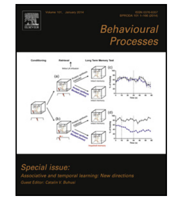
Behavioural Processes 101 (2014) 135–145

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Interactions of timing and prediction error learning

Kimberly Kirkpatrick*

Kansas State University, United States

ARTICLE INFO

Article history:
Received 20 March 2013
Received in revised form 24 June 2013
Accepted 6 August 2013

Keywords:
Timing
Prediction error learning
Motivation
Computational modeling

ABSTRACT

Timing and prediction error learning have historically been treated as independent processes, but growing evidence has indicated that they are not orthogonal. Timing emerges at the earliest time point when conditioned responses are observed, and temporal variables modulate prediction error learning in both simple conditioning and cue competition paradigms. In addition, prediction errors, through changes in reward magnitude or value alter timing of behavior. Thus, there appears to be a bi-directional interaction between timing and prediction error learning. Modern theories have attempted to integrate the two processes with mixed success. A neurocomputational approach to theory development is espoused, which draws on neurobiological evidence to guide and constrain computational model development. Heuristics for future model development are presented with the goal of sparking new approaches to theory development in the timing and prediction error fields.

Contents

Traditionally, the study of timing and associative learning has proceeded largely independently, but more recent research has suggested areas of connection between the two disciplines. Theories of timing and associative learning have also traditionally focused on one or the other process, but the last three decades have seen the emergence of hybrid theories, again reflecting overlap between the two processes (see, for example, Church and

* Correspondence address: Department of Psychological Sciences, 492 Bluemont Hall, 1100 Mid-Campus Drive, Kansas State University, Manhattan, KS 66506-5302, United States. Tel.: +1 785 532 0805; fax: +1 785 532 5401.
E-mail address: kirkpatr@ksu.edu

0376-6357/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.beproc.2013.08.005

Kirkpatrick, 2001; Kirkpatrick and Church, 1998). The present paper discusses recent developments, both empirical and theoretical, in the fields of timing and associative learning that argue for the further development of theories that couple the two processes together, as well as further research to assess the nature of interactions between the two processes. Both behavioral and neurobiological evidence are brought to bear in an attempt to understand the functioning of timing and associative learning systems.

1. Historical foundations

1.1. Prediction error learning

Prediction error learning is driven by expectancies of the occurrence or non-occurrence of events, and has been proposed to serve as the basic process that underlies associative learning in classical and instrumental conditioning procedures. Prediction error learning has historically been viewed as the process of learning to anticipate events in relation to the occurrence of other events. As a simple example, an individual might experience a tone that lasts for 10 s and is followed by food delivery, a procedure known as delay conditioning. Prediction error learning in this case would lead to an expectation of food delivery during the tone stimulus. Prediction errors play an important role during the learning process as early in learning there is no expectancy of food, but this develops over the course of repeated experiences. Prediction errors could also play an important role if the circumstances were to change by, for example, changing the properties of the tone, by changing the amount or type of food delivery, or by ceasing food deliveries altogether. Prediction error learning also plays an important role in learning connections between multiple different events, such as connections between two or more conditioned stimuli (CSs) and relationships between responses and outcomes.

1.2. Conditioning and timing

The study of classical conditioning initially proceeded largely independently of the study of timing processes, even though the procedures used to study both processes are highly similar. For example, a common procedure used in classical conditioning research is the delay conditioning procedure, described previously, in which a CS (e.g., a tone or light) is turned on for a fixed duration and then is followed by a US (e.g., food). An intertrial interval (ITI) intervenes between successive signal presentations. Although responses have no consequence in this procedure, considerable responding can be observed if the CS duration is relatively short (depending on the relevant behavioral system), if the CS precedes the US, and if there is little or no gap between CS offset and US delivery. All of these phenomena indicate that conditioning is dependent on temporal aspects of the procedure. These facets of conditioning are well established and are foundational knowledge in basic learning textbooks. In addition, conditioned responses (CRs) are not distributed evenly across the CS duration, but instead increase in frequency and/or strength as the expectancy of the US increases. Measurement of CR timing in classical conditioning has been overlooked in the majority of research reports, even though CR timing is a robust phenomenon. The fact that CRs are timed in accordance with US expectancy indicates that conditioning is resulting in learning of *whether* and *when* the US will occur. And yet, both empirical research and theoretical developments have proceeded largely independently until more recently.

1.3. Reward processing and timing

Prediction error learning plays an important role in learning to anticipate reward occurrence and the specific features of rewarding stimuli. Changes in reward magnitude or other aspects of reward lead to prediction errors and this in turn can lead to timing changes (Section 2.2). Early research examining reward effects on timing suggested that timing of responding was relatively immune to the effects of reward variables, and that reward effects were restricted to the rate of responding rather than the timing of responding. For example, Roberts (1981) reported several experiments where different aspects of a peak procedure were manipulated. A peak procedure is a variation on a fixed interval (FI) schedule of reinforcement. FI and peak trials are both cued by the same signal (e.g., a tone or light). On FI trials, food is primed at a particular time after signal onset, for example, 30 s. The first response after the prime results in food delivery and signal termination. Peak trials are cued in the same fashion and usually last 3–4 times the FI duration. There are no food deliveries on peak trials and responses have no consequence, but are recorded. The average response rate on peak trials typically increases as a function of time since signal onset until around the expected time of food delivery and then decreases thereafter.

Roberts (1981) reported that differences in the FI duration resulted in differences in the time of occurrence of the *peak time* of responding, whereas differences in the probably of reinforcement resulted in differences in the *peak rate* of responding. As a result, Roberts developed a simple model in which the timing of reinforcement was proposed to affect clock processes which would result in effects on the timing of responding whereas other factors such as probability or amount of reinforcement or the motivational state of the individual would affect the rate of responding but should have no effect on the timing of responding. As a result of this and other early studies, little attention was paid to any possible intersection of reward processes and timing processes. However, more recent research, outlined in the next section, has indicated that reward processing and timing are not entirely independent.

2. Challenges: prediction error learning and timing are not independent

In the last three decades, there has been a growth of interest (both empirical and theoretical) in examining connections between prediction error learning and timing. This section will consider the major empirical developments that have stimulated the growth of hybrid theories, which are discussed in the following section.

2.1. Timing variables and prediction error learning

One important discovery linking prediction error learning and timing is that CRs appear to be timed appropriately at their earliest point of occurrence. This has been demonstrated in appetitive conditioning in rats (Kirkpatrick and Church, 2000), aversive conditioning in goldfish (Drew et al., 2005), eyeblink conditioning in rabbits (Ohyama and Mauk, 2001), autoshaping in birds (Balsam et al., 2002), and fear conditioning in rats (Davis et al., 1989). The observation of CR timing at the start of associative learning indicates that learning to anticipate whether and when the US will occur (in relation to the CS) are most likely emerging in parallel and at a similar point in conditioning. This will be discussed further in relation to the neural substrates of timing and conditioning in Section 4.

Another important factor to consider is that interval durations directly affect the strength and/or probability of CR occurrence in simple conditioning procedures (Holland, 2000; Kirkpatrick and Church, 2000, 2003; Lattal, 1999; Kirkpatrick, 2002). This relationship appears to take the form of a power function with a slope near −1.0 in a goal-tracking procedure in rats, as shown in Fig. 1. In addition, this relationship is observed regardless of the events that cue the onset of the interval. To demonstrate this principle, the