, and entire neural circuits?
- consolidated memories are not permanent but thought to be malleable when they are retrieved or reactivated? Altered memories undergo reconsolidation, and this can be related to the phenomenon of "false memories."

Learning and memory are integrally related; one cannot have learning without memory. In fact, research on memory mechanisms in animals makes

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extensive use of the basic conditioning procedures that we described in earlier chapters. This makes the discussion of memory research appropriate at the end of a book on conditioning and learning. However, a fundamental question arises: If all learning involves memory, what distinguishes studies of memory from studies of learning? The answer is that studies of memory focus on a different stage of information processing than studies of learning.

STAGES OF INFORMATION PROCESSING

Memory involves the delayed effects of experience. For experience with stimuli and responses to influence behavior at a later time, three things have to happen. First, information about the stimuli and responses must be acquired and encoded in the nervous system in some fashion. This is the **acquisition stage** of information processing. Once encoded, the information must be stored for later use. This is the **retention stage** of information processing. Finally, when the information is needed at the end of the retention interval, it must be recovered from storage. This is the **retrieval stage**.

Acquisition, retention, and retrieval are involved in all studies of learning as well as all studies of memory. However, which stage is the focus of interest depends on whether one is primarily concerned with learning processes or memory processes (see Table 14.1). Studies of learning focus on the acquisition stage. In studies of learning, the circumstances of acquisition are manipulated or varied, while the conditions of retention and retrieval are kept constant. By contrast, in studies of memory, the conditions of acquisition are kept constant, while the retention interval and the conditions of retrieval are varied. To make matters a bit more complicated, the three stages are not entirely independent. As we will see, conditions of acquisition can determine the circumstances under which a memory is retrieved (Urcelay & Miller, 2014). However, such interactions do not undermine the basic model of memory as involving acquisition, retention, and retrieval.

THE MATCHING-TO-SAMPLE PROCEDURE

A variety of different techniques have been used to study memory mechanisms in various species. Memory procedures often require special controls to make sure that the participant's behavior is determined by its past experience rather

TABLE 14.1. Differences Between Experiments on Learning and Experiments on Memory

Stage of information processing	Learning experiments	Memory experiments
Acquisition	Varied	Constant
Retention interval	Constant (long)	Varied (short and long)
Retrieval	Constant	Varied

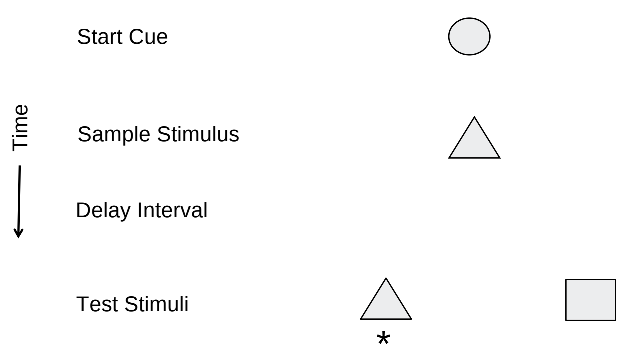
than by a clue that is inadvertently presented in the test situation. In addition, special procedures must be designed to isolate particular memory processes. To facilitate discussion of these complexities, let us begin with the matching-to-sample procedure, which is one of the most widely used and versatile techniques for the study of memory mechanisms (Zentall & Smith, 2016).

In the **matching-to-sample procedure**, the participant is first exposed to a sample stimulus. The sample is then removed for a retention interval. After the retention interval, the participant receives a multiple-choice memory test. Several alternatives are presented, one of which is the same as the sample stimulus that was presented at the start of the trial. If the participant selects the previously presented sample, it is reinforced. A well-known example of this type of task comes from the "Where's Waldo?" book series. The Waldo character appears on the front cover of the book, and then again on each page among a series of other characters. Children have to match their memory of what Waldo looks like and pick him out from the various other characters on each page.

The matching-to-sample procedure can be used to investigate memory for all sorts of stimuli and can be adapted to address a variety of research questions. The matching procedure has been used with species as diverse as dolphins, rats, and people (Baron & Menich, 1985; Forestell & Herman, 1988; Wallace et al., 1980), and the procedure has been adapted for various types of sample stimuli, including visual, auditory, and spatial cues. Figure 14.1 illustrates a version of the procedure for use with pigeons. Although our discussion will focus on the matching-to-sample technique, the conceptual issues involved are relevant to all other memory tasks as well.

Pigeons are typically tested in a Skinner box with a stimulus panel on one wall that allows the presentation of stimuli and also detects pecking responses.

FIGURE 14.1. Illustration of a Matching-to-Sample Trial



Note. The trial begins with a white circle on a touch screen that indicates the start of the trial. The sample stimulus (a triangle) is then presented in a similar location on the screen. The sample is then turned off, and a retention interval begins. At the end of the retention interval, the participant receives two test stimuli, one of which matches the sample stimulus. Responses to the test stimulus that matches the sample are reinforced, as indicated by the asterisk.

The stimulus panel is programmed to allow the presentation of stimuli in three positions, usually arranged in a row. For example, the stimuli may be three circles of the same size filled with various colors or patterns. Each trial begins with a start cue, which might be illumination of the center position with a white circle. One peck at the start cue results in presentation of the sample stimulus, also in the center position. In our example, the sample stimulus is a triangle. After a few seconds, the sample stimulus is turned off, and a retention interval begins. At the end of the retention interval, the pigeon receives two test stimuli, one on the left and one on the right. One of the test stimuli is the same as the previously presented sample (a triangle), whereas the other is different (a square). Pecks at the matching stimulus are reinforced. Pecks at the alternate test stimulus have no consequence.

Simultaneous Versus Delayed Matching to Sample

As you might suspect, the difficulty of a matching-to-sample procedure depends on the duration of the retention interval (Grant, 1976). To facilitate learning of a matching task, it is useful to begin training without a retention interval. Such a procedure is called **simultaneous matching to sample**. In simultaneous matching, after presentation of the start cue, the sample stimulus is presented in the same position. The test stimuli are then presented on the left and right sides of the sample, but the sample stimulus is not removed. Because the sample stimulus is visible at the same time as the test stimuli, the procedure is called simultaneous matching to sample.

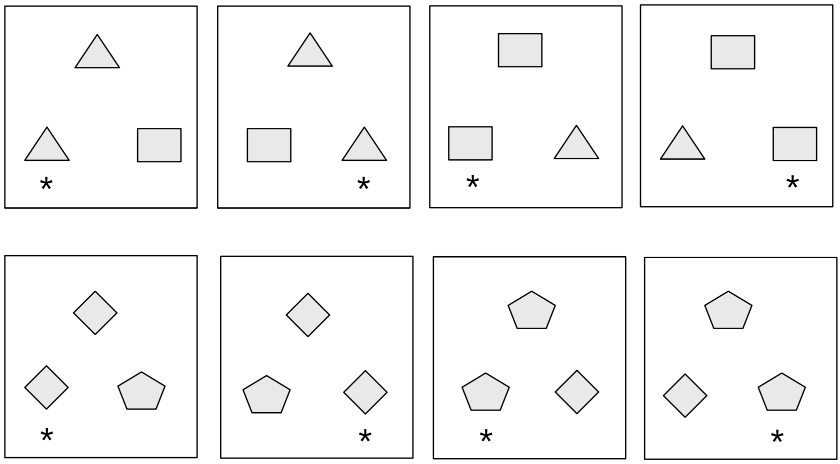
A simultaneous matching procedure is not a good test of memory because the sample stimulus remains present during the choice component of each trial. But that feature facilitates learning the task. After the participants have learned to make the accurate choice in a simultaneous matching procedure, a retention interval can be introduced between presentation of the sample and presentation of the test stimuli, as illustrated in Figure 14.1. Because in this case the test stimuli are delayed after presentation of the sample, the procedure is called **delayed matching to sample**.

Procedural Controls for Memory

Introducing a retention interval requires the participant to use what it remembers about the sample stimulus to respond accurately when the test choices are presented. However, having a retention interval in the procedure is not sufficient to make sure that the participant is remembering the sample stimulus. The sample and test stimuli must also be varied from one trial to the next.

Consider, for example, a procedure in which every trial is exactly the same as the trial illustrated in Figure 14.1. To respond accurately with repetitions of this trial, the pigeon would simply have to learn to peck the left stimulus position during the choice component of each trial. The pigeon would not have to remember anything about the shape of the triangle that was the sample on that trial.

FIGURE 14.2. Eight Types of Trials Used to Make Sure That Participants in a Matching-to-Sample Procedure Are Responding on the Basis of information Obtained From the Sample Stimulus



Note. Each panel represents a different trial type, with the sample presented on top, and the two choice stimuli are presented below. The correct choice is identified by an asterisk.

To force participants to pay attention to and remember information about the specific stimuli that are presented in a matching procedure, the sample stimulus used and the position of the test stimuli must be varied across trials. Figure 14.2 illustrates various types of trials in a matching procedure involving two pairs of shape stimuli, triangle versus square and diamond versus pentagon. There are eight possible trial types shown in the figure. With each sample stimulus, there are two types of test trials, one with the correct stimulus on the left and one with the correct stimulus on the right. If the eight trial types are varied randomly across trials during training, the participant cannot be consistently accurate unless it uses information based on the sample to guide its selection of the correct test stimulus.

TYPES OF MEMORY

Memory is not a homogeneous process. There are different kinds of memory based on the kind of information that is remembered, the types of manipulations that influence the memory, and how long the memory lasts. Common human experience often involves **episodic memory**, which is memory for a specific episode or event. Remembering who won last year's championship game, where we were when we watched the game, and when the event took place is an example of episodic memory. We are consciously aware of such memories and efforts to retrieve them. Another common form of memory that people have is **semantic memory**, which is remembering basic declarative information about the world in which we live, like who is the mayor of our town. We are consciously aware of having this knowledge, and when we try to think of the mayor's name, we are aware of our attempt to remember it, but we may not recall the specific time and place where we were when we first learned the mayor's name.

Entering the correct password on your smartphone also requires memory but you perform that task so often that you do it automatically, without thinking about each individual character. That kind of automatic and unconscious recall of learned information is called **procedural memory**. Procedural memory is characteristic of habitual behavior. Pavlovian and instrumental conditioning can result in procedural memory, but that does not mean that procedural memories are the only forms of memory evident in nonhuman species.

Throughout this book we have encountered the idea that behavior sometimes may be controlled by an underlying stimulus–response (S–R) association. That is what some have considered to be a form of procedural memory (e.g., Dickinson, 1980). However, we have also found that behavior can sometimes be controlled by much richer associative structures that could be considered the basis for declarative knowledge (e.g., knowing that a response will lead to a reward is knowledge that depends on a response–outcome [R–O] association). In this section, we review research on additional types of memories—working and reference memory, retrospective and prospective memory. We also consider whether memory involves the passive decay of learned information or more active psychological processes.

One issue that we will sidestep is whether memory in nonhuman species includes a conscious sense of remembering. Human episodic memory often includes such conscious feelings. Until we figure out how to study animal consciousness, we cannot investigate such issues with nonhuman species. However, we can examine whether other features of episodic memory occur in birds or rats. Episodic memories are complex and include information about what happened during the target episode and when and where it occurred. Numerous ingenious experiments have shown that nonhuman species also remember the what, when, and where features of a target episode and show other characteristics of human episodic memory as well (Clayton et al., 2007; Crystal, 2021). This makes animal models useful for studying disorders of episodic memory, as in Alzheimer's disease (Crystal, 2018, 2021).

Working Memory and Reference Memory

To consider reference and working memory, let us return to the matching-to-sample task. What kinds of memory are required to respond successfully in a matching-to-sample procedure? In our discussion of procedural controls for memory, we were concerned with making sure that responses to the test stimuli on a particular trial depended on what the participant remembered about the sample stimulus that was presented on that trial. However, this information was useful only until the end of the trial. Remembering the sample on a particular trial was of no help in responding on the next trial because the next trial may have involved a different sample stimulus. Memory for information that is required to complete a task or trial is called **working memory**.

Working memory is retention of information that is needed to respond successfully on one trial or task but is not useful in responding on subsequent trials or tasks. If you are baking a cake and mixing the ingredients, you start with a certain amount of flower and then add salt, sugar, and baking powder. Because all these ingredients are white and powdery, once each has been added to the mix, it cannot be distinguished by sight. Therefore, you have to remember whether you have already added the sugar or salt. But that information is only useful until you finish preparing the cake mix; it will not help you bake the next cake. Thus, this is a form of working memory.

The control procedures that we discussed previously (variations in the sample stimulus and in the location of the correct choice stimulus) make sure that matching-to-sample procedures involve working memory. However, to respond successfully, participants must remember more than just information about the sample on a particular trial. They also have to remember general features of the matching task that remain constant from one trial to the next. For example, the pigeons have to remember to peck the start cue and to peck one of the test stimuli after the retention interval. In addition, they have to remember that correct responses are reinforced and where to obtain the reinforcer once it is delivered. These pieces of information are useful on every trial. Such memory is called **reference memory**. Reference memory involves memory for features of a task that remain constant from one trial to the next. Reference memory is of considerably longer duration than working memory.

To bake a cake, you have to remember some general information about cooking. You have to know about cake pans, ovens, various ingredients, and how to measure and mix those ingredients. These general skills are useful not just for the cake you happen to be baking but also for any future cakes you might want to make. Therefore, such information involves reference memory.

Trace Decay Versus Active Memory Processes

Working memory and reference memory are distinguished by the type of information that is retained and by how long the information is remembered. Memory mechanisms can be distinguished as well by the kinds of procedures that influence them. A fundamental issue is whether memory is governed by a passive trace decay process that automatically leads to forgetting over time or involves more complex mechanisms.

The concept of **trace decay** is one of the oldest explanations of memory loss over time. According to the trace-decay hypothesis, presentation of a sample stimulus activates a neural trace that automatically fades over time after the end of the stimulus. Information about the sample is available only as long as the trace is sufficiently strong. The gradual fading or decay of the neural trace is assumed to produce progressively less accurate recall (Roberts & Grant, 1976). Although the idea of trace decay has been successfully applied in some settings (e.g., Ghirlanda et al., 2017), a growing body of evidence suggests that the simple idea of trace decay is grossly incomplete as a comprehensive account of memory loss. Numerous other factors also contribute to how well we remember something and the circumstances under which we remember those things.

According to the trace-decay hypothesis, the strength of a stimulus trace is determined primarily by the intensity and duration of the stimulus (Grant, 1976). However, the accuracy of memory also depends on the conditions of training. We are better at remembering things if we know that we will be tested on the information. That is, knowledge that memory will be required improves remembering. Two different lines of evidence support this conclusion.

One major line of research has shown that memory processes can be brought under stimulus control. These studies were originally conducted with human participants who were presented with a series of stimulus items. Some of the items on the list were followed by a remember cue (the letter R), indicating that participants would be tested on that item in a subsequent memory test. Other items on the list were followed by a forget cue (the letter F), which indicated that the item would not be included in the memory test. After the training, participants were tested for their memory for both the R- and the F-cued items. The results showed better memory for the R-cued items than the F-cued items (e.g., Dames & Oberauer, 2022; Hupbach et al., 2018; MacLeod, 2012). This shows that memory can be brought under stimulus control and is not determined by a simple trace-decay mechanism.

Students often ask whether what is being discussed in class will be on the test. In asking that question, they are asking to be provided with an R cue or an F cue. Their assumption is that an R cue will enable them to activate cognitive processes that will facilitate retention of the information.

Research on directed forgetting has been extended to nonhuman species as well, which has facilitated examination of the neural basis of the effect (e.g., Tanaka et al., 2019). In one study, for example, pigeons were trained on a matching-to-sample problem in which the sample stimulus was followed by either a high-pitched or a low-pitched tone indicating that the memory would be (or would not be) tested for the sample stimulus. Probe tests at the end of the experiment indicated better performance for R-cued sample stimuli than for F-cued sample stimuli (Milmine et al., 2008; see also Zentall, 2012).

The **directed forgetting** effect shows that memory processes can be engaged (or not) on an item-by-item basis. Broader aspects of a training procedure can also activate memory processes to different degrees. We can be trained to remember something for a short period or for a longer period. This was demonstrated in an important experiment with pigeons by Sargisson and White (2001). The birds were trained on a standard delayed matching to sample procedure. The usual practice in such experiments is to use a relatively short delay interval between the sample stimulus and the choice alternatives during training and then test the birds with longer intervals during tests of memory. The typical outcome is that memory accuracy quickly deteriorates with longer delay intervals during the test series.

Sargisson and White (2001) departed from the standard training protocol by using delay intervals of 4 and 6 seconds during the training trials. After training with the longer delay intervals, the deterioration in memory performance that is usually observed with longer test delays did not occur. That is, the pigeons learned to remember the sample stimulus over longer delays if they received a training procedure that required better retention. This shows that the ability to retain information for a longer period is a skill that can be trained given the right training procedure.

Retrospective Versus Prospective Memory

So far, we have established that the matching-to-sample task involves both working memory and reference memory and that working memory is best characterized as an active rather than passive process. Another important issue concerns the contents of working memory—that is, what does the individual remember during the retention interval that enables them to make the correct choice at the end of a trial?

Retrospective Memory

The most obvious possibility is that information about the sample stimulus is stored during the retention interval, and this enables the participant to select the correct test stimulus at the end of the trial. Presumably, during the choice test, the participant compares the memory of the sample to each of the choice alternatives to determine which alternative best resembles the sample. The participant then selects the test stimulus that best matches the sample.

Remembering attributes of the sample stimulus is a form of retrospective memory. **Retrospective memory** is memory for stimuli or events that were encountered in the past. When we think about the contents of memory, we usually think about remembering past events. However, retrospective memory for the sample stimulus is not the only type of memory that will lead to correct performance on a matching to sample problem.

Prospective Memory

Recall that, in the typical matching procedure, a small number of different trial types are repeated over and over again in random order. Figure 14.2, for example, illustrates a procedure in which there are four possible sample stimuli: a triangle, a square, a diamond, and a pentagon. For each sample, there is a specific correct test stimulus. Because of this, the matching procedure involves pairs of sample and test stimuli.

Let us represent a sample stimulus as S and a test stimulus as T. Different sample-test stimulus pairs may then be represented as S1–T1, S2–T2, S3–T3, and so on. During training, participants could learn these S–T pairings. That would then enable participants to select the correct choice stimulus by thinking of T after presentation of the sample S and storing that information during the retention interval. This strategy would involve keeping in memory information about a future choice stimulus or action and is called **prospective memory**. Prospective memory involves keeping in mind a future stimulus or response.

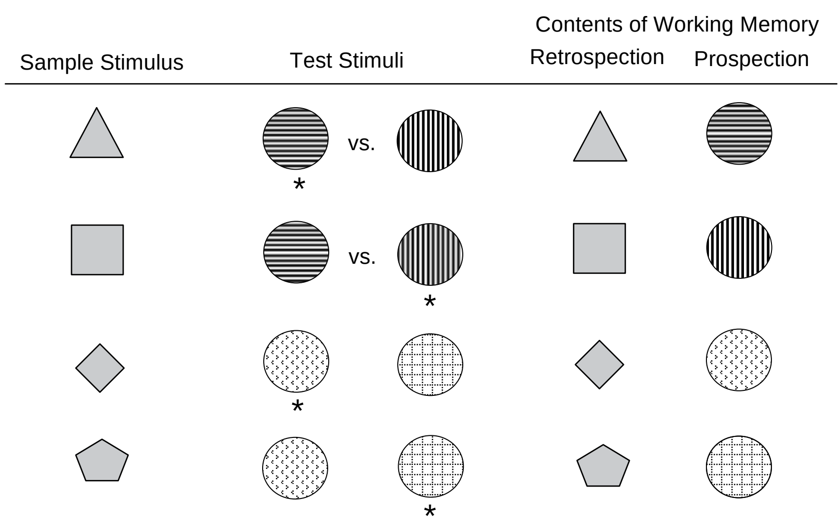
Distinguishing Between Retrospective and Prospective Memory

Retrospective memory involves remembering the sample stimulus S during the retention interval. Prospective memory involves remembering during the retention interval to choose the test stimulus T when presented with the choice. How can we distinguish between these possibilities experimentally?

In the matching-to-sample problems we have considered so far, the sample stimulus S and the correct test stimulus T are the same. If the sample is a triangle, the correct test stimulus is also a triangle. This makes it impossible to decide whether information stored during the retention interval concerns stimulus S or stimulus T. To distinguish between retrospective and prospective memory, we have to change the matching procedure somewhat, so that T is not the same physical stimulus as S. Such a procedure is called *symbolic matching to sample.*

A symbolic matching procedure is illustrated in Figure 14.3. Each row represents a different trial type in the procedure. The procedure is based on symbolic relationships between sample and test stimuli rather than the identity relationship. In Figure 14.3, responding to the horizontal grid is reinforced after presentation of a triangle as the sample stimulus, and responding to the vertical grid is reinforced after presentation of a square as the sample. In a sense, the horizontal grid is a symbol for the triangle, and the vertical grid is

FIGURE 14.3. Diagram of a Symbolic Matching-to-Sample Procedure and Illustration of the Difference Between Retrospective and Prospective Working Memory



Note. Each row shows a different trial type. The test stimuli are shown to the right of the sample for each trial type, and the correct test stimulus is indicated by an asterisk.

a symbol for the square. Symbolic relations between other shapes and visual patterns are shown in the third and fourth rows of Figure 14.3.

As with the standard matching procedure, in a symbolic matching task, the correct test stimulus appears equally often on the left and the right, and there is a delay between the sample and the test stimuli. Therefore, the task involves working memory, just as the standard matching procedure does. However, with symbolic matching, different things are remembered depending on whether the memory is retrospective or prospective. The differences are shown in the columns on the right of Figure 14.3. On trials with the triangle as the sample, retrospective memory involves retention of information about the triangle. In contrast, prospective memory involves retention of information about the horizontal-grid test stimulus, which is the correct choice after a triangle sample. On trials with the square as the sample, retrospective memory involves remembering the square, whereas prospective memory involves remembering the vertical grid.

Studies of the symbolic matching-to-sample procedure have shown that pigeons often use prospective rather than retrospective memory (e.g., Roitblat, 1980; Santi & Roberts, 1985). Research using other kinds of memory tasks has also provided evidence of prospective memory (e.g., Beran et al., 2012; Crystal & Wilson, 2015; Roberts, 2012). It may seem strange to call a plan for future action a form of memory. However, neuroscience suggests that we are on firm ground here. Functional magnetic resonance imaging of human participants has shown that prospective memory engages neural circuits that are similar to the neural circuits that are involved in retrospective memory (Schacter, 2019).

Obviously, not all instances of working memory involve prospection, or memory for events that are predicted to occur in the future. Whether organisms remember something from the past (retrospection) or a plan for future action (prospection) depends on which form of memory is more efficient in solving a particular task (Cook et al., 1985; Zentall et al., 1990). This shows that there is considerable flexibility in what information is encoded in working memory, depending on the demands of the task. In addition, the two forms of memory may operate in combination. Investigators have suggested that planning for the future is only possible with past information (Clayton & Wilkins, 2018; Schacter, 2019). Thus, retrospection may play a critical role in prospection.

SOURCES OF MEMORY FAILURE

All of us encounter frustrating instances in which we cannot remember something. You may have been introduced to a new employee but when you encounter the person several days later, you may struggle to remember their name. You may casually attribute such episodes to forgetting. Interestingly, however, forgetting is rarely used to explain instances of memory failure in the scientific literature. Forgetting implies that you learned and encoded the person's name when you were first introduced but the memory trace has since faded and no longer exists. Although that may seem plausible, true forgetting is difficult to demonstrate. There are other explanations for memory failure, and these alternative accounts are easier to document.

Memory may fail for a variety of reasons. You may not remember something because you never learned the information or properly encoded it in the first place. Memory failure may also result from failure to effectively retrieve information that was successfully encoded or stored. You may also perform poorly in a memory task because you remember several different things and are unable to choose correctly among these alternatives. In the following sections, we consider various alternative explanations of memory failure, discuss a special form of memory failure called *retrograde amnesia*, and discuss the current status of the concept of memory consolidation.

Interference Effects

One of the most common sources of memory failure is interference from information that you were exposed to before or after the event that you are trying to remember. You may not recall the name of a new employee because of the other people you met for the first time before or after that particular individual. Memory failure due to interference has been extensively investigated in studies with both human participants (e.g., Kliegl & Bäuml, 2021; Postman, 1971) and nonhuman species (e.g., Killeen, 2001; Wright et al., 2012).

There are two types of interference effects depending on whether the source of the interference takes place before or after the target even that you are trying to remember (see Exhibit 14.1). If the extraneous stimuli that disrupt memory occur before the target event, the phenomenon is called **proactive interference**. In proactive interference, the interfering stimuli act forward, or proactively, to disrupt memory for the target event. Consider, for example, going to a sociology class that deals with the issue of punishment from the standpoint of the penal system and then attending a psychology class in which punishment is discussed from the perspective of conditioning procedures. You would be experiencing proactive interference if what you learned in the sociology class disrupted your memory of the psychological analysis of punishment.

Memory disruptions can also work in the opposite direction. Something you encounter later can act backward to disrupt your memory of something

EXHIBIT 14.1

Distinction Between Proactive and Retroactive Interference

Proactive interference

Extraneous events → Target task → Memory test

Retroactive interference

Target task → Extraneous events → Memory test you learned earlier. This is called **retroactive interference**. You might be at a party, for example, where you first talk to Jane and then talk with Mary. When you think back on the experience the next day, you may have difficulty remembering what you discussed with Jane because of your subsequent discussions with Mary. In this case, your conversation with Mary acts backward or retroactively to disrupt your memory of talking with Jane.

Both proactive and retroactive interference have been investigated in nonhuman species using delayed matching to sample procedures. Proactive interference can occur if trials are scheduled close together (or massed) in matching to sample training. Recall that successive trials in a matching procedure involve different sample stimuli. With massed trials, what occurs on one trial can produce proactive interference to disrupt performance on the next trial (Edhouse & White, 1988; Jitsumori et al., 1989). One account of this effect is that participants perform poorly not because they remember too little but because they remember too much. Proactive interference is caused by remembering what happened on the preceding trial, which creates confusion about the correct choice on the current trial. Interestingly, lesions of the hippocampus can improve reference memory performance on some Pavlovian learning tasks by eliminating proactive interference caused by massed training (Han et al., 1998).

Retroactive interference has been investigated in matching to sample procedures by presenting extraneous stimuli during the delay interval between presentation of the sample stimulus and the choice alternatives. The extraneous stimulus may be provided by increasing the level of illumination in the experimental chamber to make various features of the experimental chamber more visible. Such a manipulation typically disrupts the accuracy of matching performance (e.g., Grant, 1988). In contrast to proactive interference, which results from remembering too much, retroactive interference seems to result from a failure to recall or retrieve required information. However, the precise mechanisms of retroactive interference remain under investigation (e.g., Arkell et al., 2021; Calder & White, 2014; Camats-Perna et al., 2019).

Retrieval Failure

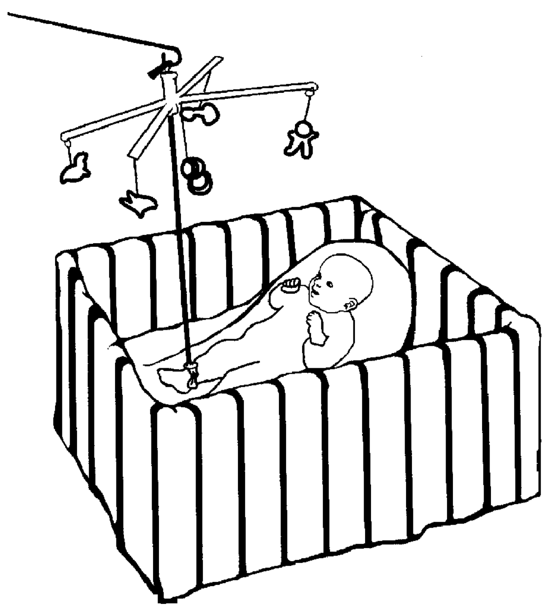
Studies of proactive and retroactive interference illustrate two causes of poor performance in a memory task. Yet another factor that contributes to memory failure is an individual's inability to effectively retrieve information that they previously learned. In principle this source of memory failure is easy to demonstrate. If poor performance on a memory task is due to retrieval failure, then procedures that facilitate retrieval should facilitate performance. Retrieval of information is facilitated by exposure to stimuli that were previously associated with the target information at the time when the target was initially encoded. Such stimuli are called **retrieval cues**.

Remarkably insignificant features of the environment may become associated with a learning task and facilitate retrieval of information relevant to that task. In one study (Borovsky & Rovee-Collier, 1990), for example, 6-month-old infants received an instrumental conditioning procedure in their playpen at home (see Figure 14.4). Each infant was placed in a baby seat in the playpen with a mobile positioned overhead in plain view. The mobile was gently attached to one foot of the infant with a satin ribbon. By moving its foot, the infant could make the mobile move. Thus, the instrumental response was a leg movement, and the reinforcer was movement of the mobile.

Infants readily acquired the leg-movement response but showed little evidence of learning if they were tested 24 hours later. Did this deterioration of performance reflect the failure to effectively learn or encode the instrumental contingency, or a failure to retrieve what was learned the day before? If the instrumental response was not learned in the first place, then there is nothing one can do to counteract the poor performance that is evident 24 hours later. In contrast, if the lack of memory was due to retrieval failure, then the presentation of retrieval or reminder cues should restore the conditioned response.

What might be an effective retrieval cue for the infants in this situation? Borovsky and Rovee-Collier (1990) found that the pattern of the cloth liner that covered the sides of the playpen served as an effective retrieval cue for the instrumental response. Sometimes the liner for the playpen had a striped pattern; on other occasions, the liner had a square pattern. Infants for whom the striped pattern was in the playpen during training responded better 24 hours later if they were tested with the striped liner than if they were

FIGURE 14.4. Experimental Situation Used by Borovsky and Rovee-Collier (1990) to Study the Effects of Retrieval Cues on the Memory of Human Infants for an Instrumental Conditioning Task



Note. The instrumental response was moving a leg, and the reinforcer was consequent movement of a mobile located in the infant's view.

tested with the square one. The reverse results were obtained with infants for whom the other liner was used during original training.

The results of this experiment are remarkable because nothing was done to direct the attention of the infants to the crib liners. The square and striped patterns were both familiar to the infants, and the patterns were not predictive of reinforcement. They served as incidental background cues rather than as discriminative stimuli. Nevertheless, the liner used during original training became associated with the instrumental task and helped to retrieve information about the task during the memory test 24 hours later.

A variety of stimuli have been found to be effective as retrieval cues in various learning situations, including exposure to a conditioned stimulus in extinction, exposure to the US, internal cues induced by psychoactive drugs, and exposure to the S– in a discrimination procedure (Spear & Riccio, 1994). In addition, retrieval cues have been found to reverse a variety of phenomena that are characterized by low levels of conditioned responding, such as extinction, latent inhibition, overshadowing, and blocking (Urcelay & Miller, 2017). Now that the effectiveness of retrieval cues has been well established in behavioral studies, investigators are turning their attention to the neuroscience of retrieval processes (e.g., Frankland et al., 2019).

CONSOLIDATION, RECONSOLIDATION, AND MEMORY UPDATING

For something to be remembered for a long time, a relatively permanent change has to occur in the nervous system. The translation of a learning episode into a long-term memory requires the process of memory **consolidation**. Memory consolidation is a complex process that operates at several levels in the nervous system. Consolidation involves changes within neurons (Langille & Gallistel, 2020), as well as cellular and molecular changes at the level of neural synapses (Hernandez & Abel, 2008). Memory consolidation also involves changes in neural circuits and neural systems (McKenzie & Eichenbaum, 2011). These various forms of consolidation take time to complete. Synaptic consolidation generally occurs faster than consolidation in neural circuits.

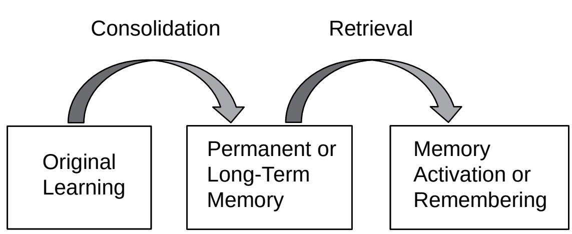
Before a memory is fully consolidated, it is in a flexible or malleable state in which it can be disrupted or changed. In fact, hypotheses about memory consolidation are typically tested by introducing manipulations that disrupt the consolidation process. For example, treatment with a protein synthesis inhibitor or electroconvulsive shock after a learning episode disrupts later recall of that conditioning trial (McGaugh, 2000; McGaugh & Herz, 1972). However, the source of disruption must occur shortly after the conditioning trial before the consolidation process has been completed. This limited period when a memory is vulnerable to disruption is called the **consolidation window**. For example, consolidation failure is one explanation for the common phenomenon that people who suffer a brain trauma from a car accident often remember few details of about the accident, but they have no trouble remembering their name or where they live.

The traditional of view of memory consolidation was that once the consolidation processes have been completed, the memory was solidified and permanent: It could no longer be disrupted by the inhibition of protein synthesis or the administration of electroconvulsive shock. A previously consolidated memory could be retrieved to help deal with current situations. Retrieval or recollection moves the memory from an inactive or stored state to an active state in which the memory can guide decisions and behavior. However, the assumption was that moving the memory to an active state did nothing to change the durability or strength of the original memory. Because the original memory remained pretty much intact, each attempt at retrieval operated on the original consolidated memory (see Figure 14.5).

The traditional view that memory consolidation creates a permanent memory has been challenged in recent years by the phenomenon of **reconsolidation** or **memory updating**. When a memory is reactivated or retrieved, the information is moved from its inactive (or stored) state to an active state. New evidence suggests that when brought into this active state, even well-consolidated memories can be further modified or changed. In other words, reactivating a memory is thought to make that memory more labile and vulnerable to change. Modifications of the old memory can then become incorporated into a new form of long-term memory through the process of reconsolidation (Auber et al., 2013; Lee et al., 2017). Interestingly, reconsolidation appears to involve many of the same neural mechanisms as original consolidation (Josselyn & Tonegawa, 2020; McKenzie & Eichenbaum, 2011; Nader & Hardt, 2009). This type of process may be at least partly responsible for the phenomenon of "false memories" (e.g., Schacter & Loftus, 2013; Sinclair & Barense, 2019).

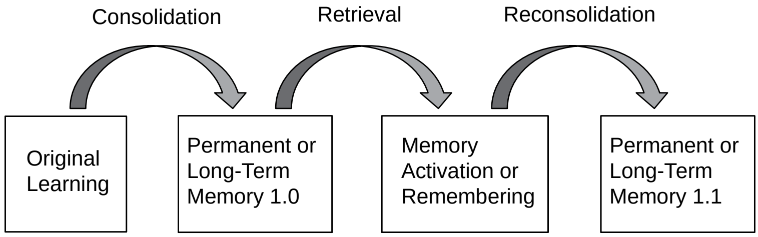
The concept of reconsolidation is illustrated in Figure 14.6. Original learning and consolidation of that learning establishes the first form of a long-term memory, something we may label as memory 1.0. Retrieval of that memory makes the memory subject to alteration, and these changes are then reconsolidated into a modified form of the long-term memory, which we may label as 1.1. This process of memory retrieval and reconsolidation can be repeated multiple times, with the consequence that the original memory becomes substantially modified as a result of the repeated recollections.

FIGURE 14.5. Traditional View of Learning and Memory Consolidation



Note. Once a new memory has been consolidated, it is available for retrieval, but this was assumed to leave the contents of the original memory unchanged.

FIGURE 14.6. Contemporary View of Learning, Memory Consolidation, and Reconsolidation



Note. When a memory is retrieved, it becomes labile and susceptible to reconsolidation, permitting changes in the contents of long-term memory with each episode of retrieval.

Recent research on reconsolidation has revolutionized how we think about memory mechanisms. Traditionally, we considered a well-consolidated memory to be like a photograph that does not change each time you look at it. The concept of reconsolidation suggests that when you look at a photograph and then return it to storage, the photo that you store may have been modified by your current thoughts and reactions to it. In principle, the more often you retrieve a photo, the more chances you have to modify it. Through repetitions of this process, you could end up with an entirely different photo.

Not all reactivated memories are changed during the process of recall. If the reactivated memory is not accompanied by new elements (or some form of prediction error), it is not likely to activate reconsolidation processes (Sevenster et al., 2013). Much remains to be discovered about the circumstances that make a memory susceptible to long-term modification, and the boundary conditions of such modifications (Zhang et al., 2018). The fact that long-term memories are susceptible to alteration helps us better understand how false and distorted memories develop through repeated efforts at recollection (Hardt et al., 2010). But memory reconsolidation is not necessarily bad; it allows us to update memories to incorporate new relevant information. Investigators are also exploring ways to use memory reconsolidation to change maladaptive memories that are the source of clinical problems such as anxiety and threat-related disorders, drug addiction, and posttraumatic stress disorder (Astill Wright et al., 2021; Lee et al., 2017).

SUMMARY

Learning and memory are integrally related. Studies of learning focus on the acquisition stage of information processing, whereas studies of memory focus on the retention and retrieval stages. Working memory is used to retain information that is required just long enough to complete a trial or task. In contrast, reference memory involves aspects of the task or trial that remain constant from one occasion to the next. Early studies considered memory to be passive and retrospective. However, more recent evidence suggests that in many cases memory involves active processes and that the stored information often involves information about the future (prospective memory) rather than past (retrospective memory).

Studies of what individuals forget can tell us as much about memory mechanisms as studies of successful performance. Memory failure may occur because of proactive or retroactive interference or because of retrieval failure. Proactive interference is often due to remembering both useful and irrelevant information and not being able to select between these. Retroactive interference can be due to disruptions of rehearsal processes needed for successful encoding. Proper rehearsal, however, does not guarantee good memory. Information that is properly retained may not be retrieved during a memory test. Retrieval cues, some of which may be seemingly trivial features of the training situation, can facilitate memory performance in cases of retrieval failure.

Establishing a long-term memory involves processes of consolidation that operate at the level of neurons and neural circuits. However, a consolidated memory is not immune to modification. The recollection of a memory returns the memory to an active state in which it can be modified, and those modifications can then be incorporated into the old memory through a process called reconsolidation or memory updating. With repeated recollections, significant aspects of a memory can be altered. This type of memory updating can create false memories, which may be problematic. However, research on memory updating may also enable scientists to develop more effective treatments for forms of psychopathology that are based on the maladaptive memories.

SUGGESTED READINGS

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Lee, J. L. C., Nader, K., & Schiller, D. (2017). An update on memory reconsolidation updating. *Trends in Cognitive Sciences, 21*(7), 531–545. https://doi.org/10.1016/j.tics.2017.04.006.

TECHNICAL TERMS

acquisition stage, page 226
retention stage, page 226
retrieval stage, page 226

matching-to-sample procedure, page 227
simultaneous matching to sample, page 228
delayed matching to sample, page 228
episodic memory, page 229
semantic memory, page 229
procedural memory, page 230
working memory, page 231
reference memory, page 231
trace decay, page 231
directed forgetting, page 232
retrospective memory, page 233
prospective memory, page 234
proactive interference, page 236
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