9 The Role of Associative Processes in Spatial, Temporal, and Causal Cognition

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Associative processes build the structural-representational framework upon which cognitive processes of computation and inference can act. I review evidence I have collected showing how associative processes are involved in building spatial, temporal, and causal maps. Evidence comes from studies on simple associative acquisition such as Pavlovian and instrumental conditioning, higher-order conditioning procedures such as sensory preconditioning and conditioned inhibition, and from cue-competition studies. Parallels are drawn between acquisition and integration of information in conventional associative paradigms on the one hand and cognitive paradigms on the other.

1 Introduction

One of the great psychological debates of the twentieth century involved an exchange between Tolman and Guthrie. Tolman, originally a behaviorist himself, conducted experiments with rats that lead him to develop a nascent cognitive framework during the first half of the twentieth century—a period dominated by the S-R behaviorist ideology. He suggested that rats held expectations about impending events, rats could learn without explicit (i.e., food) reinforcement, and that rats formed cognitive maps while navigating a maze. Tolman was ridiculed by many of his colleagues for these heretical notions. Guthrie, one of behaviorism's chief proponents, even accused Tolman of "leaving the rat buried in thought" (Guthrie, 1935, p. 172). Tolman planted the seed, however, that led to the cognitive revolution of the 1960s and 1970s. The cognitive framework finally found acceptance and hypotheses about mental states and cognitive processes in both humans and animals became commonplace. Today, the cognitive framework is the dominant ideological stance, though currents of behaviorism still exist. This is not to say that one framework, such as the cognitive, provides a more accurate depiction than the other, such as behaviorism. Rather, both frameworks continue to have heuristic value, and the tension between them epitomizes the

Hegelian dialectic—a process that can lead to a synthesis of new ideas and enlightenment. In fact, the more we understand about the neural underpinnings of learning and behavior, the more difficult it is to distinguish between behaviorist and cognitivist explanations of psychological processes.

Despite the acceptance of cognitive explanations of behavior in general, learning theorists have been slow to adopt a truly rich cognitive framework. Even now, the dominant conventional view is that only the strength of the CS-US association is encoded during Pavlovian conditioning. Likewise, theories of instrumental conditioning are largely focused on the strengths of S-R and R-O associations with only a minority focus on the quality of these associations. Evidence has been accumulating over the past two decades, however, suggesting that subjects acquire a much richer representation of their experiences during associative learning. These representations include information about time, space, and qualitative attributes of a CS and US (e.g., Blaisdell, Denniston, and Miller, 1997). Moreover, there is evidence that both humans and animals learn cause-effect relationships during even the most simple of Pavlovian procedures. In this chapter, I review this accumulating evidence presenting key examples from my own laboratory and from my work with Dr. Ralph Miller.

2 Spatial Cognition

Since its introduction by Tolman (1948), the cognitive map has gained widespread use as a conceptual tool for understanding spatial memory and cognition. Spatial abilities are fundamentally important for navigating the world in order to migrate, avoid dangers such as predators, and to locate biological necessities such as food, shelter, and mates. The concept of a cognitive map usefully describes many aspects of spatial behavior and continues to facilitate the discovery of new behavioral phenomena and processes (Gallistel, 1990; Healy, 1998; Shettleworth, 1998). The cognitive map has also been useful in understanding processes of timing in associative memory (Honig, 1981, see Section 3). One important feature of cognitive maps is that they can be used to compute novel routes between separate spatial locations (Tolman, 1948). Despite some criticisms (Bennett, 1996; Gibson and Kamil, 2001; Shettleworth, 1998), I have found the cognitive map to be a useful concept in describing the results of recent experiments from my and others' laboratories.

For example, the demonstration that pigeons learn to use visual landmarks on a touchscreen or in an open field to find a hidden goal supports the interpretation that they learned the spatial vector between the landmark and the goal (Blaisdell and Cook, 2005; Cheng, 1994; Cheng and Spetch, 1995, 1998; Kamil and Cheng, 2001; Sawa, Leising, and Blaisdell, 2005; Spetch, Cheng, and MacDonald, 1996; Spetch et al., 1997; Spetch, Cheng, and Mondloch, 1992; Spetch and Mondloch, 1993). A vector is a metric encoding both distance and direction between two points in space occupied by specific objects. The direction is coded in reference to a larger framework of orientation, such as the sides of the touchscreen monitor or the walls of the room containing the open field. A vector is easily conceptualized as an allocentric spatial map between two objects: A and B. Object A may be a junk object located in the open field and Object B may be a food goal buried under sand on the floor of the

open field. Alternatively, Object A may be a colored shape presented on the surface of the monitor and Object B may be a spatial location on the monitor at a fixed distance and direction relative to Object A. Work carried out in my lab has investigated the role of associative processes in the acquisition and expression of spatial maps. The fundamental issue is whether learning the spatial relationship between objects, such as landmarks and goals, obeys the same principles as learning and expression of associations in conventional Pavlovian and instrumental conditioning procedures. We adopted a method used by others of testing specific functional parallels between spatial learning and conventional associative learning. The existence of functional parallels strongly suggests a common process underlying learning in both domains.

2.1 Acquisition of Spatial Maps

Figure 1 (inset) shows an example of a procedure used in our lab to train pigeons to use a visual cue presented on a touchscreen in an operant box as a landmark to a hidden goal also located on the touchscreen. Pigeons were reinforced with mixed gain from a food hopper below the touchscreen for pecking at the goal location which could be any one of 56 dots in an 8 x 7 grid. Each dot was centered within a 2-cm^2 response area that served as a possible goal location. The goal was initially marked with the 2-cm^2 white square that was gradually faded out until only the dot was visible (see Sawa et al., 2005 for details). The training landmark (denoted by the "T" in Figure 1) bore a fixed spatial location relative to the goal. By the completion of fading out the goal marker, subjects were able to locate the hidden goal based solely on its spatial relationship with the training landmark. Because the location of the goal was randomly determined on each trial, subjects were not able to predict its location on a given trial other than to attend to the landmark. The main panel of Figure 1 shows peck location data collected on 30-s nonreinforced probe trials with LM T. The strong spatial control over pecks by LM T shows that pigeons had encoded the T➔Goal spatial vector.

The benefit of studying allocentric representations of space on the touchscreen is that it is virtually free of confounding spatial processes that are engaged when navigating three-dimensional space, such as optic flow, dead reckoning, and motion parallax. Nevertheless, it is important to verify the validity of results from touchscreen experiments by conducting similar tests in a more ecologically valid setting such as the open field. To this end, some of the experiments reported here include replications in an operant open-field procedure called ARENA recently developed in our lab (Badelt and Blaisdell, 2008; Leising, Garlick, Parenteau, and Blaisdell, in press).

2.2 Integration of Spatial Maps

If a Landmark-Goal spatial map is encoded during first-order associative conditioning in which two events are directly paired, then multiple spatial maps between landmarks and goals could be integrated during higher-order associative conditioning such as second-order conditioning and sensory preconditioning. In second-order conditioning, a CS1-US association is learned prior to a CS2-CS1 association. In sensory preconditioning, the CS2-CS1

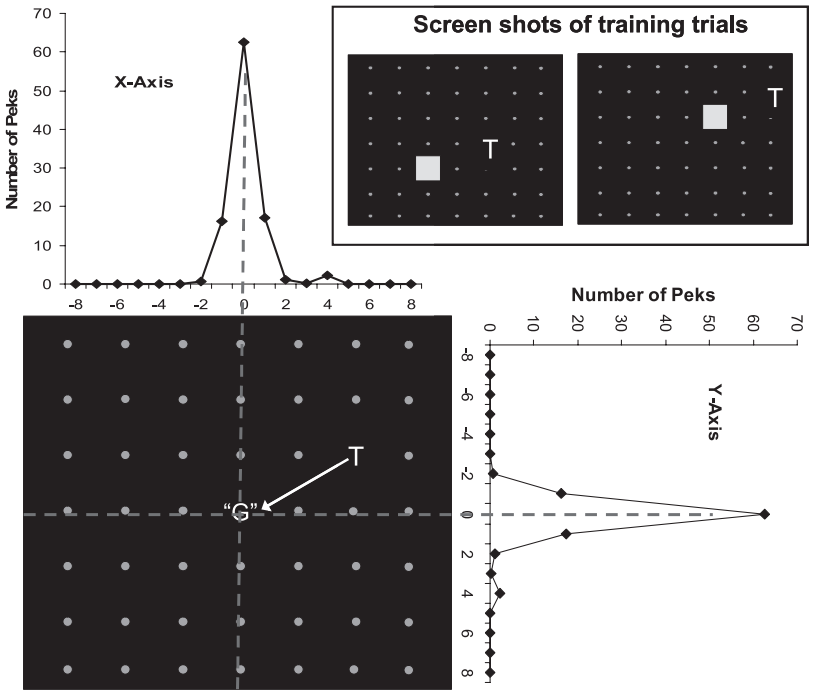

Figure 1. Inset: An example of two trials during initial training of the landmark-based search task. The dots mark the center of each unit of the response grid. The white square marked the goal location. "T" is the training landmark. Main panel: Total number of pecks to the screen on nonreinforced probe trials with LM T. "G" marks the screen location (relative to LM T) where pecks were reinforced on training trials. This location was unmarked during nonreinforced test trials. The arrow (not visible during the trial) indicates the LM T➔Goal spatial map. Distribution of pecks shown separately for X and Y screen axes. Data were pooled across trials so that the goal was zeroed to location (0, 0).

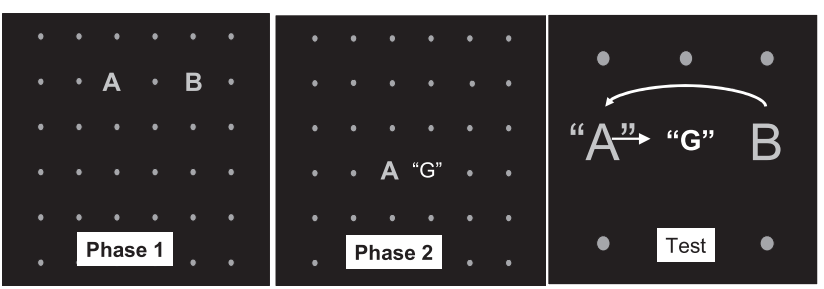

Figure 2. Left panel: LM A and LM B are paired without food in Phase 1 of sensory preconditioning. Middle panel: LM A signals the location of the hidden goal ("G") in Phase 2. Right panel: Hypothetical maps at test (not to same scale as other two panels.)

association is learned prior to the CS1-US association. According to this associative integration hypothesis of cognitive map formation, complex spatial representations can be built by linking together simpler representations that share common elements. The simplest conceivable spatial association encodes the spatial relationship between two events: A and B, such as two landmarks, or a landmark and a food goal (see Section 2.1). A spatial representation containing three events (A, B, and C) can be built in one of two ways. On the one hand, all three events could be presented simultaneously, in which case the subject could construct a spatial or configural representation containing all three elements. For example, presenting LMs A and B together with a food goal could establish a spatial map containing all three elements. On the other hand, the same three-element spatial map could be constructed in a piecemeal fashion by joining together two simpler representations, each containing two of the three elements. This process would allow subjects to construct the same three-element representation without experiencing all three elements at the same time. An integrated map allows the subject to extrapolate novel relationships beyond its direct experience.

Consider the example in Figure 2 (from Sawa et al., 2005). Pigeons received pairings between two visual landmarks (A and B; actual landmarks were colored geometric shapes) in Phase 1 of sensory preconditioning. The screen location of the pair of landmarks varied across trials, but they always bore the same spatial relationship to each other. Pigeons then received first-order conditioning in Phase 2 consisting of A➔Goal pairings. The screen location of the goal was randomly determined from trial to trial. LM A maintained a stable spatial relationship to the goal, thereby signaling the goal location. After pigeons were reliably finding the goal in the presence of LM A, pigeons received nonreinforced test trials with LM B alone which terminated after 30 s without food. We recorded the screen location of all pecks during these test trials. If pigeons had acquired the B➔A map during Phase 1 and the A➔Goal map during Phase 2, then they should search the location one grid unit to the left of LM B (right panel of Figure 2; arrows represent spatial maps acquired between the landmarks and the goal; events enclosed in quotes indicate memories retrieved by way of the associations between events).

Figure 3 shows the results of LM B test trials. The response density peak was located one grid unit to the left of LM B. Thus, through an inference-like process the pigeon arrived at the three-item representation without the concurrent presentation of all three elements (A, B, and goal). That is, associative integration allowed subjects to compute a novel B-Goal spatial relationship despite the fact that B had never been directly paired with the goal. These results suggest that associative learning may serve as a mechanism for the acquisition and expression of spatial behavior guided by both simple and complex maps. According to the associative integration hypothesis, only maps that share linking, common elements are bound together. In our example, the B➔A and A➔Goal associations were integrated into a B➔A➔Goal map through the common element LM A. Unpaired controls (not shown) revealed that associative integration depended on the Phase 1 and Phase 2 pairings (see Sawa et al., 2005). Similar findings have been reported by Blaisdell and Cook (2005) and Chamizo, Roderigo, and Mackintosh (2006).

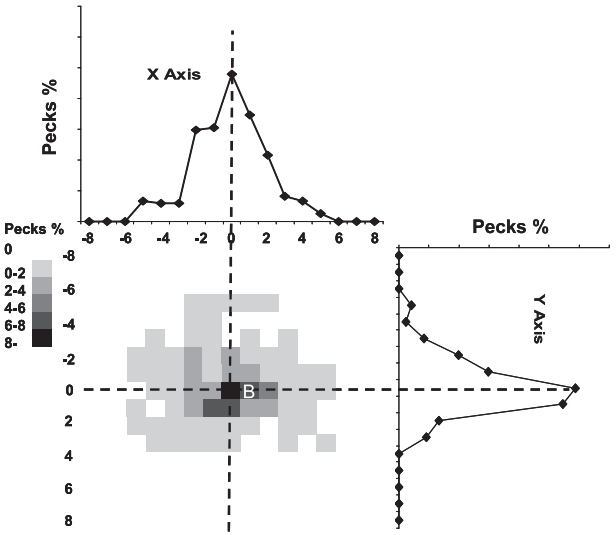

Figure 3. Test trial data for LM B plotted both as a density plot of screen locations pecked and as separate frequency histograms for the X and Y screen axes. The location of LM B in relation to the predicted location of the goal (0, 0) based on integration of the B➔A and A➔Goal spatial maps. Sawa, Leising, and Blaisdell, 2005. Sensory preconditioning in spatial learning using a touch screen task in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* **31**, 368-375, APA, adapted with permission.

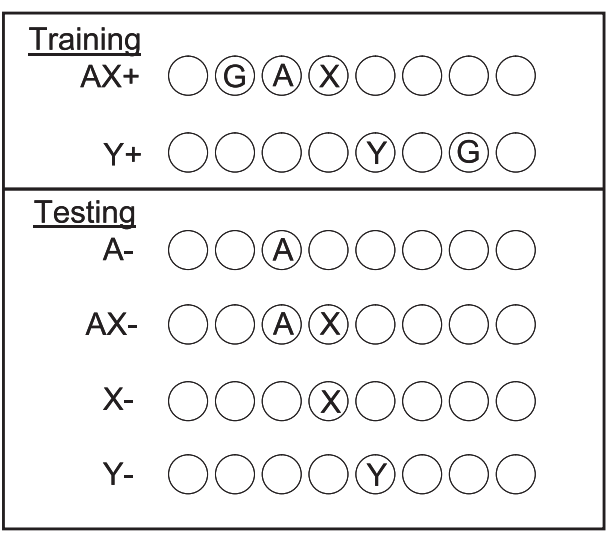

Figure 4. Top panel depicts the overshadowing procedure separately for AX+ and Y+ trials. Bottom panel shows test trial types separately for A-, AX-, X-, and Y- trials.

2.3 Cue Competition Effects in Spatial Maps

Learning theorists have used the technique of presenting multiple cues in compound to study the selective nature of learning and performance (Blaisdell, 2003). How the learning process selects among potential CSs or other antecedent events to form associations with the US or other consequences can be studied by varying different stimulus attributes—such as duration and salience—and the relationship between paired events—such as their contiguity and correlation. The results of such cue-competition experiments is that only a subset of the available cues acquires control over behavior. In addition to the long history of demonstrating cue-competition effects in conventional associative learning paradigms, cue-competition also occurs in spatial learning tasks, such as overshadowing (Cheng, Collett, Pickhard, and Wehner, 1987; March, Chamizo, and Mackintosh, 1992; Sanchez-Moreno, Rodrigo, Chamizo, and Mackintosh, 1999; Spetch, 1995; Spetch and Wilkie, 1994) and blocking (Diez-Chamizo, Sterio, and Mackintosh, 1985; Rodrigo, Chamizo, McLaren, and Mackintosh, 1997; see Leising and Blaisdell, in press for a review).

Overshadowing of Spatial Associations. Overshadowing is the attenuated response to a CS X after having been paired with a US in the presence of a more salient CS A (Pavlov, 1927). For example, if CS X (a soft tone) is paired with the US in the presence of CS **A** (a loud noise; boldface indicates **A** is more intense than X), responding to X is reduced relative to a control group that received X-US pairings in the absence of CS **A**. Thus, the more salient CS **A** overshadows the development of conditioned responding to the less salient CS X. When adapted to the spatial domain, if a more salient LM **A** is able to overshadow the less salient LM X, then subjects should be less accurate at locating the goal in the presence of LM X compared to subjects which learned to find the goal in the presence of X alone (i.e., in the absence of **A**). In conventional Pavlovian conditioning experiments, salience is typically manipulated by adjusting the relative intensity of auditory and visual cues. A brighter visual cue typically overshadows a dimmer one, and a louder auditory cue typically overshadows a quieter one. The salience of spatial cues, however, may be determined by factors other than intensity. For example, landmarks closer to the goal tend to overshadow more distal landmarks (e.g., Cheng, Collett, Pickhard, and Wehner, 1987; Spetch, 1995; Spetch and Wilkie, 1994).

The top panel of Figure 4 shows the design of recent spatial overshadowing experiments in our lab. Eight visual disks located on the surface of the touchscreen or eight ARENA modules located on the floor of the ARENA open field were linearly arranged (see Leising and Blaisdell, submitted, for details). Subjects were first trained to find the goal (G) in the presence of **A**X+ (Figure 4, first row) on some trials, and Y+ on other trials (Figure 4, second row). On **A**X+ trials, two adjacent locations were lit with a different color (one color for A and one for X) that served as landmarks that signaled the location of the goal (indicated by 'G' in the figure). The goal was one location to the left of LM **A** and two locations to the left of LM X. On Y+ trials, one location was lit with a third color that served as LM Y that signaled a goal two locations to the right of LM Y. Pecks at the goal location were reinforced. The landmarks and goal could be placed at different spatial locations within the array across trials, but always had the same relative spatial relationships to each other. After goal pecking

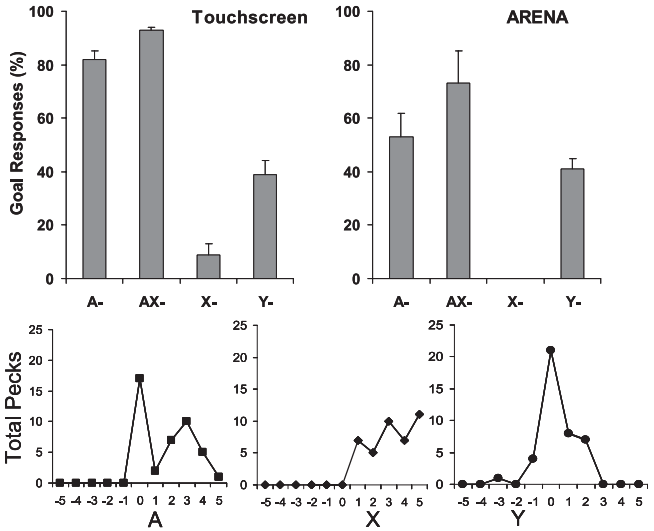

Figure 5. Top panel: Mean percentage of goal responses in the presence of each test landmark for both the Touchscreen and ARENA apparatus. Bottom panel: Response distributions of one representative pigeon on A, X, and Y test trials from the ARENA procedure.

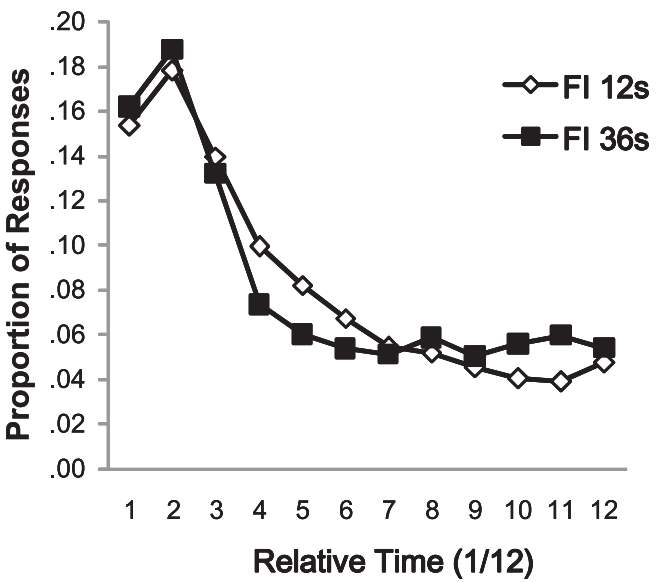

Figure 6. Mean proportion of responding as a function of proportion of elapsed interval on peak interval trials for two separate intervals.

was established for both types of trials, pigeons received 30-s nonreinforced probe trials of **A**, **A**X, X, and Y (bottom panel of Figure 4). Figure 5 shows the results of these tests for the touchscreen and ARENA. We found a robust overshadowing effect in both preparations, with fewer pecks at the training goal location on LM X trials than on LM Y trials. Furthermore, spatial control of search was equally good on tests of overshadowing LM **A** alone as on the **A**X probe trials. This suggests that the poorer control by X than by Y was not due to generalization decrement from a configural **A**X training landmark (see Leising and Blaisdell, submitted for further tests of generalization account of overshadowing). The response distributions from one representative bird (bottom panel) reveal better spatial control by LMs **A** and Y than by X.

3 Temporal Cognition

Much of our everyday behavior is governed by psychological processes involving timing intervals and integrating temporal intervals into sequences. For example, waiting for the next train depends on when the previous train left the station platform and the posted intertrain interval. Likewise, many simple procedures and motor tasks require performing a set of steps in the correct order and at the correct time. There is a wealth of experimental evidence that animals are sensitive to the temporal parameters of perceived events, such as stimulus-reinforcer and response-reinforcer relationships, as indicated by the control temporal relationships exert over behavior (Balsam, 1984; Brown, Hemmes, and Cabeza de Vaca, 1997; Church, 1989; Gibbon and Allan, 1984; Gibbon and Balsam, 1981; Maier and Church, 1991).

3.1 Acquisition of Temporal Maps

Pavlov (1927) reported that conditioned responding becomes maximal at the time after CS onset when the US had previously been presented, indicating encoding of the CS-US interval. Skinner documented the important role time plays in instrumental responding (Ferster and Skinner, 1957). Fixed-interval (FI) schedules of reinforcement—in which reward is given for the first operant response after an FI (e.g., 15 s) elapses—result in a "scalloped" response function. Response rates are low at the beginning of the interval and accelerate as the interval approaches the time of reinforcement. The scalloped nature of the response-rate histogram reflects the subjects' ability to accurately predict the time that reinforcement becomes available. Such scallops generally do not develop under variable-interval (VI) schedules of reinforcement on which the availability of the reinforcer cannot be precisely timed.

The Peak Interval (PI) procedure is a variant of the FI procedure and consists of a mixture of two types of trials (Catania, 1970; Roberts, 1981). FI trials are as described above. For example, a rat might receive food reward for the first lever press it emits 20 s after the onset of a tone. On PI trials, the tone is presented for three to four times the duration as on FI trials (e.g., 60 to 80 s) but no reinforcement is delivered. After extensive training on FI trials, the rate of responding on PI trials increases during the first part of the interval, peaks

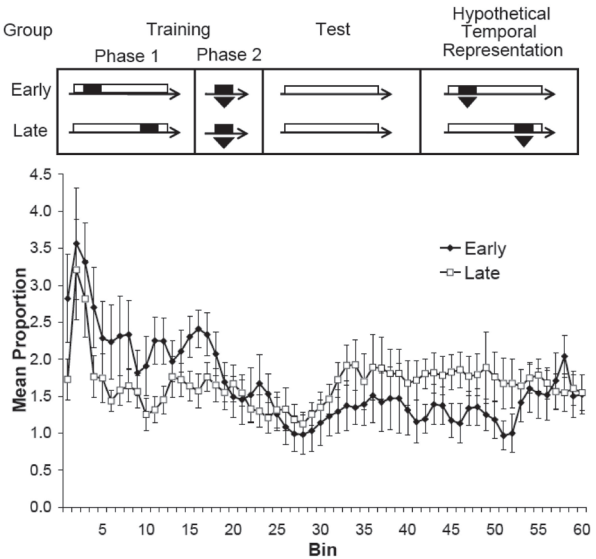

Figure 7. Design (top panel) and data (bottom panel) from Leising, Sawa, and Blaisdell (2007). Bottom panel shows mean proportion of nose pokes recorded in each 1-s bin on CS 2 test trials for Groups Early and Late.Reprinted with permission.

at around the interval reinforced on FI trials, and declines afterward. Figure 6 provides an example from a rat lever press experiment in our lab involving concurrent training on FI-12 and FI-36 s schedule of reinforcement. The location of peak response rate reflects the Stimulus-Reinforcement interval (i.e., temporal map) encoded by the subject.

3.2 Integration of Temporal Maps

There is evidence that time is encoded as an attribute of Pavlovian associations as well (Honig, 1981). The temporal coding hypothesis developed by Ralph Miller and colleagues describes the role time plays in associative learning experiments (Arcediano, Escobar, and Miller, 2003; Miller and Barnet, 1993; Savastano and Miller, 1998). The four tenets of the temporal coding hypothesis are that a) contiguity between events is sufficient for the formation of an association between those events, b) the temporal relationship (order and interval) between associated events is automatically encoded as an attribute of the association (i.e., subjects encode a temporal map), c) the temporal relationship plays a critical role in the nature, magnitude, and timing of the conditioned response, and d) separately acquired temporal maps can be superimposed when they contain common elements, thereby forming an integrated map. This integrated map can be used to compute temporal relationships between events that had never been physically paired. Temporal integration has been shown using a variety of Pavlovian tasks such as second-order conditioning and sensory preconditioning.

Our lab has recently demonstrated temporal integration in an appetitive sensory

preconditioning procedure with rats (Leising, Sawa, and Blaisdell, 2007). The design in Figure 7 (top panel) employed a modified operant Peak Interval procedure. During Phase 1 of sensory preconditioning, rats received a 60-s auditory CS2 in compound with a 10-s visual CS1. For the rats in Group Early, CS1 onset 5 s after the onset of CS2 and terminated 10 s thereafter (thus ending 45 s before CS2 did). For the rats in Group Late, CS1 onset 45 s after the onset of CS 2 and terminated 10 s thereafter (thus ending 5 s before CS2 did). In Phase 2, all subjects received simultaneous pairings between CS1 and food. If rats acquired the CS2-CS1 and CS1-US temporal maps, then they should be able to compute the CS2-US temporal relationship and thus should expect the US at a specific time relative to CS2 onset (see right side of top panel). The bottom panel of Figure 7 shows that on subsequent non-reinforced probe tests of CS2 the highest rate of responding occurred early in the test trial in Group Early and later in the test trial in Group Late. [Note, there was also an initial response peak in the early portions of CS2 in Group Late, but unpaired control groups also show these early peaks and are thus non-associative.] Most important, responding during the early portions of CS2 was higher in Group Early than in Group Late, while responding during the later portions of CS2 was higher in Group Late than in Group Early. This interaction between the CS2-CS1 training interval and response levels to CS2 at test provides strong evidence for temporal integration.

3.3 Temporal Maps in Conditioned Inhibition

Evidence for integration of temporal maps also comes from studies using the Pavlovian conditioned inhibition procedure. Pavlov (1927) discovered that a stimulus that predicts the explicit absence of an otherwise expected US acts to inhibit responses to other excitatory stimuli when presented in compound. The standard procedure Pavlov used to study conditioned inhibition intersperses A-US pairings with nonreinforced presentations of an AX compound. After extensive training, CS X acquires the ability to suppress responding to CS A. Furthermore, the inhibitory properties of X transfer to other excitors. The inhibitory properties of X also manifest themselves in retarded acquisition of excitatory responding to X if it is subsequently paired with the US. The inhibition to CS X mediated by the excitatory X-A and A-US associations is analogous to second-order conditioning, except that CS A negatively—rather than positively—mediates responding to CS X.

Temporal integration has been demonstrated in conditioned inhibition procedures with rats (Barnet and Miller, 1996; Burger, Denniston, and Miller, 2001; Denniston, Blaisdell, and Miller, 1998, 2004; Denniston, Cole, and Miller, 1998). For example, in one experiment (Denniston et al., 2004) rats received four types of trials interspersed in each session: serial delay pairings between training excitor A and a foothshock US (A➔US); serial delay pairings between transfer excitor C and the US (C➔US); simultaneous compound trials of excitor A and inhibitor X (AX); and serial compound trials of excitor A and inhibitor Y (Y➔A). After a month of training, rats received nonreinforced summation tests of each inhibitor (X and Y) with transfer excitor C. The temporal relationships between each inhibitor and C were manipulated on these probe tests, so that rats were tested either on a simultaneous compound (CX and CY) or a serial compound (X➔C and Y➔C). The left panel of Figure 8

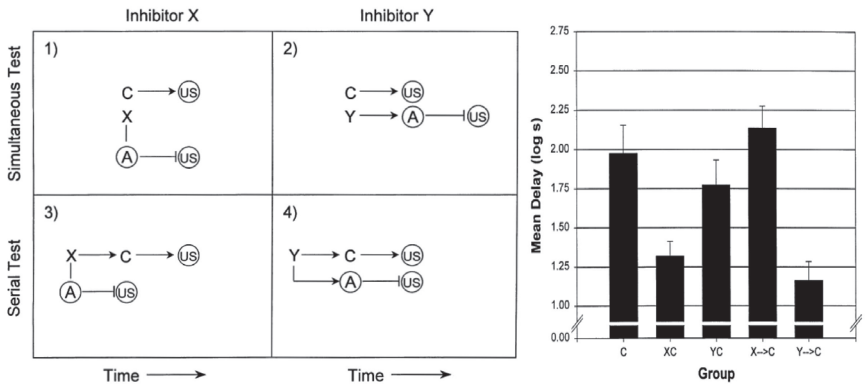

Figure 8. Left Panel: Hypothetical temporal relationships as a result of conditioned inhibition training and transfer excitor testing. Right panel: Mean times to complete 5 cumulative seconds of drinking in the presence of the test stimuli. From Experiment 1 of Denniston, Blaisdell, and Miller, 1998. Reprinted with permission.

depicts the hypothetical temporal relationships that should govern responding on each of these tests. The temporal coding hypothesis predicts maximal inhibition when the inhibitory CS predicts the omission of the US—represented in the figure by the inhibitory link between the inhibitor's training excitor A and the US—at the same time that the transfer excitor predicts the presentation of the US—represented by the excitatory arrow between transfer excitor C and the US. The right panel of Figure 8 shows that conditioned inhibition was maximal when the expectation of US omission evoked by the conditioned inhibitor was temporally aligned with the US expectation evoked by transfer excitor C, independent of whether the inhibitor was trained as a serial or simultaneous signal for US omission (higher scores indicate more conditioned suppression, low scores mean less conditioned suppression).

3.4 Cue Competition in Temporal Maps

As with the spatial domain, cue-competition effects have also been demonstrated in the temporal domain. Blaisdell, Denniston, and Miller (1998) have shown, for example, that overshadowing of X by **A** in a conditioned suppression procedure with rats is strongest (i.e., suppression to X is weakest) when X and **A** have the same temporal map with the US, while little overshadowing is seen when the X➔US and **A**➔US temporal maps differ. Figure 9 summarizes the results of three experiments in Blaisdell et al. (2008) in which the **A**➔US temporal interval was manipulated within each experiment and the X➔US temporal interval was manipulated across experiments. Little conditioned suppression to X (i.e., a strong overshadowing effect) was observed at test when **A** and X were both paired with a forward (Experiment 1), simultaneous (Experiment 2), or backward (Experiment 3) temporal relation to the US (see Barnet, Grahame, and Miller, 1993 for similar effects in a blocking design).

Data Table (adapted from Blaisdell, Denniston, & Miller, 1998)

A-US temporal relationship	X-US temporal relationship		
	Forward (Ex. 1)	Simultaneous (Ex. 2)	Backward (Ex. 3)
Forward	**0.92**	1.73	1.70
Simultaneous	1.59	**1.00**	1.70
Backward	1.70	1.52	**0.86**
Acquisition Control	1.64	1.71	2.15

Figure 9. Mean times (log s) to complete 5 cumulative seconds of drinking in the presence of overshadowed CS X at test. From Blaisdell, Denniston, and Miller, 1998.

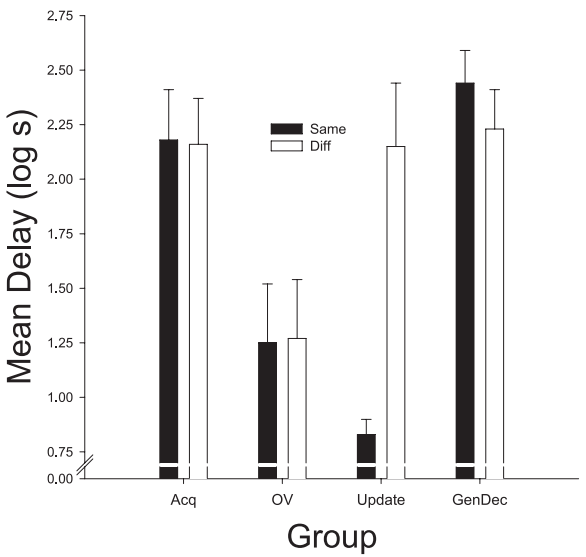

Figure 10. Mean times (log s) to complete 5 cumulative seconds of licking in the presence of CS X at test. Error bars represent standard errors of means. From Experiment 1 of Blaisdell, Denniston, and Miller, 1999. Blaisdell, Denniston, Miller, 1999. Posttraining shifts in the overshadowing stimulus-unconditioned stimulus interval alleviates the overshadowing deficit. *Journal of Experimental Psychology: Animal Behavior Processes* **25**, 18-27, APA, reprinted with permission.

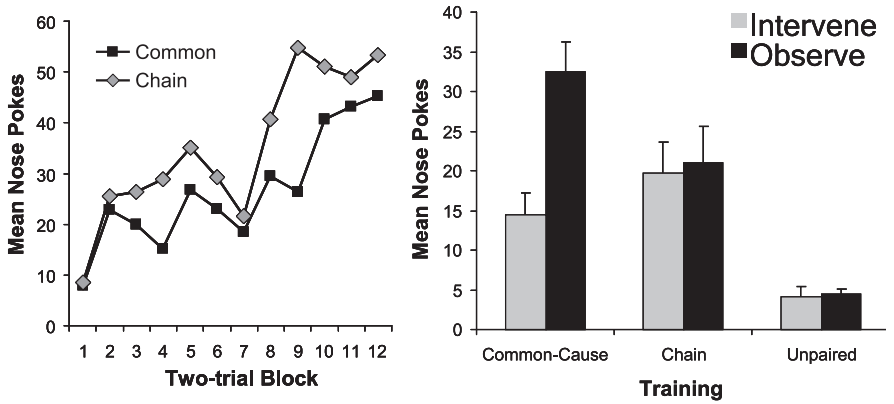

Figure 11. Left panel: Mean nose pokes during the Light during Phase 2 Light➔Food pairings. Right panel: Mean nose pokes during the Tone at test. Error bars denote standard errors of the means. From Experiment 2a of Blaisdell et al., 2006. (Adapted with permission of Science).

In a follow-up experiment, Blaisdell, Denniston, and Miller (1999) gave rats overshadowing treatment in which **A** and X both had the same temporal interval to the US. After overshadowing treatment was complete, some rats received further **A**-US pairings with either the same or different temporal relationship as during the overshadowing phase. As seen in Figure 10, updating the **A**➔US temporal map so that it was different from the X➔US temporal map abolished the overshadowing effect (and responding to X was equally strong as in the acquisition control groups). Updating the **A**➔US temporal map, but maintaining the same map as for X if anything made overshadowing of X stronger when compared to overshadowing groups that did not receive updating of the A➔US temporal map. Thus, the magnitude of overshadowing is determined by the similarity of the **A**➔US map to the X➔US map at the time of testing, not of training (see Blaisdell, Denniston, and Miller, 2001 for similar findings for the overexpectation effect, and Denniston, Blaisdell, and Miller, 2004 for similar findings in Pavlovian conditioned inhibition.)

4 Causal Cognition

There is growing evidence that both humans and animals engage in top-down causal cognitive processes that defy simple bottom-up, contingency based accounts of assessing cause-effect relations (Waldmann, Hagmayer, and Blaisdell, 2006). This evidence does not deny, however, that these top-down processes operate on a framework of knowledge previously acquired through bottom-up processes such as associative learning.

4.1 Acquisition and Integration of Causal Maps

Despite the explosion of research investigating the parallels between associative phenomena

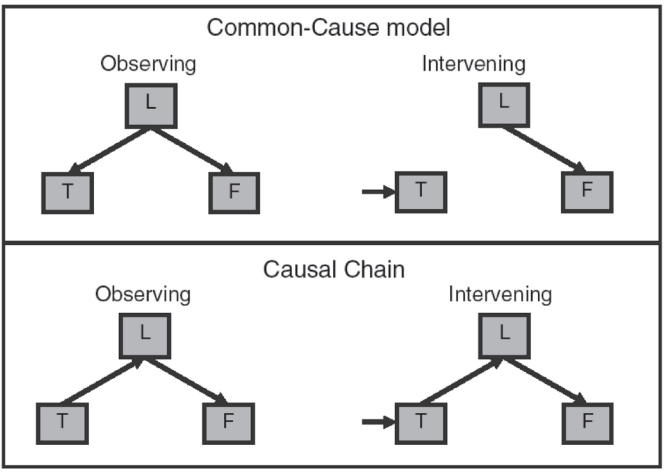

Figure 12. Causal models of the relationships among events in Experiment 2a of Blaisdell et al., 2006. (Adapted with permission of Science).

on the one hand and causal judgment and contingency assessment by humans on the other (see reviews by Allan, 1993; Dickinson, 2001; Young, 1995). One could actually take the opposite approach and look for evidence in animal conditioning experiments for the acquisition of causal maps from purely associative (i.e., contingency) input. It is difficult to ask a nonverbal subject directly whether or not they represent an association between two stimuli as causal or merely predictive. A procedure recently developed in our lab (Blaisdell, Sawa, Leising, and Waldmann, 2006) for studying causal inferences, however, can yield such an answer. Rats received sensory preconditioning treatment consisting of Light➔Tone (Group Common Cause) or Tone➔Light (Group Causal Chain) pairings in Phase 1 and Light➔Food pairings in Phase 2 (Blaisdell et al., 2006; Experiment 2a). Conditioned nose-poke responding to the Light during Phase 2 developed at the same rate in both groups (Figure 11, left panel). As we saw in Section 3.2, rats learn the temporal maps between paired events and integrate these maps into higher-order maps. Temporal priority is a potent cue to causality, with causes preceding their effects in time (Waldmann, 1996; Young, 1995). If an associative integration process builds causal maps as it builds spatial and temporal maps, then these sensory preconditioning treatments should have resulted in the causal maps depicted in Figure 12. Rats in Group Causal Chain should have formed a Tone➔Light➔Food causal chain representation (bottom panel, left side). Likewise, rats in Group Common Cause should have formed a Tone⬅Light➔Food common cause representation with Light as a common cause of both Tone and Food (top panel, left side). Given these causal maps causal model theory makes certain predictions (Waldmann, Cheng, Hagmayer, and Blaisdell, 2008; Waldmann, Hagmayer, and Blaisdell, 2006). Specifically, an intervention on the Tone should lead to an expectation of Food in Group Causal Chain, but not in Group Common Cause (right side of each panel).

To test these predictions, Blaisdell et al. (2006; see also Leising, Wong, Waldmann, and

Blaisdell, 2008) inserted a lever into the conditioning chamber during the test phase after Phase 2 training was complete. Half of the rats in each group received an Intervention test treatment for which each press of the lever resulted in a 10-s presentation of the Tone. The remaining rats in each group received an Observation test treatment for which a lever press had no consequence. Figure 11 (right panel) shows that for the Common-Cause group Tones contingent on a lever press (Intervene test condition) elicited much less nose poking compared to Tones noncontingent on lever presses (Observe test condition). No difference in nose poking was seen, however, between the same two test conditions for the Chain group. By supporting the predictions of causal model theory, these results provide evidence that the rats had represented the associative links as causal links. That is, sensory preconditioning treatment in the Common-Cause condition resulted in rats acquiring a causal map of Tone←Light→Food. A Tone produced by a lever press resulted in discounting of the Light→Tone causal relationship (Waldmann et al., 2008), and as a consequence discounting of other effects caused by the Light, such as Food. Sensory preconditioning treatment in the Causal-Chain condition, on the other hand, resulted in rats acquiring a causal map of Tone→Light→Food. For this causal map, it didn't matter whether or not the Tone was produced by a lever press intervention—all the effects of the Tone (i.e., Light and then Food) were expected to follow. These results show that associative relationships established in a conventional Pavlovian conditioning procedure supported the attribution of causal relationships. In the case of sensory preconditioning, this allowed the formation of integrated causal maps. Causal maps are therefore a direct analogy to the spatial and temporal maps discussed in the previous sections.

5 Summary

We have shown how spatial, temporal, and causal maps can be acquired during associative learning procedures such as Pavlovian and instrumental conditioning. Once established by associative processes these maps can be used to compute novel relationships among elements in the map that have not had prior directly-shared experiences. We showed this in simple conditioning, higher-order conditioning procedures such as sensory preconditioning and conditioned inhibition, and in associative cue competition. For example, after sensory preconditioning in which Event A is paired with Event B in Phase 1 and Event B is paired with Event C in Phase 2, a relationship between Events A and C can be computed. This computed A-C relationship allows for behavior indicative of spatial, temporal, and causal inferences. Although the associative integration hypothesis was derived from Ralph Miller's temporal coding hypothesis, it has been successfully extended to spatial and causal cognition. This suggests that associative processes of acquisition, integration, and expression may play an important role generally in cognitive processes, especially those yielding cognitive structures (i.e., representations). These cognitive structures could then be used in a flexible manner to make inferences about specific relationships between different parts of the representation. The power of such a model is that inferences could be derived for relationships between elements that had never physically occurred together. Put another way, this proc-

esses can serve as the means to go beyond the information given by direct experience. We hope this chapter provides a framework by which to open up new avenues in computational and neuroscientific exploration.

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