Behavioural Processes 130 (2016) 53–64

Contents lists available at ScienceDirect

Behavioural Processes

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

Effects of variable sequences of food availability on interval time-place learning by pigeons

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ARTICLE INFO

Article history:
Received 4 March 2016
Received in revised form 11 July 2016
Accepted 13 July 2016
Available online 15 July 2016

Keywords:
Time-place learning
Timing
Pigeon

ABSTRACT

The effects of within session variability of the sequences of food availability in a 16 period Time Place Learning (TPL) task on the performance of pigeons were assessed. Two groups of birds were exposed to two conditions. For group 1 (N = 3), the first condition consisted of a TPL task in which food could be obtained according to a Random Interval (RI) 25 s schedule of reinforcement in one of four feeders, the correct feeder changed every 3 min. The same sequence was repeated four times within every training session (Fixed Sequence). The second condition was exactly the same as the first one with the exception that the sequence in which the correct feeder changed was randomized, yielding a total of four randomized sequences of food availability each session (Variable Sequence). An Open Hopper Test (OHT) was conducted at the end of each condition. Birds in group 2 (N = 3) experienced the same conditions but in the reverse order. Results showed high percent correct responses for both group of birds under both conditions. However, birds were able to time the availability period's duration only under the Fixed Sequence condition, as shown by anticipation, anticipation of depletion and persistence of visiting patterns on the OHT. The implications of these results to Gallistels (1990) tripartite time-place-event memory code model are discussed, pointing out that these results are in line with previous findings about the important role that spatial parameters of a TPL task can play, for accurate timing was precluded when a variable sequence was employed.

1. Introduction

Time-Place Learning (TPL) has been usually considered to be the ability to find and exploit resources with a spatiotemporally limited availability (Biebach et al., 1989; Wilkie and Wilson, 1992; Thorpe et al., 2007). Sincethis availability is not always perfectly predictable, Thorpe et al., (2007) have proposed that TPL is "... the ability of animals to learn the spatiotemporal variability of biologically significant events such as food." (p. 55).

TPL has long been considered an essential animal behavior feature because it seems to be critical for many species to be able to anticipate the location and duration of biologically relevant events in order to ensure survival (Biebach et al., 1989; Saksida and Wilkie, 1994; Carr and Wilkie, 1997). Therefore, no surprise comes from the fact that a wide variety of species including rats (Carr and Wilkie, 1997, 1998, 1999; Widman et al., 2000), mice (Van der Zee et al., 2008; Mulder et al., 2015) fish (Reebs, 1993, 1996, 1999; Delicio and Barreto, 2008), ants (Schatz et al., 1994) pigeons (Wilkie and Wilson, 1992; Saksida and Wilkie, 1994; Wilkie et al., 1994), garden warblers (Krebs and Biebach, 1989; Biebach et al., 1991, 1994), and other birds (Falk et al., 1992), have been shown to display TPL under many different circumstances. Since most TPL definitions typically refer to animals, it comes as no surprise that the use of human participants is more recent and the evidence of them showing TPL is still somewhat controversial (Thorpe et al., 2012 García-Gallardoet al., 2015).

A typical TPL task is defined by two features: 1) There is more than one place where any given resource can be found and 2) The *correct* place (i.e. the one where the resource can be found) changes according to a temporal criterion.

A usual consideration is that there are two different kinds of TPL tasks (Carr and Wilkie, 1997; Thorpe et al., 2003; Crystal, 2009): a)Daily TPL, where the correct place changes according to the time of day (e.g. Biebach et al., 1989; Carr and Wilkie, 1997; Pizzo and Crystal, 2002), b)Interval TPL, where changes are scheduled within minutes or seconds since the start of an experimental session (Carr et al., 2001; Crystal and Miller, 2002; Pizzo and Crystal, 2004). Both tasks can be solved using a number of different strategies, one of

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http://dx.doi.org/10.1016/j.beproc.2016.07.008

them could be to respond on any given option until no more food is available in that option (i.e. a win/stay – lose/shift strategy). However a widely accepted view of these types of TPL tasks is that daily TPL is solved by using an endogenous circadian mechanism (Biebach et al., 1989, 1994; Widman et al., 2004; Deibel and Thorpe, 2013; Mulder et al., 2013) and that animals solving an interval TPL task rely primarily on an interval-timing mechanism with functions that resemble a stopwatch (Crystal and Miller, 2002; Thorpe et al., 2002a, 2002b, 2007; Thorpe and Wilkie, 2002, 2005; Pizzo and Crystal 2004).

Three common findings have usually been considered as evidence that animals exposed to an interval TPL task do not rely on a win/stay-lose shift strategy, but that they are timing the availability periods in each option: A) **Anticipation of depletion.** – The temporal distribution of response during availability periods describes an ascendant-descendent function that sometimes has a peak (Wilkie and Willson, 1992; Wilkie et al., 1994; Carr et al., 2001), and others has a plateau (Thorpe et al., 2002a, 2002b, 2007; Pizzo and Crystal, 2002; Thorpe and Wilkie, 2005) around the middle of the period and the descendent fraction at the end of it. This suggest that subjects are keeping track of how long have they been responding on any given option, and they are thus capable of switching prior to the resource depletion on that option. B) **Anticipation.** – Subjects start responding on any given option, with the obvious exception of the first one, just before it becomes the temporally correct one, suggesting that they are keeping track of time. C) **Persistence of patterns.-** Many TPL experiments (e.g. Carr et al., 2001; Thorpe et al., 2002a, 2002b; Thorpe and Wilkie, 2006) include probe sessions in which food can be obtained in any place at any time. These tests are commonly referred to as Open Hopper Tests (OHT). During these sessions, if subjects were relying on a win/stay- lose/shift strategy, they would never stop responding on the first option they chose, since they can obtain food there throughout the entire session. Most papers find that animals do not do this, instead, they tend to maintain the visiting patterns displayed during training, which suggests that they are timing the intervals they learned during training.

Gallistel (1990) proposed a theory about animal learning that has been recovered by some authors to explain behavior under circumstances like those involved in a TPL task (e.g., Wilkie, 1995; Thorpe et al., 2007). He posited that whenever an animal encounters a biologically relevant event like food or water, the animal forms a tripartite code, consisting of information about what was found, the place where it was found and the time when it happened. These codes are later retrieved to find and exploit these resources. This way, they can learn about the spatio-temporal regularities involved in TPL tasks.

With Gallistel's model on mind, research on the effects of variability of the TPL task parameters is of particular relevance, especially considering that, in their natural environments, animals could be faced with a certain degree of variability in location or duration of food availability. Understanding the learning processes involved in the solution of TPL tasks with some degree of variability could be useful for a more naturalistic approach to TPL.

A previous experiment explored the effects of some degree of variability in the parameters of a TPL task was conducted by Thorpe et al., 2007. They exposed rats to a modified TPL task in which either the temporal or spatial parameters of the task could be changed from day to day, thus precluding the animals from forming the tripartite codes proposed by Gallistel (1990). One group of rats experienced always the same sequence of food locations but a different duration each session (SEQ group), and the other was subject to a different sequence of food locations each day but always with the same duration (DUR group).

The rationale was that rats should be unable to solve the TPL task under both conditions, since effective TPL performance, according to Gallistel (1990), depends on the animal's ability to form these tripartite event-time-place codes. Thorpe et al. (2007) found that rats in the SEQ group were able to solve the task, while rats in the DUR group were not. These results are rather troublesome when analyzed in light of Gallistelís proposal, the results of SEQ group could imply that regularity on the three components of the code is not critical for an adequate performance on a TPL task while the results of the DUR group suggests the opposite.

Thorpe et al. (2007) interpreted their results as evidence that tripartite codes might not be absolutely necessary for effective performance under a TPL task. They also proposed that there must be an asymmetrical role played by spatial and temporal information under these tasks, suggesting that spatial information might be more relevant than the temporal one (Thorpe et al., 2007).

Thorpe et al. (2007) study allows the understanding of animalís performance under a different sequence of food availability from day to day (between sessions variability). As noted above, one of the main conclusions is that spatial variability alone is sufficient to preclude effective timing performance on the TPL task (Thorpe et al., 2007). Thorpe et alís findings were clear, and they raise the question about whether the same detrimental effect of spatial variability could be found under intrasessions variability. The reason why this could be an important question is that Interval TPL is widely said to depend on learning mechanisms that are regulated by relatively brief events and durations (Thorpe and Wilkie, 2002; Wilkie et al., 1994; Carr and Wilkie, 1997; Crystal, 2009), which makes it reasonable to suppose that the effects of spatial variability could be different when explored from day to day and within a single session. Answering this question could yield important insight to understand how animals adjust their behavior to variable food availability conditions. If the same effect could be replicated even when animals face a different sequence of food location within a single session, this could be further evidence that spatial information is crucial for an adequate TPL performance.

Therefore, the purpose of the present study is to assess the effects of intrasessions variability in the sequence of food availability on the temporal distribution of response in a TPL task with pigeons.

If Gallistel's (1990) model stands even under local variability conditions, then we should see that birds should be unable to accurately time the availability period duration under a variable sequence condition, for the tripartite time-place-event memory code would not be configured. On the other hand, if birds were to time the availability periods under this condition, that could be troublesome for a joint time-place information processing model like that of Gallistel.

2. Materials and methods

2.1. Subjects

Six experimentally naïve White Carneaux pigeons were used. Subjects were housed in individual cages and maintained at 70% + −10 g of their free feeding weight. They had free access to water throughout the experiment.

2.2. Apparatus

An experimental chamber 64 cm long, 64 cm wide and 33 cm tall was used in this experiment. The experimental chamber had four identical side walls. Each of these walls comprised seven panels. A solenoid operated magazine was mounted on the central panel and the remaining six were filled with Plexiglas plates that covered the entire panel. The magazine opening was 8 cm wide and 6 cm tall and was located 10 cm above the chamber floor. Each feeder was