

Timing in simple conditioning and occasion setting: a neural network approach

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Abstract

We present a neural network model of Pavlovian conditioning in which a timing mechanism, by which a CS can predict when the US is presented, activates an architecture in which a stimulus acts as a simple CS and/or as an occasion setter. In the model, stimuli evoke multiple traces of different duration and amplitude, peaking at different times after CS presentation [Grossberg and Schmajuk, 1989. *Neural Netw.* 2, 79–102]. These traces compete to become associated directly and indirectly (through hidden units) with the US [Schmajuk and DiCarlo, 1992. *Psychol. Rev.* 99, 268–305]. The output of the system predicts the value, moment, and duration of presentation of reinforcement. Importantly, in contrast to the model by Schmajuk and DiCarlo [Schmajuk and DiCarlo, 1992. *Psychol. Rev.* 99, 268–305], in the present model a stimulus may assume different roles (simple CS, occasion setter, or both) at different time moments. Moreover, while in the Schmajuk and DiCarlo model [Schmajuk and DiCarlo, 1992. *Psychol. Rev.* 99, 268–305], competition between CSs is purely associative, in the present model competition between CSs is both associative and temporal. CSs compete to predict not only the presence and the intensity of the US, but also its temporal characteristics: time of presentation and duration. The model is able to address both the temporal and associative properties of simple conditioning, compound conditioning, and occasion setting. © 1999 Elsevier Science B.V. All rights reserved.

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1. The content of learning in Pavlovian conditioning

In simple Pavlovian conditioning, animals learn not only that the presentation of the conditioned stimulus (CS) precedes the unconditioned stimulus (US) but also the time at which the US follows

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the CS. For example, Smith (1968) reported that for different CS–US interstimulus intervals (ISI), the conditioned response (CR) shows a peak at the time of the US presentation and the duration of the CR increases with increasing ISIs. Similar results were reported in operant conditioning with fixed interval schedules in rats (Meck and Church, 1982, 1987) and pigeons (Roberts et al., 1989).

Temporal information also seems to play a role in paradigms involving multiple CSs, such as blocking. Reduced conditioning (blocking) is not simply observed when a new stimulus is reinforced in the presence of a good predictor of the US (Kamin, 1969), but only when the blocked stimulus, B, is paired in the same temporal relationship with the US as the blocking stimulus, A (Schreurs and Westbrook, 1982; Goddard and Jenkins, 1988; Barnet et al., 1993; Esmoriz-Arranz et al., 1997). In summary, in simple and compound Pavlovian conditioning, when a stimulus acts as a simple CS, the content of learning seems to be sensitive to both the presence of the US and the timing of the US presentation.

In the above-mentioned paradigms, stimuli are considered to act as simple CSs when they elicit CRs by signaling the occurrence of the US. Alternatively, a stimulus can play the role of an ‘occasion setter’ when it controls the responses generated by another CS by indicating the relation between that second CS and the US (Holland, 1983, 1992). When a stimulus acts as an occasion setter, the content of learning is sensitive to the timing of the target presentation. For example, in a feature-positive (FP) discrimination, animals have to respond when feature stimulus X is paired with target stimulus A, and to refrain from responding to the target stimulus A when presented alone. Holland (1992) demonstrated that the content of learning in this paradigm is different when feature X and target A are presented simultaneously ($XA + /A -$) or serially ($X \rightarrow A + /A -$). Moreover, recent data (Holland et al., 1997) show that training with a specific feature-target interval (FTI) in a serial FP discrimination ($X \rightarrow A + /A -$), results in better discrimination when the $X - A$ delay matches the training interval than at other shorter or longer $X - A$ intervals. Thus, temporal information

seems to be acquired not only in simple and compound conditioning, but also in occasion setting.

Although a number of hypotheses have been advanced to address the properties of conditioning in paradigms such as those described above, possibly due to the complexity of the phenomena, these hypotheses tend to separately address their temporal and associative aspects. Classical learning theories develop around notions like ‘associative strength’ and ‘surprise’, largely ignoring the timing of the CR. For example, in order to deal with blocking, Kamin (1969) proposed that the failure of B to be associated with the US is due to the US already being signaled by A, and thus being unsurprising. This (and other) phenomena prompted Rescorla and Wagner (1972) to propose that association is gained in proportion to the difference between the actual and the predicted value of the US. In their model, Rescorla and Wagner assume that the content of learning includes only predicted values of reinforcement. Therefore, although the Rescorla and Wagner (1972) model correctly describes many Pavlovian conditioning phenomena, it does not address their temporal properties.

Some associative and temporal characteristics of conditioning can be jointly described by associative models that depict conditioning in ‘real-time’. Such models (Moore and Stickney, 1980; Sutton and Barto, 1990; Schmajuk and Moore, 1988; Schmajuk and DiCarlo, 1992; Buhusi and Schmajuk, 1996) are able to capture temporal aspects of conditioning such as the effect of CS duration, US duration, and ISI interval. However, they do not speak to the temporal specificity of conditioning.

Among these ‘real-time’ models, Schmajuk and DiCarlo (1992) proposed an associative network that describes not only simple and compound conditioning, but also some of the associative and temporal properties of occasion setting (Schmajuk et al., 1998). In the model, each CS activates a single short-term memory trace which can become associated directly and indirectly (through hidden units) with the US. This feature enables the model to describe the distinction between simple conditioning and occasion setting: a CS acts as a simple

stimulus through its direct connections with the output units and as an occasion setter through its indirect configural connections through the hidden units. Although the model by Schmajuk and DiCarlo (1992) is able to describe some the effects of temporal parameters on occasion setting (Schmajuk et al., 1998), the model still cannot describe the timing of the CR.

On the other hand, a number of timing models have been proposed in classical (Grossberg and Schmajuk, 1989; Grossberg and Merrill, 1992; Moore and Choi, 1998) and operant conditioning (Gibbon, 1977; Killeen and Fetterman, 1988; Church and Broadbent 1990; Machado, 1997; Staddon and Higa, 1999). These theories concentrate on the idea that peak time CR and CR duration increase with increasing ISIs, and propose various timing mechanisms by which the temporal properties of these phenomena can be explained: a pacemaker/accumulator process (Gibbon, 1977; Meck and Church, 1987), a set of oscillators (Church and Broadbent, 1990), a sequence of behaviors (Killeen and Fetterman, 1988), or a set of memory traces (Grossberg and Schmajuk, 1989; Schmajuk, 1990; Machado, 1997; Staddon and Higa, 1999).

For example, the spectral timing model by Grossberg and Schmajuk (1989) assumes that a CS activates multiple memory traces. Those traces active at the time of the US presentation become associated with the US in proportion to their activity. The outputs generated by all traces are added in order to determine the magnitude of the CR. The CR shows a peak at the time when the traces that have been active simultaneously with the US are active again. Although the model is able to describe CR timing with single and multiple USs, and a Weber law for temporal generalization, the model cannot describe important associative phenomena such as compound conditioning and occasion setting.

Finally, a few models aim at describing both temporal and associative properties conditioning (Desmond and Moore, 1988; Grossberg and Merrill, 1992; Moore and Choi, 1998). Although the models by Desmond and Moore (1988), Grossberg and Merrill (1992), Moore and Choi (1998) address temporal specificity in simple and com-

pound conditioning, they do not describe the complex properties of occasion setting.

In order to describe temporal specificity in simple conditioning, compound conditioning, and occasion setting, we present a computational model of Pavlovian conditioning in which stimuli compete to predict the value, moment, and duration of presentation of reinforcement. The model incorporates three notions. Firstly, it is a real-time model, therefore being able to describe various temporal relations between stimuli, and between stimuli and the reinforcement. The real-time properties of the model follow the hypothesis proposed by Grossberg and Schmajuk (1989) which assumes that stimuli evoke multiple traces with different temporal properties. Secondly, we assume that these traces become associated directly and indirectly (through hidden units) with a representation of the reinforcement (Schmajuk and DiCarlo, 1992), thus allowing for the description of the difference between simple CSs and occasion setters. In contrast to Schmajuk and DiCarlo (1992), the present model assumes that a stimulus may adopt the roles of a simple CS and/or an occasion setter at different moments in time, thus providing support for the description of the temporal specificity of the action of a CS. Thirdly, while in the Schmajuk and DiCarlo (1992) model competition between CSs is purely associative (CSs compete to predict the presence and the value of the US), in the present model competition between CSs is both associative and temporal. CSs compete to predict the presence and the value of the US, as well as the moment and duration of US presentation. Thus, the model can address both the associative and temporal characteristics of the competition between CSs in conditioning paradigms such as blocking.

We demonstrate that the model is able to address temporal specificity and associative properties characterizing conditioning paradigms of different levels of complexity. We detail computer simulations of CR topography in simple conditioning (Smith, 1968), temporal competition between simple CSs in paradigms like blocking (Barnet et al., 1993), and temporal specificity of serial FP discriminations (Holland et al., 1997). The paper suggests that a necessary characteristic

of any putative timing mechanism is to co-operate (operate in conjunction) with associative mechanisms in order to describe both the temporal and associative properties of conditioning.

2. A brief description of the model

In order to describe temporal specificity in simple conditioning and occasion setting, we introduce a real-time neural network model of conditioning in which stimuli compete in predicting the value, time of presentation, and duration of the reinforcement. The model incorporates three notions, which refer to timing, associations, and stimulus competition.

The first notion is that, in line with the spectral timing hypothesis (Grossberg and Schmajuk, 1989), a stimulus CS_i evokes k multiple memory traces, denoted τ_{ik} . These traces have three (related) properties. They peak at different moments in time, have different peak amplitudes, and are active over different time intervals. Fast τ_{ik} traces peak closer to the onset of CS_i , have large amplitudes, and are active for a relatively short period of time. Slow τ_{ik} traces peak far away in time from the onset of CS_i , and are active for a relatively long period of time, but have smaller peak amplitudes than fast traces. The topography of the traces is a key issue in the model, in that it determines the moment of the peak, the amplitude and the duration of the CR.

The second notion refers to the type of associations that are assumed to be part of the content of learning. In a manner consistent with the model by Schmajuk and DiCarlo (1992), we assume that stimuli are associated directly and indirectly (through 'hidden' units) with a representation of the US. Each trace τ_{ik} is independently associated through direct connections V_{ik} with the US, and through indirect connections VH_{ikj} with hidden unit H_j . Thus, each trace is capable of separately exciting or inhibiting a representation of the US, and to excite or inhibit hidden units. On the other hand, each hidden unit H_j activates a trace τ_j which becomes associated with the US through connection VN_j . A CS acts as a simple CS through the direct connections of its traces with

the US, and as an occasion setter through the indirect connections of its traces with the US via the hidden units H_j .

However, while in the model by Schmajuk and DiCarlo (1992), a CS can adopt the role of a simple CS and/or an occasion setter, throughout the duration of the trial, in the present model, a CS can have different roles at different moments during the trial. The CS can act as a simple CS at one moment in time, and as an occasion setter at another moment in time, and as both at other time moments, by the activation of the different traces evoked by the stimulus. Therefore, in the present model an occasion setter is a stimulus that controls both the associative and temporal properties of the relation between another CS and the US.

The third notion is that the multiple traces of the CSs and of the hidden units compete to predict the value of the US. We assume that the prediction of the US is the sum of the direct and indirect associations (Schmajuk and DiCarlo, 1992). However, while in the model by Schmajuk and DiCarlo (1992), the competition between CSs is purely associative (CSs compete to predict the presence and the value of the US), in the present model the competition between CSs is both associative and temporal. CSs compete to predict not only the presence and intensity of the US, but also its duration and time of presentation.

Importantly in the model, timing is mapped onto trace-specific associations, i.e. the US is predicted at specific time moments after CS onset by the differential activation of specific CS–US and hidden-US associations. As mentioned, traces τ_{ik} are most active (peak) at different moments in time. Therefore, the fact that a specific trace τ_{ik} is associated with the US signifies that the US representation is more active (or inhibited) at a specific moment in time. Similarly, hidden units are more active (or inhibited) at a specific moment in time. The fact that hidden units are co-activated by the (multiple) traces of all the CSs present, allows them to be active (or inhibited) when specific temporal relations among CSs hold. In sum, the competition between traces for the prediction of the value of the US is also a temporal competition for the prediction of the time and duration of US presentation.

Fig. 1 summarizes the main features of the model. Each conditioned stimulus, CS_1 and CS_2 , activates k multiple memory traces, τ_{1k} and τ_{2k} . The context CX is assumed to activate constant traces τ_{CXk} . Note that CS_1 and CS_2 can be presented with different ISIs. Their traces are associated directly with a representation of the US through direct connections V_{1k} and V_{2k} (although not shown in the figure, the context CX can also activate the representation of the US.) Spectral traces τ_{1k} , τ_{2k} , and τ_{CXk} jointly activate the hidden units H_j through indirect connections VH_{1kj} , VH_{2kj} , and VH_{CXkj} . In order to illustrate the idea that hidden units are active when stimuli CS_1 and CS_2 are in a specific temporal relation, Fig. 1 depicts the hypothetical activation of the hidden units, τ_j . Each hidden unit H_j becomes associated with the representation of the US, through indirect connection VN_j . The US prediction is computed as the sum of US predictions based on direct connections, $\tau_{1k}V_{1k}$, $\tau_{2k}V_{2k}$ and indirect connections τ_jVN_j . As in the Rescorla–Wagner rule (Rescorla and Wagner, 1972), the difference between the actual and predicted value of the US is used to adapt direct connections V_{ik} . The same error is used in a variation of the back-propagation algorithm (Werbos, 1974; Rumelhart et al., 1986) introduced by Schmajuk and DiCarlo (1992) to train the hidden connections VH_{1kj} , VH_{2kj} , and VH_{CXkj} . The specifics of the model are

presented in Appendix A. Parameter values used in the simulations are shown in Appendix B.

In the following sections, we present computer simulations obtained with the model for different learning paradigms. We demonstrate that the model is able to address not only the associative but also the temporal properties of conditioning paradigms of different complexity. We present computer simulations of the CR topography in simple conditioning (Smith, 1968), the effect of changing the temporal CS–US interval between the phases of a blocking paradigm (Barnet et al., 1993), and the temporal specificity of the action of a CS acting as an occasion setter in a serial FP discrimination (Holland et al., 1997).

3. CR topography in simple conditioning

An important property of the CR topography in simple conditioning is that CR peak time and CR duration are proportional to the CS–US interval. Smith (1968) recorded the nictitating membrane response (NMR) in rabbits that received a 50-ms tone paired with a 50-ms periocular shock of intensity 1, 2, and 4 mA, with an ISI of 125, 250, 500, and 1000 ms. Smith (1968) found for different CS–US intervals, that the NMR is centered around the time of US presentation and CR duration increases for longer CS–US intervals.

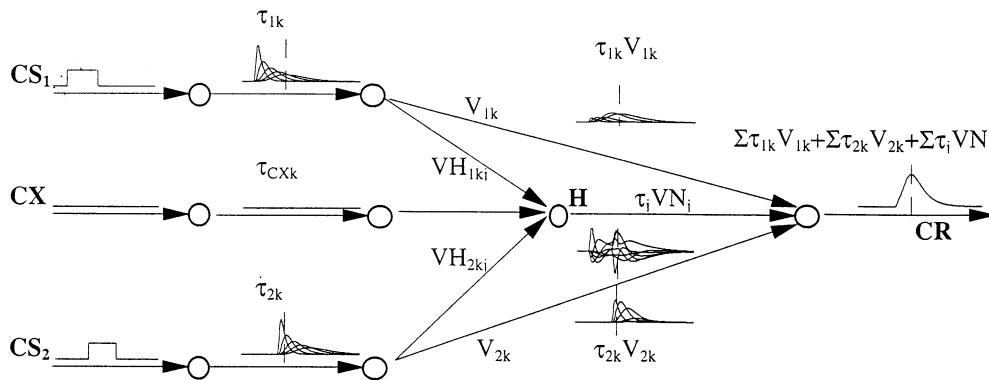


Fig. 1. The main features of the model. CS_1 , CS_2 : conditioned stimuli; CX : experimental context; τ_{1k} , τ_{2k} : spectral traces; VH_{1kj} , VH_{2kj} : direct CS–US connections; VH_{1kj} , VH_{2kj} : indirect CS–hidden unit H_j connections; VN_j : direct hidden unit H_j –US connections; τ_j : activation trace of the hidden unit H_j ; $\tau_{1k}V_{1k}$, $\tau_{2k}V_{2k}$: US predictions by direct traces; τ_jVN_j : US prediction by hidden units; CR : conditioned stimulus, proportional to the sum of US predictions based on direct and indirect connections.

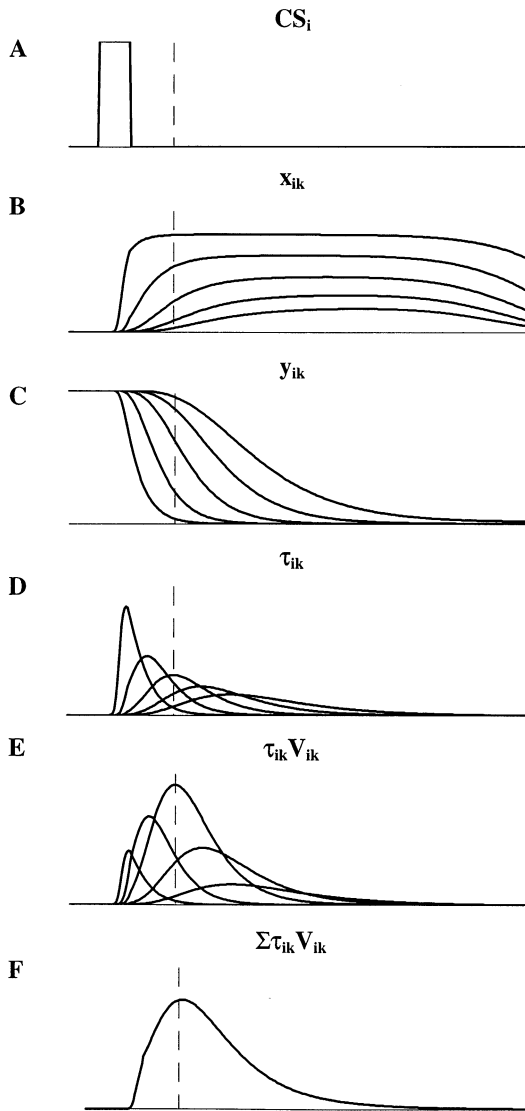


Fig. 2. Spectral traces and CR topography. Presentation of conditioned stimulus CS_i (panel A) determines two families of potentials, x_{ik} (panel B) and y_{ik} (panel C), which combine to form the memory traces τ_{ik} (panel D). Traces τ_{ik} that peak closer to the moment of US presentation (dotted line) are reinforced more (panel E). Therefore, traces that peak closer to the moment of US presentation dominate the prediction of the US, $\tau_{ik}V_{ik}$, and thus control the peak and the duration of the CR (panel F).

On the other hand, US intensity determines the strength of the response, but not its timing.

The present model is able to describe these phenomena due to the topography of the traces.

Fig. 2 illustrates the way traces contribute to the peak and duration of the CR. Each panel presents the value of a specific variable of the model during a test trial after simple conditioning. Panel A shows conditioned stimulus CS_i . The dotted line shows the moment of presentation of the US. Panels B and C show that stimulus CS_i activates potential x_{ik} , which in turn activates potential y_{ik} . When combined (panel D), x_{ik} and y_{ik} form the spectral traces, τ_{ik} (see Appendix A for details).

The topography of the traces determines the CR to peak at the moment of US presentation. Traces τ_{ik} peak at different moments in time. They increase their associations V_{ik} in proportion to their overlap (co-activation) with the US, and decrease (extinguish) their associations at moments when they are active in the absence of the US. Therefore, traces τ_{ik} that peak close to the moment of US presentation will be reinforced more (will gain a larger V_{ik}) than those that peak at other moments. Also, due to the associative competition, strong traces (of higher peak amplitude) will tend to overshadow the weak ones. The predictions of the US based on direct associations V_{ik} , $\tau_{ik}V_{ik}$, are presented in panel E of Fig. 2, which shows that the combination of predictions is governed by the traces whose peak time is close to the moment of US presentation. Therefore, the CR, which is proportional to the sum of the predictions $\sum_i \tau_{ik}V_{ik}$ (panel F), will peak at the moment of US presentation.

The topography of the traces also determines the duration of the CR to be proportional to the ISI (scalar timing). By Eq. (1) in Appendix A, spectral traces that peak further away in time vary more slowly in time and last longer (panel D). Since the CR peaks at the moment of US presentation, its duration will be proportional to the ISI (panel F). Should the ISI increase, correspondingly slower traces would be closer to the moment of US presentation, would be reinforced more, and the CR would be accordingly of increased duration.

The model correctly describes the CR topography when the ISI and US intensity are varied. The upper panels of Fig. 3 show the topography of the

nictitating membrane response (NMR) as reported by Smith (1968). The left upper panel shows that the CR peaks approximately at the moment of US presentation and that the duration of the response increases with the ISI. The upper right panel shows that an increase in US intensity does not greatly affect either the peak time or the duration of the CR. Lower panels present simulations with the model showing that the model correctly addresses the experimental data. The CR peaks approximately at the moment of US presentation (left lower panel), and an increase in US intensity (right lower panel) minimally affects the peak time and the duration of the CR.

These results demonstrate that spectral traces are able to correctly describe CR topography (Grossberg and Schmajuk, 1989; Grossberg and Merrill, 1992). Section 4 examines the competition between simple stimuli for the prediction of the value, moment, and duration of US presentation.

4. Temporal competition in simple conditioning

Barnet et al. (1993) examined the temporal specificity of blocking. In the first phase of the experiments, stimulus A was paired with the US (shock) simultaneously ($A +$, common onset and offset) or serially ($A \rightarrow +$, US onset at CS termi-

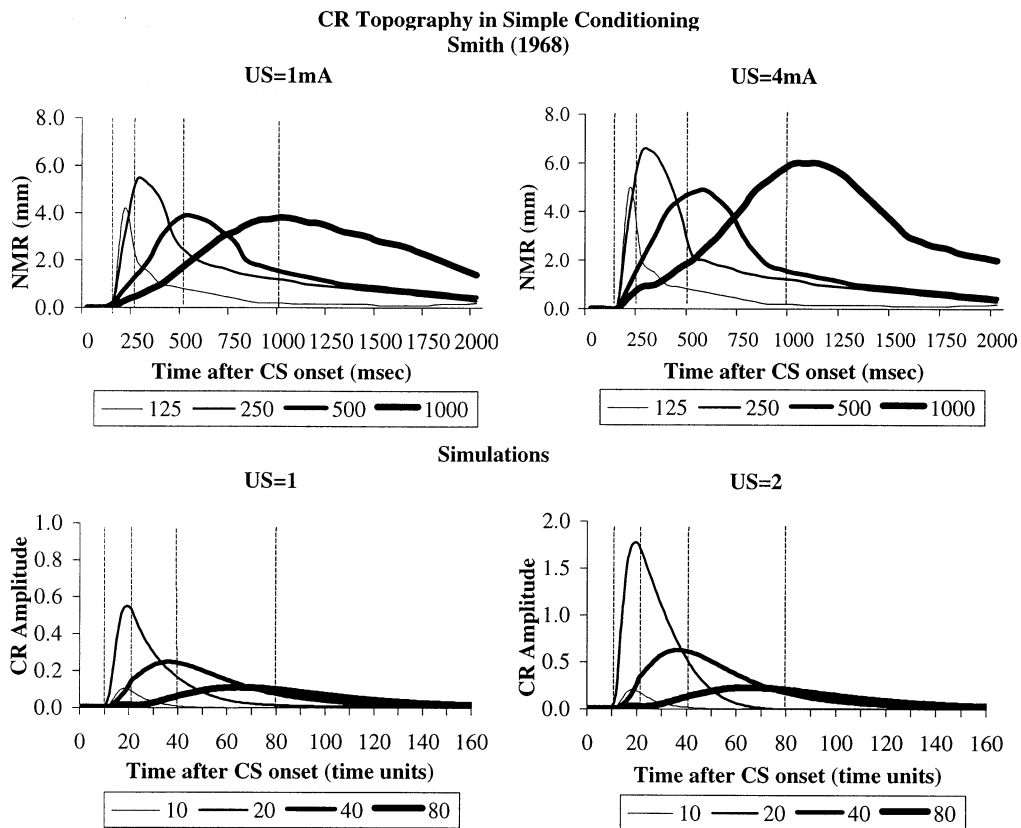


Fig. 3. CR topography in simple conditioning. Upper panels: Mean CR topography of the nictitating membrane response (NMR) after 10 conditioning days in which a 50 ms CS was paired with a periocular shock US, at four different CS–US intervals: 125 ms, 250, 500, and 1000 ms (Smith, 1968). Left upper panel: CR topography for 1 mA US shock (Smith, 1968). Right upper panel: CR topography for 4 mA US shock (Smith, 1968). Lower panels: Simulated CR amplitude after 50 CS–US pairings at four different CS–US intervals: 10, 20, 40, and 80 time units. Left lower panel: Simulated CR amplitude for US = 1. Right lower panel: Simulated CR amplitude for US = 2.

Table 1
Temporal specificity of blocking as examined by Barnet et al. (1993)^a

Group		Phase 1	Phase 2	Phase 3
F–F(f)	Experimental	A → +	AB → +	
	Control		AB → +	
S–F(f)	Experimental	A +	AB → +	
	Control		AB → +	
S–S(s)	Experimental	A +	AB +	C → B
	Control		AB +	C → B
F–S(s)	Experimental	A → +	AB +	C → B
	Control		AB +	C → B
S–F(s)	Experimental	A +	B → A +	
	Control		B → A +	
F–S(f)	Experimental	A → +	A → B +	C → B
	Control		A → B +	C → B

^a In the simulations presented in Figs. 4 and 5, we considered only the first two phases of the paradigm.

nation). In the second phase, stimuli A and B were paired with the shock, either simultaneously or serially. In the test phase, animals were required to complete 5 cumulative seconds of licking in the presence of the CSs. A high latency in the presence of the stimulus was taken as evidence for conditioning, while a reduced latency was taken as evidence for blocking.

Importantly, in their setting, Barnet et al. (1993) observed a significantly reduced conditioning for simultaneous pairing than for serial pairing. When B is reinforced in a simultaneous position, this phenomenon could partly obscure unblocking of B. Therefore, Barnet et al. (1993) further subjected animals for which B was reinforced in the second phase in simultaneous position to second-order conditioning to B. In a third phase of the paradigm, a new stimulus, C, was paired serially with the blocked stimulus B (C → B). A high latency in the presence of the stimulus C was taken as evidence for conditioning to B, while a reduced latency was taken as evidence for B blocking.

Table 1 shows details of the experimental procedures used by Barnet et al. (1993). Following Barnet's notations (Barnet et al., 1993), we use the letters 'S' or 's' for simultaneous CS–US pairings, CS +, and the letters 'F' or 'f' for serial ('for-

ward') CS–US pairings, CS → +. The first letter of the name of the group refers to the A–US interval in phase 1, the second refers to the B–US interval in phase 2, while the third refers to the A–US interval in phase 2. Each group consists of experimental animals that receive all phases, and control animals that do not receive phase 1 of the paradigm. For example, in group S–F(f), while experimental animals receive simultaneous A + pairings in phase 1, and serial AB → + pairings in phase 2, control animals receive only serial AB → + pairings (phase 2).

In our simulations, we assume that latency is proportional to CR. The larger the CR, the longer it takes to complete the required licking period (see Appendix B for details). Since in the model the difference in conditioning between simultaneous and serial pairing is not extremely large, and since the model does not address second-order conditioning, simulations comprise only the first two phases of the Barnet et al. (1993) experiments.

In summary, in the test phase animals were required to complete 5 cumulative seconds of licking in the presence of the blocking stimulus A, the blocked stimulus B, or the second-order CS, C. Barnet et al. (1993) reported a reduced latency (blocking) in the presence of stimuli B or C in the groups that receive A training in phase 1 in the same temporal relation to the US as B in the second phase. In the following subsections we demonstrate that the model correctly accounts for these results.

4.1. Competition to predict the moment of US presentation

Part of the temporal specificity of blocking can be accounted for by assuming that the 'surprise' that drives learning (Kamin, 1969) includes a temporal component (Schreurs and Westbrook, 1982; Goddard and Jenkins, 1988). According to this account—that we refer to as 'temporal surprise'—in the first phase of the blocking experiment, animals learn not only that A predicts the US, but also the moment of US presentation. In the second phase of the paradigm, when stimuli A and B are paired with the US, B is blocked if the

moment of US presentation is rendered unsurprising by presenting the US in the same temporal relation with A as in the first phase. In line with this idea Barnet et al. showed that when the temporal A–US interval in both phase 1 and 2 is the same, latency to respond in the presence of

stimuli B or C is reduced (blocking) (Barnet et al., 1993, Experiments 1 and 3). On the other hand, a change in the temporal A–US interval from phase 1 to phase 2, renders the US unpredicted in time and unblocks B (increased latency to respond in the presence of stimuli B or C).

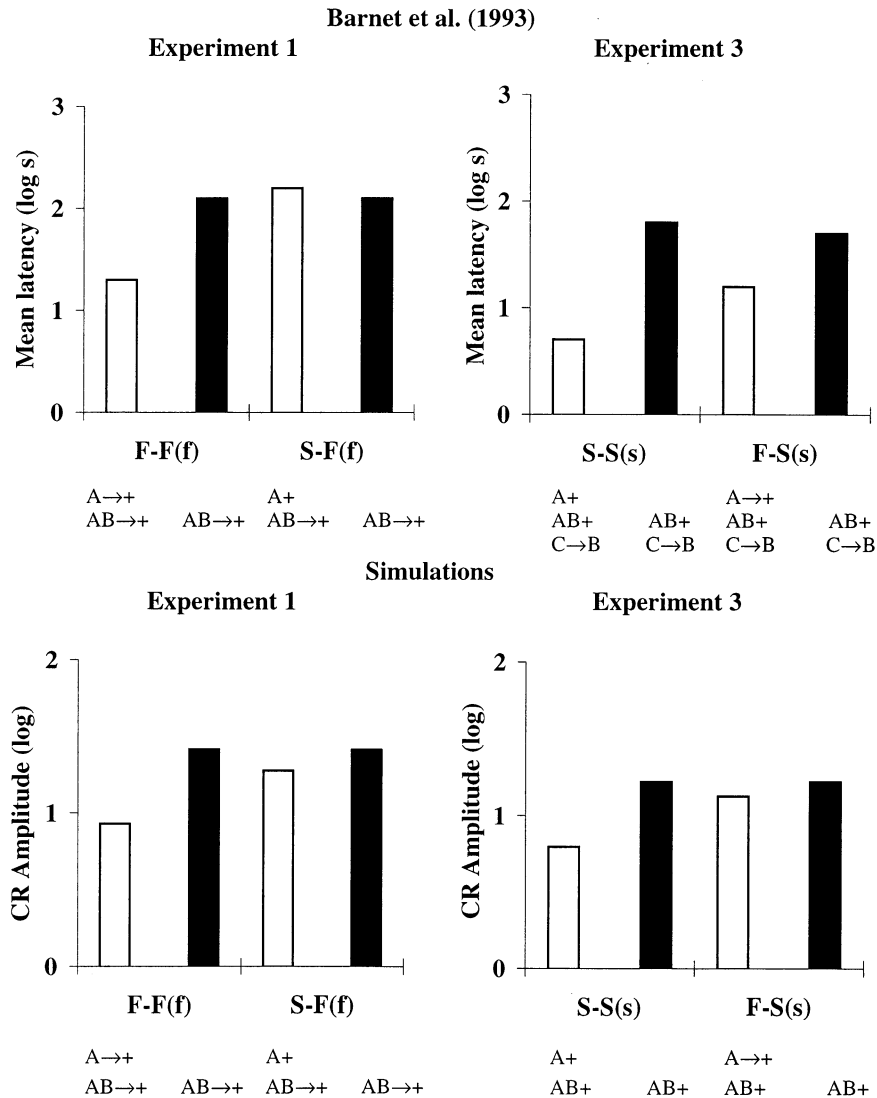


Fig. 4. Temporal specificity of blocking. Upper panels: Mean latency to complete 5 consecutive seconds of licking (in log scale). Open bars: experimental; closed bars: controls. Left upper panel: Latency in the presence of the blocked stimulus B in groups F–F(f) and S–F(f) (Barnet et al., 1993, Experiment 1). Right upper panel: Latency in the presence of a second-order CS paired with the blocked stimulus B in groups S–S(s) and F–S(s) (Barnet et al., 1993, Experiment 3). Lower panels: Simulated conditioned response amplitude (in log scale) after 100 trials of phase 1 and 100 trials of phase 2 of the blocking paradigm (Table 1). Open bars: experimental; closed bars: controls. Left lower panel: Simulated CR to the blocked stimulus B in groups F–F(f), S–F(f). Right lower panel: Simulated CR to the blocked stimulus B in groups S–S(s) and F–S(s).

As shown in the upper panels of Fig. 4, blocking (reduced latency) is present in experimental animals (open bars) relative to controls (closed bars) in groups F–F(f) and S–S(s), in which the temporal A–US interval in phases 1 and 2 is the same, but not in groups S–F(f) and F–S(s), in which the temporal A–US interval is changed from phase 1 to phase 2.

The lower panels of Fig. 4 show the simulated conditioned response amplitude to the blocked stimulus B for experiments 1 and 3 from Barnett et al. (1993). Details of simulations are given in Appendix B. As shown in the lower panels of Fig. 4, in general agreement with the results of Barnett et al. (1993), blocking is present in simulated experimental animals (open bars) relative to controls (closed bars) in F–F(f) and S–S(s) groups, but not in S–F(f) and F–S(s) groups.

In the model, stimuli compete to predict the moment of US presentation. Thus, blocking is observed in experimental animals (open bars) of both groups F–F(f) and S–S(s) relative to controls (closed bars) because in the second phase A is a good predictor of the moment of US presentation. Since the value and moment of US presentation do not change from phase 1 and 2, when A and B are paired with the US, the reinforcement is ‘unsurprising’, the error in prediction is small, and B gains little associative strength, as shown in the lower panels of Fig. 4.

However, a change in A–US interval from phase 1 to phase 2 renders the US ‘temporally’ surprising and unblocks B. When A predicts the reinforcement at a specific moment but animals receive the reinforcement at a different moment, two types of surprise (error) occur. At the moment predicted by A, the US is expected but is not delivered, and the error in prediction is negative. Therefore, the A traces that predict the US will extinguish. By contrast, at the moment when the US is presented in the second phase, the US is unexpected, the error in prediction is positive, and both A and B traces that are most active at that moment will gain associative strength. In sum, blocking is absent in the experimental animals (open bars) of both groups S–F(f) and F–S(s), relative to their controls (closed bars) because in the second phase A is a good predictor of the

presence of the US, but a rather imprecise predictor of the moment the US will be delivered.

4.2. *Competition to predict the intensity and the duration of the US*

Although the ‘temporal surprise’ notion is able to account for the unblocking of B when the A–US interval is different in the two phases of the paradigm, this concept can not explain the unblocking of B in groups S–F(s) and F–S(f), as reported by Barnett et al. (1993, Experiments 2 and 4). In these groups, latency to respond to stimuli B or C is increased although the A–US interval is the same in the two phases of the blocking paradigm, and thus A is presumably a good predictor of the presence and timing of the US.

4.2.1. *Competition to predict the intensity of the US*

In the S–F(s) experimental group, animals receive simultaneous A–US pairings, A + , in phase 1 and 2, but B is paired serially with the US, B → + , in phase 2. The ‘temporal surprise’ notion implies that B would be blocked, because the presence and timing of the US are predicted by A. However, the left panel of Fig. 5 shows that blocking is absent in experimental animals (open bars) relative to controls (closed bars) in group S–F(s). According to Barnett et al. (1993), these results suggest that animals associate a specific time-to-US-presentation with each CS. Only if this interval is the same for A in phase 1 and for B in phase 2, B-to-US timing is superfluous, and blocking occurs. As an alternative, here we demonstrate that the result can also be explained if one assumes that each CS evokes spectral traces, which compete not only to predict the time of US presentation, but also to predict the US value.

In the model, the form of the traces imply that in the associative competition between traces, serial conditioning is favored over simultaneous conditioning (Fig. 3). During phase 1, the simulated experimental S–F(s) animals (open bars) receive simultaneous A + pairings, so that the spectral traces of stimulus A gain V_{Ak} associative

($C \rightarrow B$), thus allowing C to reveal the associative strength acquired by B . A reduced latency to respond to C shows that B was blocked, while an increased latency shows that B acquired associative strength (unblocked). The left panel of Fig. 5 shows latency to respond to C . The results suggest that B blocking is absent in experimental animals (open bars) relative to control animals (closed bars) in group $F-S(f)$ (Barnet et al., 1993, Experiment 4).

In the model, traces that match the ISI better are promoted over faster or slower traces. A trace gains associative strength when the trace is active in the presence of the US (overlaps with the US), and loses associative strength when the trace is activated in the absence of the US. Slow traces are long in duration, and hence less precise in predicting the moment and the duration of the US. They are co-active with the US for a longer duration, but also lose more association when they are active in the absence of the US. Fast traces overlap less with the US, but are also less active in the absence of the US. Therefore, fast traces, although short in duration, when simultaneously paired with the US (short ISI), predict the moment and duration of US presentation better than slow traces. In this case, their balance is better: they gain little associative strength, but lose less.

In summary, when competing to predict the US in simultaneous position, fast traces, which predict the duration and the moment of the US presentation more accurately, are favored over slow traces. During phase 1, the experimental $F-S(f)$ animals (open bars) receive serial $A \rightarrow +$ pairings, so that the slow spectral traces of stimulus A gain V_{Ak} associative strength to predict the reinforcement at A offset. However, as explained above, fast B traces are favored against slow A traces, because they predict more accurately the moment and the duration of US presentation. The right panel of Fig. 5 shows that in general agreement with the results of Barnet (Barnet et al. 1993, Experiment 4) results, little (if any) blocking is observed in the $F-S(f)$ experimental group, relative to its controls. Details of the simulations are given in Appendix B.

4.3. Summary of blocking simulations

In a blocking paradigm, A and B traces compete to accurately predict the value, time, and duration of the US presentation. Blocking is observed only if the $A-US$ interval in phase 1 matches the $B-US$ interval in phase 2, because the US is already accurately predicted both in value, time, and duration. By contrast, if the $A-US$ interval is changed between the two phases of the experiment, the error in predicting the moment of reinforcement renders B unblocked (Barnet et al., 1993, Experiments 1 and 3).

In the model, traces that better match the ISI are promoted over faster or slower traces. For example, even if the $A-US$ interval does not change (i.e. the moment of US presentation is correctly predicted by A), if B is able to predict the time and duration of US presentation more accurately than A , B is unblocked (Barnet et al., 1993, Experiment 4).

Interestingly, in the Barnet et al. (1993) setting, and in the model, the scalar property is counter-balanced by an asymmetry between serial and simultaneous CS-US pairing in gaining associative strength. Simultaneous $A +$ pairings are not capable of completely blocking serial $B \rightarrow +$ pairings even if the US is predicted more accurately after simultaneous pairings (Barnet et al., 1993, Experiment 2), and this effect reflects the competition between traces to better predict the intensity of the US.

The simulations presented above demonstrate that competition between traces is a viable mechanism for explaining temporal specificity in a class of paradigms in which stimuli act as simple CSs. In the next section we explore the temporal properties of a class of paradigms in which stimuli act as occasion setters.

5. Temporal specificity of the action of an occasion setter

Recently, Holland et al. (1997) investigated temporal specificity in a serial FP discrimination ($X \rightarrow A + / A -$), a paradigm in which feature X acts as an occasion setter, and showed that tem-

poral information not only determines the type of solution but is also part of the content of learning. Here we show that by allowing the CSs to evoke multiple spectral traces, an associative structure in which stimuli may act as simple CSs or as occasion setters (Schmajuk and DiCarlo, 1992) is able to correctly address the temporal and associative characteristics of serial FP discriminations.

More importantly, because in the model by Schmajuk and DiCarlo (1992), a CS evokes a single trace, it can adopt the role of a simple CS and/or an occasion setter throughout the duration of the trial. If in a serial FP discrimination feature X were an occasion setter throughout the $X \rightarrow A +$ trial (as in the model by Schmajuk and DiCarlo, 1992), the solution would lack temporal specificity. In contrast, since in the present model a CS evokes multiple traces, it can have different roles at different moments in time by the differential activation of its traces. While one of its traces might behave as a simple CS (through a direct trace-US association), another trace can assume the role of an occasion setter (through indirect trace-hidden unit associations). By allowing a CS to have different roles at different moments in time, the present model is able to address the temporal specificity of occasion setting. Therefore, the present model extends the notion of occasion setter to describe a stimulus that controls both the temporal and associative relations between another CS and the US.

5.1. Temporal specificity of an occasion setter

Holland et al. (1997) trained rats to chain pull in order to receive a food reward, and placed chain pulling under the control of to-be-target CSs. Afterwards, two groups of rats were trained in two serial FP discriminations with 5- or 25-s $X-A$ FTI. After training, the rats were tested at different FTIs. Both groups were tested at short FTIs ranging from 0 to 30 s (Test 2). The 25 s group was also tested at long FTIs ranging from 25 to 55 s (Test 3). A short latency to pull was taken as evidence of conditioning.

The experimental results of Holland et al. (1997) are shown in the left panel of Fig. 6, which

depicts the difference in latency to chain pull to A alone or $X \rightarrow A$ for different FTI ($X-A$). Three points should be noted. Firstly, when tested at both short (Test 2) and long (Test 3) FTIs, both groups seem to discriminate better when tested at FTIs similar to that used in training than at shorter or longer FTIs. Secondly, discrimination in the 5 s $X-A$ group is sharper than in the 25 s $X-A$ group, which suggests that the temporal specificity of serial FP discriminations follows a scalar property (a shallower temporal gradient for longer FTIs). Thirdly, better discrimination (larger peak) is observed in the 5 s $X-A$ group than in the 25 s $X-A$ group, although the 25 s $X-A$ group received more training (40 training sessions) than the 5 s group (only 15 training sessions). In sum, the above observations favor the suggestion (Holland et al., 1997) that the content of learning includes the $X-A$ temporal interval, and that the data is consistent with scalar timing.

The right panel of Fig. 6 presents simulation results from Holland et al. (1997). The model was trained (separately) in two serial FP discriminations ($X \rightarrow A + / A -$) with 15 or 75 time unit FTIs. After the training stage, the model was tested for different FTIs. Latency to respond was assumed to decrease linearly with the CR. Therefore, difference in latency is proportional to difference in CR amplitude (Appendix B).

The right panel of Fig. 6 demonstrates that in the model, serial FP discrimination qualitatively follows the properties reported by Holland et al. (1997). Firstly, the difference in the simulated conditioned response to the presentation of $X-A$ and A alone is larger at the training FTI than at other shorter or longer intervals. Secondly, the difference in CR shows the scalar property, i.e. its duration is proportional with the FTI. Finally, the 25 s $X-A$ group shows less discrimination after 800 alternated $X \rightarrow A + / A -$ trials, than the 5 s $X-A$ group after only 300 alternated $X \rightarrow A + / A -$ trials.

Although simulations generally agree with data, differences do exist. For example, discrimination gradient in the 25 s group is more shallow in the data (left panel) than in the simulations (right panel). The difference in latency is relatively large

in the 25 s group animals tested with 5 and 10 s FTIs, but the difference in CR is null in the model for these intervals. Possible explanations for this discrepancy are worth discussing.

Firstly, in the present model a CS can have different roles (simple CS and/or occasion setter) at different moments in time. For example, in a serial FP discrimination with a long FTI, slow X traces are occasion setters (act through hidden units) and fast X traces become direct inhibitors of the US, and sharpen the discrimination gradient in the 25 s group. If feature X were an occasion setter throughout the $X \rightarrow A +$ trial, the solution would lack temporal specificity and the discrimination gradient would be shallower.

Secondly, the simulated gradient depends on the assumed relation between the CR magnitude and latency to respond. In the present simulations, we simply assumed that latency responds by decreasing linearly with the CR. Therefore, a difference in latency is assumed proportional to a difference in CR magnitude (see Appendix B).

Thirdly, in the model the shape of the gradient varies with the number of training trials and the number of traces evoked by a stimulus. By increasing the number of training trials, the discrimination increases along with the temporal specificity. In our simulations, we used a number of training trials proportional to the number of experimental training sessions. Also, by increasing the number of traces evoked by one stimulus, the discrimination gradient becomes more symmetrical. However, an increase in the number of traces evoked by one stimulus would also increase the computational complexity of the model. Therefore, in the present simulation, we used a relatively low number of traces, $k = 5$.

Fourthly, although the model describes classical conditioning, we applied it to the description of operant conditioning, given that in operant conditioning discriminative stimuli become classically conditioned to the US (Mackintosh, 1983). Therefore, the discrepancy between data and simula-

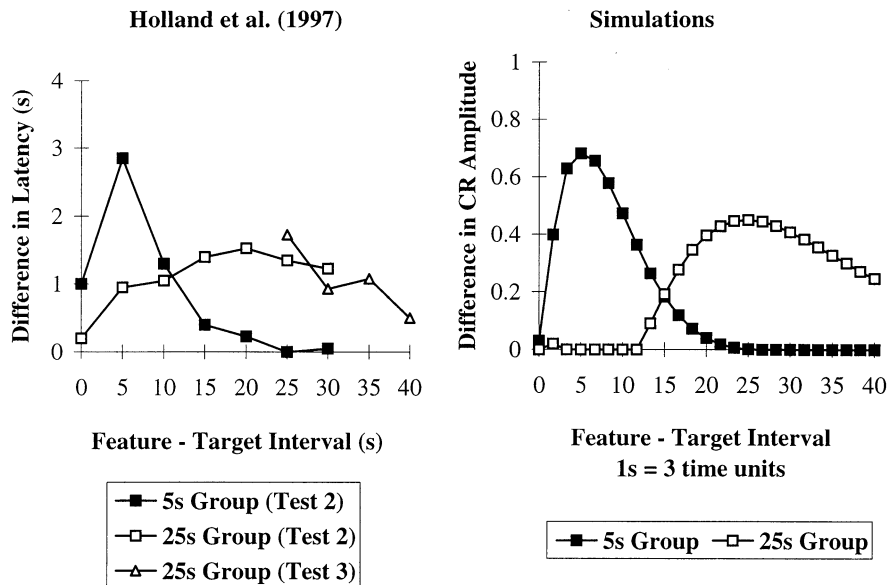


Fig. 6. Temporal specificity of serial FP discrimination. Left panel: Difference in latency to chain pull in the presence of A alone or $X \rightarrow A$ for different FTI ($X \rightarrow A$) (Holland et al., 1997), in two groups of animals that were trained for serial FP discriminations with 5 s FTI (5 s Group), or 25 s FTI (25 s Group) (see text). Right panel: Difference in simulated conditioned response to the presentation of $X \rightarrow A$, or A alone, for different FTI ($X \rightarrow A$), after 300 alternated $X \rightarrow A + /A -$ trials with 15 time-units $X \rightarrow A$ interval (5 s group), or 800 alternated $X \rightarrow A + /A -$ trials with 75 time-units FTI (25 s group). Latency to respond is assumed to decrease linearly with the CR: $\text{Latency} = 1 - \text{CR}$. Therefore, difference in latency $\text{Latency}_A - \text{Latency}_{X \rightarrow A} = (1 - \text{CR}_A) - (1 - \text{CR}_{X \rightarrow A}) = \text{CR}_{X \rightarrow A} - \text{CR}_A$.

tions might be due to the differences between the experimental (operant) procedure and the simulated (classical) one. Indeed, a much steeper gradient was recently reported by Holland (1998) by using a classical conditioning procedure. While temporal specificity of occasion setting seems to be procedure-independent, the discrimination gradient might be procedure-dependent.

In summary, the model qualitatively describes the temporal specificity of serial FP discrimination. Importantly, besides describing its temporal characteristics, the model is also able to describe the type of associations learned by animals.

5.2. The feature controls both temporal and associative mechanisms

Figs. 7 and 8 show that at both short and long FTIs, the feature controls both the temporal and associative properties of the solution learned by the animals. Fig. 7 shows that for short FTIs the discrimination is solved mainly through direct X–US, and indirect H–US connections. Indeed, the prediction of the US by the target, $B_{A,US}$ is very small. When presented alone (right panels), the small prediction of the US by the target, $B_{A,US}$ is cancelled by a small negative prediction of the US by the hidden units, $B_{H,US}$, so that A alone does not evoke any response. By contrast, on $X \rightarrow A$ presentation (left panels) the US is predicted by the feature and by the hidden units, so that the sum of these predictions (CR) is positive. Importantly, since feature directly controls the temporal and associative properties of the solution (the CS acts as a simple CS), these properties do not survive after feature extinction (see Section 5.3).

Fig. 8 shows that at long FTIs the feature indirectly controls (through hidden units) both the temporal and associative properties of the solution learned by the animals. Fig. 8 shows that in this case the discrimination is solved mainly through direct target A–US, and indirect H–US, connections controlled by the feature. Indeed, both panels show that the prediction of the US by the feature, $B_{X,US}$, is very small. When the target is presented alone (right panels), the large prediction of the US by the target, $B_{A,US}$ is cancelled by

a large negative prediction of the US by the hidden units, $B_{H,US}$, so that A alone evokes a response small in amplitude and duration. By contrast, on $X \rightarrow A$ presentations (left panels of Fig. 8) the US is predicted mainly by the target and by the hidden units (controlled by X) so that the sum of these predictions (CR) is positive and large, both in amplitude and duration.

It is important to note the control of the discrimination by the feature through hidden units. The US prediction by hidden units changes sign (at the moment of US presentation marked by the dotted line) from positive ($X \rightarrow A$, left panels) to negative (A alone, right panels). As will be shown in the next section, since the feature controls (through hidden units) the temporal and associative properties of the solution indirectly (the CS acts as an occasion setter), these properties survive after feature extinction.

5.3. Temporal specificity of serial FP discrimination after feature extinction

Whereas feature X extinction eliminates a simultaneous FP discrimination in which X acts as a simple CS, it does not affect a serial FP discrimination in which X acts as an occasion setter (Holland, 1992). Therefore, in order to further characterize the solution found by the animals (simple conditioning or occasion setting), Holland et al. (1997) tested the two groups of animals after feature cue was extinguished and also examined the effect of feature extinction on the temporal specificity of serial FP discrimination.

Fig. 9 shows that after feature extinction, discrimination decreases dramatically in the 5 s X–A group but not in the 25 s X–A group, suggesting that in the two cases animals use different solutions to solve the discrimination (Holland et al., 1997). The upper panels of Fig. 9 show the results of the test before (left upper panel) and after (right upper panel) feature extinction (Holland et al., 1997), in two groups of animals trained with 5 and 25 s X–A intervals. The bars represent difference in latency to chain pull in the presence of $X \rightarrow A$ or A alone. The left upper panel of Fig. 9 shows that animals discriminate better at the

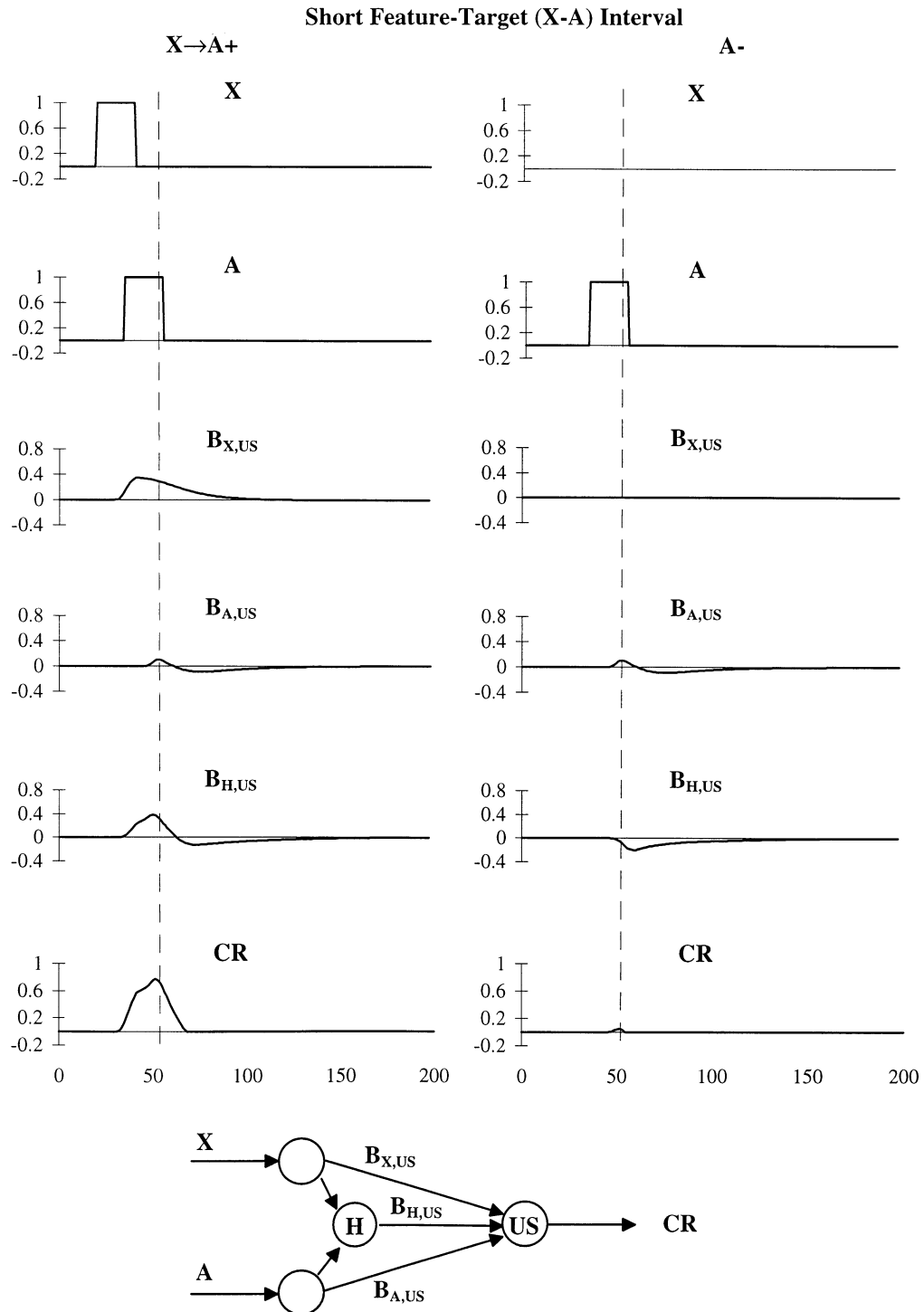


Fig. 7. Feature directly controls the temporal and associative mechanisms of a serial FP discrimination with short FTI. Two test trials after 300 alternated $X \rightarrow A + / A -$ trials with a 15 time unit FTI. Left panels: Temporal map of the activation of the model during the first 200 time units of an $X \rightarrow A$ test trial. Right panels: Temporal map of the activation of the model during the first 200 time units of an A test trial. Bottom Panel: A schematic of the associations involved in solving the discrimination. X : feature; A : target; $B_{X,US}$: US prediction by feature X ; $B_{A,US}$: US prediction by target A ; $B_{H,US}$: US prediction by hidden units; CR : conditioned response. The dotted line: moment of US presentation during training.

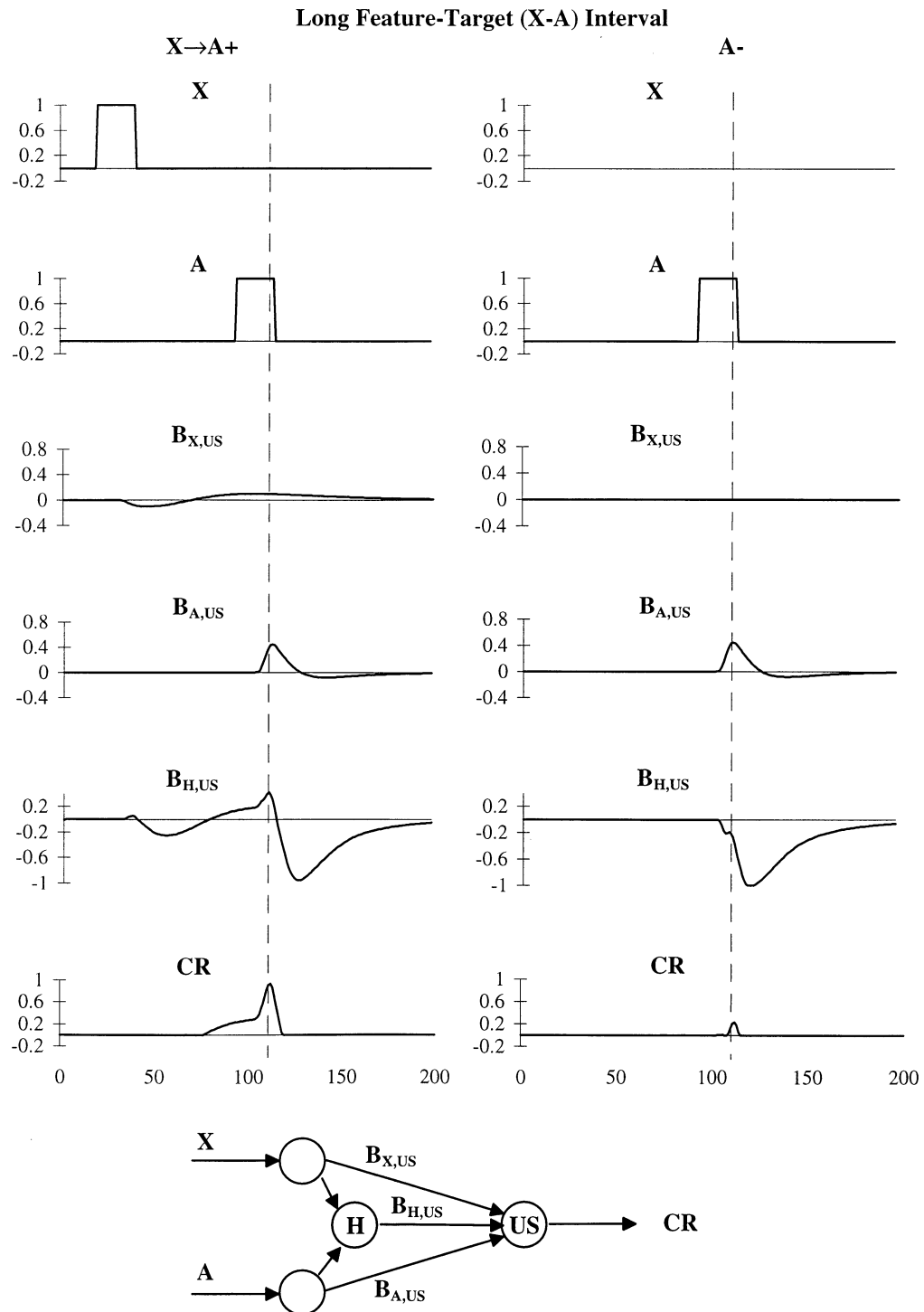


Fig. 8. Feature indirectly (through hidden units) controls the temporal and associative mechanisms of a serial FP discrimination with long FTI. Two test trials after 800 alternated $X \rightarrow A + / A -$ trials with a 75 time unit FTI. Left panels: Temporal map of the activation of the model during the first 200 time units of an $X \rightarrow A +$ test trial. Right panels: Temporal map of the activation of the model during the first 200 time units of an $A -$ test trial. Bottom Panel: A schematic of the associations involved in solving the discrimination. X: feature; A: target; $B_{X,US}$: US prediction by feature X; $B_{A,US}$: US prediction by target A; $B_{H,US}$: US prediction by hidden units; CR: conditioned response. The dotted line: moment of US presentation during training.

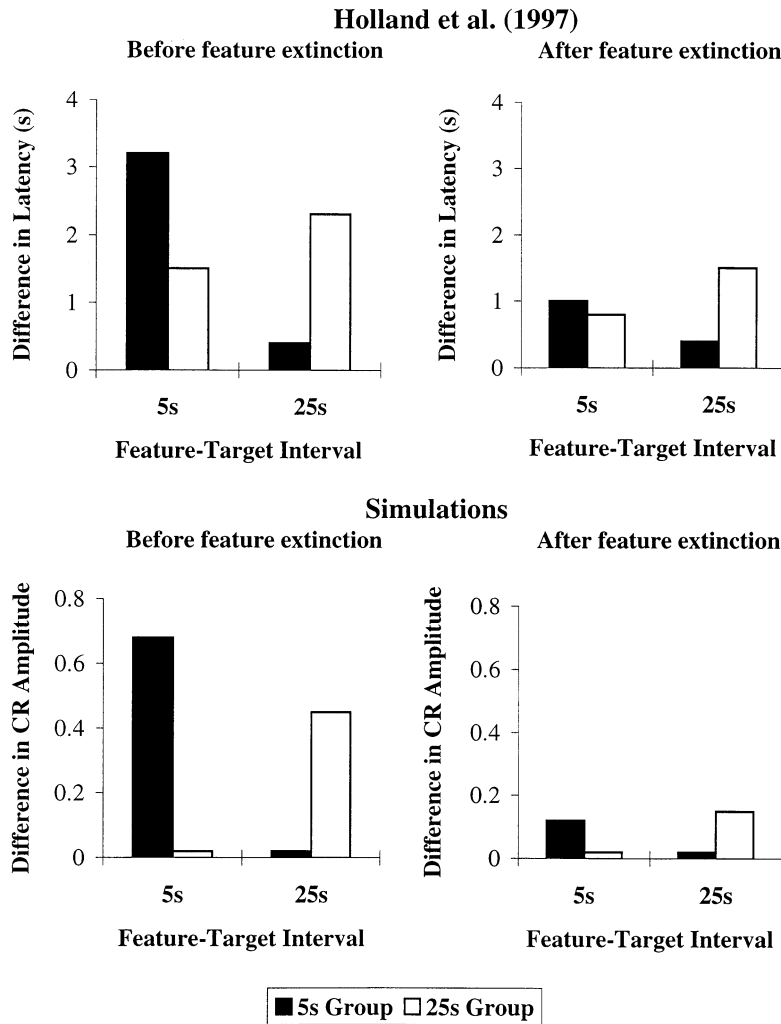


Fig. 9. Temporal specificity of serial FP discrimination before and after feature extinction. Upper panels: Difference in latency to chain pull in the presence of A alone, or $X \rightarrow A$, for two FTIs, 5 and 25 s (Holland et al., 1997). Left upper panel: Difference in latency before feature X extinction (Holland et al., 1997). Right upper panel: Difference in latency after feature X extinction (Holland et al., 1997). Lower panels: Simulated difference in CR to $X \rightarrow A$, or A alone, before and after 40 trials of feature X extinction, in two simulated groups that received 300 alternated $X \rightarrow A + /A -$ trials, with 15-time units FTI (5 s group), or 800 alternated $X \rightarrow A + /A -$ trials, with 75-time unit $X \rightarrow A$ interval (25 s group). Left lower panel: Difference in latency before feature X extinction. Right lower panel: Difference in latency after feature X extinction. Latency to respond is assumed to decrease linearly with the CR: $\text{Latency} = 1 - \text{CR}$. Therefore, difference in latency $\text{Latency}_A - \text{Latency}_{X \rightarrow A} = (1 - \text{CR}_A) - (1 - \text{CR}_{X \rightarrow A}) = \text{CR}_{X \rightarrow A} - \text{CR}_A$.

training FTI than at the other interval. The right upper panel shows the effect of feature extinction. In the 5 s $X \rightarrow A$ group, feature extinction almost eliminates discrimination, suggesting that the solution of the discrimination relies on direct feature-US associations. In the 25 s $X \rightarrow A$ group,

feature extinction has less effect on the discrimination, suggesting that the solution does not depend on direct feature-US associations.

The lower panel of Fig. 9 shows that the model is able to correctly describe the effect of feature extinction on serial FP discrimination. The left

lower panel of Fig. 9 demonstrates that before feature extinction, the model discriminates better at the training FTI than at the other interval. The right lower panel of Fig. 9 shows the effect of 40 feature extinction trials on serial FP discrimination. Discrimination decreases dramatically in the 5 s X–A group (closed bars), but only moderately in the 25 s X–A group (open bars).

In summary, the model is not only able to describe the temporal specificity of serial FP discrimination, but also the associative relations that would allow feature extinction to eliminate FP discrimination in the 5 s group, but not in the 25 s group. The simulated 5 s X–A group solves the discrimination by engaging direct X–US connections and positive H–US connections activated by the presentation of X in the experimental context (Fig. 7). When these associations extinguish, discrimination is abolished. However, as shown in Fig. 8, in the simulated 25 s X–A group, discrimination is solved by engaging direct A–US connections, and inhibitory H–US connections inhibited by the presentation of X in the experimental context. Extinguishing the direct X–US associations, and the few H–US associations activated by X in the experimental context, has only a moderate effect on the discrimination.

5.4. Summary of serial FP discrimination simulations

Simulations show that by allowing the CSs to evoke multiple spectral traces the model is able to correctly address both the temporal specificity and the associative relations involved in a serial FP discrimination. The model is qualitatively in accord with the data by Holland et al. (1997) showing that animals discriminate better when tested at the training FTI than at shorter or longer FTIs, the discrimination gradient is consistent with scalar timing, and animals discriminate better when trained with short, but not long FTIs.

Importantly, the model incorporates the associative structures that would allow feature extinction to eliminate FP discrimination in the short, but not long, FTI group. Further research remains to explore if other properties of occasion setting (Buhusi and Schmajuk, 1996; Schmajuk

and Buhusi, 1997; Lamoureux et al., 1998; Schmajuk et al., 1998) are preserved in the model.

6. Discussion

Perhaps due to the complexity of conditioning, it is common to develop theories and models which deal with very specific properties of learning. For example, theories tend to separately address the associative and temporal aspects of Pavlovian conditioning.

Associative models largely ignore temporal properties and concentrate on the type of associations that seem to be involved in conditioning. For example, a popular associative model, the Rescorla and Wagner (1972) model assumes that animals learn to predict the value of the US, but ignore its timing. Although ‘real-time’ models of associative learning (Moore and Stickney, 1980; Schmajuk and Moore, 1988; Schmajuk and DiCarlo, 1992; Buhusi and Schmajuk, 1996) are able to address some temporal aspects of conditioning, they do not speak to the temporal specificity of these phenomena. Other theories (Grossberg and Merrill, 1992; Moore and Choi, 1998) although addressing timing in simple and compound conditioning, do not apply to the more complex characteristics of occasion setting.

Similarly, a wide range of models describe the temporal properties of classical (Grossberg and Schmajuk, 1989; Grossberg and Merrill, 1992) and operant conditioning (Gibbon, 1977; Killeen and Fetterman, 1988; Church and Broadbent, 1990; Machado, 1997; Staddon and Higa, 1999), and the neurophysiological aspects of timing (Meck and Church, 1987), but ignore all other aspects of the paradigms. Various mechanisms were proposed to underly timing: a pacemaker/accumulator process (Gibbon, 1977; Meck and Church, 1987), a set of oscillator processes (Church and Broadbent, 1990), a sequence of behaviors (Killeen and Fetterman, 1988), or a set of memory traces (Grossberg and Schmajuk, 1989; Machado, 1997; Staddon and Higa, 1999).

A central problem from the perspective of timing theories is to differentiate between ‘clock’-based (pacemaker- or oscillator-based) timing

mechanisms, and ‘clock-free’ timing mechanisms (Staddon and Higa, 1999). Although this approach is useful to investigate particular timing mechanisms, it says little about how these mechanisms are used in conjunction with other learning mechanisms, given that animals seem to learn not only ‘when’ the US is presented, but also other aspects of the conditioning paradigm, such as ‘what’ are the best predictors of the US. In contrast, this paper suggests that efforts towards addressing timing questions should be complemented by a combined analysis of the temporal and associative characteristics of these paradigms.

The present model describes timing in classical conditioning by assuming that CSs activate a set of processes that develop at different time scales. These processes and their configurations compete to become associated with the US. Based on these properties, the model is able to describe ISI curves in simple conditioning, the temporal specificity of blocking, and the temporal specificity of the action of occasion setters. The results presented here suggest that the spectral timing hypothesis has an important characteristic: it can work in conjunction with associative mechanisms to explain timing in associative learning.

For example, we suggest that in a blocking paradigm, stimuli compete to accurately predict the value, time, and duration of US presentation. In line with Barnet et al. (1993), more blocking is observed if A–US interval in phase 1 matches the B–US interval in the second phase of the blocking paradigm, because the US is already accurately predicted. According to the model, the accuracy of US prediction implies not only a precise moment but also an appropriate CR duration. If these criteria are not satisfied, unblocking occurs. In particular, if B is able to predict the value, time and duration of the US more accurately than A, B is able to gain associative strength and predict the appropriate properties of the US.

In order to deal with conditioning paradigms that involve multiple CSs, Grossberg and Merrill (1992) extended the model by Grossberg and Schmajuk (1989) by assuming that: (a) internal representations of the CSs compete among them

thereby modifying their magnitude; (b) spectral traces controlled by CS internal representations establish associations with the US in proportion to their magnitude; and (c) trace-US associations change in proportion to the moment-to-moment change in the US internal representation. Therefore, their model is able to describe some aspects of timing in simple and compound conditioning, including second-order conditioning. By contrast, the model presented here follows the assumption that the unchanged internal representations (traces) of the CSs compete to gain association with the US (Moore and Stickney, 1980; Schmajuk and Moore, 1988; Schmajuk, 1997).

A model that is also able to address some temporal aspects of blocking and second-order conditioning was presented by Desmond and Moore (1988) and Moore and Choi (1998). In their model, each CS evokes a cascade of activations that compete in predicting the value and the time of US presentation through a time-derivative rule (Sutton and Barto, 1990). Although in the original formulation the model does not describe the scalar property of CR topography (increased CR duration for larger CS–US intervals), the model might address this issue by allowing parameter δ to progressively vary with elapsed time after CS onset (John W. Moore, personal communication, April 1998).

Importantly, the present model and the above competing models differ in their predictions relative to the blocking paradigm. The models by Desmond and Moore (1988), Grossberg and Merrill (1992) and Moore and Choi (1998) are able to account for the unblocking due to a change in the A–US interval between the two phases of the blocking paradigm. Also, as an outcome of their description of second-order conditioning they might be able to account for unblocking when A–US duration is the same in both phases (A +), but B is paired serially with A and the US, B → A + , as in group S–F(s) (Barnet et al., 1993, Experiment 2). However, while the models by Desmond and Moore (1988), Grossberg and Merrill (1992) and Moore and Choi (1998) would presumably predict that in this case animals learn the B–A interval, the present model predicts that animals learn the B–US interval. Unlike the

present model, these models have also problems accounting for unblocking when $A-US$ duration is the same in both phases ($A \rightarrow +$) and B is paired simultaneously with the US, $A \rightarrow B +$, as in group $F-S(f)$ (Barnet et al., 1993, Experiment 4). The present model describes this result due to competition between spectral traces to predict the US duration. Thus, the present model also predicts that in this case animals learn the $B-US$ interval.

Furthermore, in contrast to these models (Desmond and Moore, 1988; Grossberg and Merrill, 1992; Moore and Choi, 1998), the present model is also able to address temporal specificity in a different class of phenomena that seems to require, besides competition between simple $CS-US$ associations, the involvement of hidden $H-US$ associations. More precisely, we showed that when activated by spectral traces, a structure consistent with Schmajuk and DiCarlo (1992) model is able to correctly address temporal specificity of serial FP discriminations. At short FTIs, the associative solution is similar to simple conditioning, and therefore is abolished by feature extinction. When trained with large FTIs the associative solution is similar to occasion setting, and therefore is not abolished by feature extinction. In sum, for both short and long FTIs, the model describes both the temporal and associative properties of serial FP discrimination.

However, while in the model by Schmajuk and DiCarlo (1992), the competition between CSs is purely associative, in the present model the competition between CSs is both associative and temporal. In short, CSs compete to predict not only the presence and intensity, but also the duration, and time of presentation of the US. For example, blocking is observed only when specific temporal relationships occur. Similarly, in a serial FP discrimination, feature X simultaneously controls both the associative and temporal properties of the solution found by animals.

Most importantly, while in the model by Schmajuk and DiCarlo (1992), a CS assumes the same role (simple CS, and/or occasion setter) throughout a trial duration, in the present model a CS can assume different roles at different time moments. Thus, a CS can act as a simple CS at

one moment in time, and as an occasion setter at other moments in time, by the activation of its different traces. In the model by Schmajuk and DiCarlo (1992), $X \rightarrow A + / A -$ discrimination with a long FTI is solved indirectly (through hidden units) while direct $X-US$ associations are null. At no moment during the trial does the feature directly activate the US representation. Therefore, the solution is not time specific. In contrast, in the present model, in a $X \rightarrow A + / A -$ discrimination with a long FTI slow X traces are occasion setters (act through hidden units) and fast X traces become direct inhibitors of the US. Feature X directly inhibits the US representation shortly after X presentation, but indirectly activates it (through hidden units) later on in time. Feature X assumes different roles during the trial, thus allowing for temporal specificity of the solution. Therefore, in the present model, temporal specificity is incorporated into the solution found by the system by allowing any CS to have different roles at different moments in time. The present model extends the notion of occasion setter to describe a stimulus that controls both the temporal and associative relations between another CS and the US.

Further research is nonetheless necessary to resolve some conflicting assumptions incorporated in the present model, assumptions that were favored in the past by the separate analysis of conditioning from the timing, or associative, perspective. For example, the temporal assumption adopted in the present model that CSs evoke spectral traces that are independent of CS duration (Grossberg and Schmajuk, 1989) precludes the description of the effect of CS duration on conditioning, a feature well described by other 'real-time' associative models (Moore and Stickney, 1980; Schmajuk and Moore, 1988; Schmajuk and DiCarlo, 1992; Buhusi and Schmajuk, 1996). On the other hand, since in the present model a CS can have different roles (simple CS or occasion setter) at different time moments, the description of the multiple associative features of occasion setting (Schmajuk and Buhusi, 1997; Lamoureux et al., 1998; Schmajuk et al., 1998) is partly obscured by the temporal interactions between multiple traces.

Despite the shortcomings discussed above, the present model gives an adequate description of both temporal and associative aspects of some conditioning protocols, and can guide the independent study of both timing and associative mechanisms engaged in animal learning. Nonetheless, the paper suggests that a combined analysis of timing and associative learning is needed for a better understanding of conditioning phenomena.

7. Summary

In order to describe the temporal specificity in simple conditioning and occasion setting, we present a computational model of Pavlovian conditioning in which stimuli compete to predict the value, duration, and time of presentation of the reinforcement. The model develops three basic notions. Firstly, it is a real-time model, and therefore able to describe various temporal relations between stimuli, and between stimuli and the reinforcement. The real-time properties of the model follow from the hypothesis that stimuli evoke multiple traces with different temporal properties (Grossberg and Schmajuk, 1989). Secondly, spectral traces become associated directly and indirectly (through hidden units) with a representation of the reinforcement, in a manner consistent with the model by Schmajuk and DiCarlo (1992). Therefore, the model is able to describe the difference between simple CSs and occasion setters. However, in contrast to Schmajuk and DiCarlo's model, in the present model a stimulus may assume different roles (simple CS, occasion setter, or both) at different time moments, thus providing support for the description of the temporal specificity of occasion setting. Therefore, the present model extends the notion of occasion setter to describe a stimulus that controls both the temporal and associative relations between another CS and the US.

Thirdly, the direct and indirect (hidden unit) traces compete to predict the presence and characteristics of the US. Importantly, while in the model by Schmajuk and DiCarlo (1992), competition between CSs is purely associative (CSs compete for the prediction of the presence and value

of the US), since in the present model timing is mapped onto trace-specific associations, competition between CSs is both associative and temporal. The associative competition for the prediction of presence and value of the US is also a temporal competition for the prediction of the temporal properties (time of presentation and duration) of the US. Thus, the model can address associative and temporal competition between CSs, as in the blocking paradigm.

Computer simulations demonstrate that the model is able to address temporal specificity in conditioning paradigms in which stimuli act as simple CSs or as occasion setters. We show that the model describes the CR topography in simple conditioning (Smith, 1968), the temporal competition between simple CSs in paradigms like blocking (Barnet et al., 1993), and the temporal specificity in serial FP discriminations (Holland et al., 1997).

The paper suggests that efforts towards characterizing animal timing should include a joint analysis of the temporal and associative mechanisms that allow animals to simultaneously learn both 'what' and 'when' significant events occur.

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Appendix A. The model

Conditioned stimulus CS_i evokes k spectral traces, with different temporal properties. These traces are computed using activities x_{ik} and y_{ik} . Activity x_{ik} is given by:

$$\Delta x_{ik} = (k_1/k)(1 - x_{ik})(CS(i) + k_2 f_1(i)) - k_3 x_{ik} \quad (1)$$

where $CS(i)$ is 1 when CS_i is present and 0 otherwise, k_1 is a growth rate parameter, k_3 is a decay parameter, and k_2 and function f_1 denote

the combined feedback contribution of the traces corresponding to stimulus CS_i . According to Eq. (1), each activity x_{ik} increases at a different rate, which is inversely related with index k of the trace. Activities x_{ik} are initialized with null values. The feedback function f_1 is given by Eq. (5).

Activity y_{ik} is given by:

$$\Delta y_{ik} = k_4(1 - y_{ik}) - k_5 f_2(x_{ik}) y_{ik} \quad (2)$$

where f_2 is the sigmoid function

$$f_2(a) = \frac{a^\alpha}{a^\alpha + k_6^\alpha} \quad (3)$$

According to Eq. (2), for each CS_i , the set of k activities y_{ik} increases with growth rate k_4 , and decays in proportion to activity x_{ik} . While x_{ik} increases with a rate inversely related to index k of the trace, y_{ik} decreases with a rate inversely related to index k of the trace. Activities y_{ik} are initialized with values 1.

The k spectral traces of stimulus CS_i are given by:

$$\tau_{ik} = y_{ik} f_2(x_{ik}) \quad (4)$$

The spectral traces peak at different moments in time, and rise and decay in proportion to index k of the trace. For each CS_i , traces τ_{ik} are feed back into activities x_{ik} , through function f_1 given by:

$$f_1(i) = f_3\left(\sum_k x_{ik}\right) \quad (5)$$

where f_3 is the sigmoid function

$$f_3(a) = \frac{a^\beta}{a^\beta + k_7^\beta} \quad (6)$$

The context, CX is assumed to activate k traces, τ_{CXk} , of constant intensity.

The spectral traces, τ_{ik} of each CS_i are configured in the hidden unit H_j through indirect connections VH_{ikj} . The activity of hidden unit H_j is given by:

$$\text{act}_j = \sum_i \sum_k \tau_{ik} VH_{ikj} \quad (7)$$

Each hidden unit H_j evokes a memory trace τ_j proportional with its activity:

$$\tau_j = k_8 f_4(\text{act}_j) \quad (8)$$

where f_4 is the sigmoid function

$$f_4(a) = \frac{a^\gamma}{a^\gamma + k_9^\gamma} \quad (9)$$

Hidden units H_j are associated with the US through connections VN_j . The prediction of the US by the hidden unit H_j is given by:

$$B_{H_j US} = \tau_j VN_j \quad (10)$$

Spectral traces, τ_{ik} of each CS_i are directly associated with the US through direct connections V_{ik} . The direct prediction of the US by stimulus CS_i is given by:

$$B_{CS_i US} = \sum_k \tau_{ik} V_{ik} \quad (11)$$

The aggregate prediction of the US is given by the sum of the direct and indirect contributions of all the stimuli, CS_i and of all hidden units H_j :

$$B_{US} = \sum_i B_{CS_i US} + \sum_j B_{H_j US} \quad (12)$$

Importantly, in order to prevent the extinction of conditioned inhibition by the presentation of CS alone (Zimmer-Hart and Rescorla, 1974), B_{US} is considered non-negative. If $B_{US} < 0$, then $B_{US} = 0$.

The conditioned response, CR is considered proportional with the aggregate prediction of the US:

$$CR = k_{10} B_{US} \quad (13)$$

Direct associations V_{ik} are adapted according to:

$$\Delta V_{ik} = k_{11} \tau_{ik} (US - B_{US}) (1 - |V_{ik}|) \quad (14)$$

where the growth rate k_{11} is equal to k'_{11} if $US \geq B_{US}$, or equal to k''_{11} if $US < B_{US}$.

Similarly, the direct hidden-US associations VN_j , are adapted according to:

$$\Delta VN_j = k_{12} \tau_j (US - B_{US}) (1 - |VN_j|) \quad (15)$$

where the growth rate k_{12} is equal to k'_{12} if $US \geq B_{US}$, or equal to k''_{12} if $US < B_{US}$.

The indirect, CS_i -US associations, VH_{ikj} are adapted by:

$$\Delta VH_{ijk} = k_{13} \tau_{ik} \tau_j (US - B_{US}) VN_j \quad (16)$$

Appendix B. Simulation parameters

Simulations assume 20 hidden units and $k = 5$ traces per stimulus, including the context CX. Context traces, τ_{CXk} are 0.01 in intensity. The initial values of V_{ik} and VN_j are null. Input-hidden unit association weights, VH_{ijk} are randomly assigned using a uniform distribution ranging between ± 0.25 in all simulations.

Each simulation trial consists of 400 time steps. The simulations assume 20-time unit CSs, and a 3-time unit US of intensity $US = 1$ if not otherwise specified.

All simulations use the same set of parameters: $\alpha = 8$, $\beta = 2$, $\gamma = 1.5$, $k_1 = 0.05$, $k_2 = 2$, $k_3 = 0.01$, $k_4 = 0.0001$, $k_5 = 0.125$, $k_6 = 0.8$, $k_7 = 0.005$, $k_8 = 1.5$, $k_9 = 0.35$, $k_{10} = 5$, $k'_{11} = 0.005$, $k''_{11} = 0.0045$, $k'_{12} = 0.015$, $k''_{12} = 0.018$, and $k_{13} = 0.5$.

In the simulations presented in Fig. 3, the CS is presented between time units 20–40. The CS–US intervals are 10, 20, 40, or 80. US intensity is $US = 1$ or 2, respectively. In the simulations presented in Fig. 3, the nictitating membrane response is assumed to be proportional to the CR, $NMR = CR$.

Figs. 4 and 5 present simulations of the first two phases of the paradigms described in Table 1. The CS–US interval is 14-time units for simultaneous CS–US pairing, CS+, and 34-time units for serial ('forward') CS–US pairings, CS→+. In the simulations presented in Figs. 4 and 5, latency to complete the licking period is assumed to be proportional to the CR, $Latency = CR$.

In the simulations presented in Figs. 6–9, feature X is presented between time units 20–40. The target is presented between time units 35–55 for group 5 s, and between time units 95–115 for group 25 s. The target-US interval is 13-time units. In the simulations presented in Figs. 6–9, latency to respond is assumed to decrease linearly with the CR: $Latency = 1 - CR$. Therefore, difference in latency is proportional to a difference in CR: $Latency_A - Latency_{X \rightarrow A} = (1 - CR_A) - (1 - CR_{X \rightarrow A}) = CR_{X \rightarrow A} - CR_A$.

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