UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
PROGRAMA DE MAESTRÍA Y DOCTORADO EN PSICOLOGÍA
ANÁLISIS EXPERIMENTAL DEL COMPORTAMIENTO

Distribución espacio-temporal de eventos biológicamente relevantes: Regularidad vs Irregularidad en la estructuración del comportamiento

TESIS
QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN PSICOLOGÍA

PRESENTA
DANIEL ANTONIO GARCÍA GALLARDO

TUTOR PRINCIPAL
DR. CLAUDIO ANTONIO CARPIO RAMÍREZ
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA, UNAM.

COMITÉ TUTOR
DRA. JUDITH MARINA MENEZ DÍAZ
FACULTAD DE PSICOLOGÍA, UNAM

DR. EDWARD ARNOLD WASSERMAN
DEPARTMENT OF PSYCHOLOGICAL AND BRAIN SCIENCES, THE UNIVERSITY OF IOWA

Los reyes Iztacala, Tlalnepantla, Estado de México. Septiembre de 2016

We cannot look out into space
without seeing back in time

Neil de Grasse Tyson – *Cosmos:
A spacetime odyssey*

Al día siguiente, Miércoles, José
Arcadio Buendía volvió a entrar al
taller. "Éste es un desastre" -dijo-.
Mira el aire, oye el zumbido del
sol, igual que ayer y antier.
También hoy es Lunes.

Gabriel García Márquez – *Cien
años de soledad.*

El "Aquí" y el "Ahora" sólo
significan algo en términos del
"antes", el "después" y el "allá"

Emilio Ribes – *Sobre el tiempo y
el espacio psicológicos*

Agradecimientos

A mi esposa, Areli, por darme mi pasado, regalarme mi presente y reinventar mi futuro

A mis padres, Leti y Paco, por darme mi vida y enseñarme cómo vivirla

A mis hermanos, Paco, Héctor y Rubén, porque sus batallas me han inspirado a continuar la mía

A mis abuelos, Quico y Lupita, por ser inspiración de cultura, devoción y cariño

A mis abuelos, Toñita y Juan, porque son prueba de que la existencia trasciende el último suspiro

A mis sobrinas, Naty, Camy, Vicky, Vale, y Julieta, porque con cada latido crean y evocan memorias perennes

A mi Familia García Pérez: Cris, Toño, César y Muny, por su demostración ininterrumpida de voluntad y fuerza para los suyos

A mis cuñadas, Idalid y Nallely, porque han sabido ser piedra angular de la vida de seres que amo

Al Dr. Claudio Carpio, por mostrarme las entrañas de la Universidad y enseñarme a vivir en Ella

Al Dr. Edward Wasserman, por la humildad y paciencia que le llevaron a abrirme las puertas de su laboratorio

A la Dra. Marina Menez, por siempre tener a la mano una sonrisa y apoyo para este trabajo

A mis amigos del Laboratorio De Análisis Experimental de la Conducta: Francisco, Mitzi y Sergio. Este trabajo es de Ustedes.

A mis maestros, Virginia, César, German, Héctor y Rosy, porque de ellos he aprendido a ser Universitario

A los peleles, por la amistad y lealtad imperecederas

Index

RESUMEN

Se evalúan los efectos de variabilidad y constancia en la secuencia de localizaciones o en la duración del período de disponibilidad de una tarea de time-place learning de 16 períodos. En un experimento, se expuso a 3 palomas a una tarea de TPL en el que se las respuestas en uno de 4 comederos fueron reforzadas con un programa IA 25s. El comedero correcto cambió cada 3 minutos siguiendo la misma secuencia 4 veces en cada sesión: 1→2→3→4. Posteriormente, se condujeron 50 sesiones en las que la duración permaneció constante en 3 minutos, pero la secuencia de localización del alimento fue aleatoria. Al final de cada condición se corrió una Prueba de Comedero Abierto (OHT). Otro grupo de 3 palomas experimentó las mismas condiciones en orden inverso. Los resultados muestran que ambos grupos fueron capaces de mostrar hallazgos típicos de TPL en la condición de secuencia fija. Por otro lado, no se encontró lo mismo al usar una secuencia variable. En el experimento 2 se entrenó a un grupo de 3 palomas en la condición de secuencia y duración fija durante 50 sesiones para posteriormente someterlos a una condición en la que la duración de cada período de disponibilidad varió entre 1, 2, 3 o 6 min. Otro grupo experimentó las mismas condiciones en el orden inverso. Los resultados muestran que los sujetos pueden mostrar todos los indicadores de TPL bajo la condición de secuencia y duración fijas. Por otro lado, cuando los pichones fueron expuestos a condiciones de variabilidad temporal, no se impidió que los sujetos aprendieran la secuencia de localizaciones y se observa que los sujetos muestran anticipación y otros indicadores típicamente sugerentes de timing a pesar de la variabilidad temporal. Se discuten alternativas explicativas al hallazgo de que la variabilidad espacial genera disrupción en el comportamiento relacionado con las regularidades temporales, pero la variabilidad temporal no impide el contacto con las regularidades espaciales de una tarea de TPL.

Abstract

The effects of regularity or irregularity on the location sequence or the duration of the availability periods in a time-place learning (TPL) task involving 16 availability periods were assessed. In experiment 1, a group of 3 pigeons was exposed to a TPL task in which food could be obtained for responses in 1 of 4 feeders according to a RI 25s schedule of reinforcement. The correct feeder changed every 3 minutes following the same sequence 1→2→3→4 for four times each session. Afterwards, these birds were exposed to a similar condition with the exception that the 4 sequences of food locations in each session were randomized. Birds in group 2 (N= 3) experienced the same conditions in the reverse order. An Open Hopper Test (OHT) was conducted at the end of each session. 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. For experiment 2, a group of 3 birds was exposed to the Fixed sequence and Fixed Duration condition for 50 sessions. Afterwards, birds were put in a second condition in which the same sequence was used but the duration of the availability period was variable: 1, 2, 3, or 6 min long. An OHT followed each training condition. Results from this experiment showed, that birds are able to anticipate both the depletion and upcoming location of food under our 16 period fixed sequence fixed duration task. On the other hand, when put on a variable duration condition, birds are able to learn the fixed sequence involved, moreover, they seem to be timing the periods despite their variable duration. In the general discussion, explanatory alternatives are considered to the main finding that spatial variability precludes subjects from accurately timing regular durations but variable durations do not have the same disruptive effect over them learning the fixed sequences.

INTRODUCTION

THE EXPERIMENTAL STUDY OF BEHAVIOR

A well established fact of the scientific evolution of psychology is that the soul has been historically conceived as an entity of a different ontological nature than that of the body (Ribes, 1990; Carpio, 1992). While one is corruptible and mortal, the other has been thought as incorruptible and transcendental. This dichotomy dominated for centuries all work that would try to shed light on any given aspect of the mental life. This supremacy resulted in logical and philosophical inquiries about the nature of mental life that relied on deduction and induction as their source of data (Hume, 1772/2004, Locke, 1690/1956, Descartes, 1637/1973), thus precluding the use of systematic observation and the hypotheses formulation and testing by means of observation (Like the observation of the stars by Galileo) or direct manipulation of some characteristics of the event (Like Mendel's experiments on genetics).

It was until 1879 in Leipzig, that, an attempt was made to use experimental methods to investigate aspects about mental life, particularly those related to the consciousness and the prints that the objects leave on it as a product of experience. However, this first step kept the assumption that mental life occurs in a different plain of existence than that of the *sensibilia*, while acknowledging the possibility that humans are capable of gaining access to the contents of consciousness via extended training, thus developing the widely described introspeccionist method (Titchener, 1894; 1914).

Roughly at the same time but in a different place, the Russian physiologist Ivan Pétrovich Pavlov (1849-1936) stumbled upon a problematic finding on the course on his research on the gastric reflexes in the dog: The experimental subjects would start to salivate before actually having the food in their mouth (Keller & Schoenfeld, 1950; Le Ny, 1965; Pavlov, 1993). Pavlov (1927) reports having searched the psychological treaties of the time looking for an explanation, but found theoretical developments still deeply embedded with the transcendentalist tradition, and thus he tried to develop his own objective system of methods, descriptions, data, relations and laws reported in his famous work about *The conditioned reflexes* (Pavlov, 1927). In his book, Pavlov describes the method that came to be known as classical conditioning: The approximately simultaneous presentation of two events, one of them, the Unconditioned Stimulus (US) has the power to elicit a strong adaptive response [the Unconditioned Response (UR)], while the other, called Conditioned Stimulus (CS) has no such effect. The typical and widely reported result of such a procedure is that the CS develops the power to produce a similar response to the UR: the Conditioned Response (CR). Pavlov (1927) reported different features of the RC development, maintenance and elimination under a wide number of conditions, such as different temporal relations of the stimuli, the physical nature of the CS and the occasional or definitive omission of one of them among many others.

Just like Keller and Schoenfeld (1950) described, several years before the first English translation of Pavlov’s work, Edward Lee Thorndike (1874-1949) developed an experimental method that turned out to be quite useful to explore the development of novel behavior in problematic situations in animals, particularly cats, dogs and chickens. The general method consists of introducing a hungry animal in a closed box that can be open via a given mechanism, once the box has been open, a piece of food is delivered to the animal. Thorndike (1911) reported that, as training progressed, the animals needed less time to release themselves from the box, suggesting that they learned the effective response to open it.

One extremely valuable aspect of Thorndike’s research is the nature of his methodological description, for, while the theoretical interpretation does keep some transcendentalism, his work laid out the foundations for a psychological science that claimed behavior as a specific and legitimate object for study. The first example of such an attempt was made by Watson (1913) who proposed to eradicate all theories that posited that psychological life was transcendental, metaphysical, unobservable and inaccessible to the scientific scrutiny; and substitute them with the idea that behavior should be the object study of psychology, for it is perfectly observable, measurable, and quantifiable. Moreover, based on Thorndike's (1911) and Pavlov's (1927) findings, he suggested that the laws of causation of behavior should not be looked for in some inner entity, but in environmental factors.

This *behaviorist manifesto,* had a huge impact on the emerging experimental discipline of psychology particularly in the United States, where figures such as Tolman, Guthrie, Hull and Skinner attempted to develop comprehensive theoretical systems, which, while different, shared at least two fundamental assumptions:

- Psychology should be objective and rigorous in its observation, recording, experimental methods and data analysis.
- The observable and measurable behavior should be the critical datum around which to build theories, assumptions and hypotheses.

For many reasons, the impact of Skinner's work (Skinner, 1938) had the biggest immediate impact in psychology (Schwartz, 1978). He posited that behavior should be understood as the actions carried on by any given organism in response to any given environmental situation, and that this, and only this, should be the object of psychological studies. He also identified two different kinds of behavior. The first one, respondent behavior was defined as an action that is produced by an antecedent stimulus. The second one lacks of a clearly identified provoking stimulus and produces changes in the environment: Operant behavior. Pavlov's (1927) work would be a prototypical example of respondent conditioning; while Thorndike (1911) was considered to be conditioning operant responses.

The basic notions described and proposed by Skinner served to create an enormous theoretical, but mainly methodological tradition. Procedures like the free operant (Skinner, 1938; Ferster, 1953; Morris, 1987), stimulus control (Reynolds, 1961; Terrace, 1966; Dube & McIlvane, 1997; Carpio, Serrano & Camacho, 2006), schedules of reinforcement (Ferster & Skinner, 1957; Dews, 1962; Farmer & Schoenfeld, 1966; Felton & Lyon, 1966; Schoenfeld, 1970; Schoenfeld & Farmer, 1970), and avoidance (Sidman, 1953; 1955; Anger, 1963; Bolles & Popp, 1964), were widely used to explore a large number of basic psychological phenomena and to work on applied scenarios (e.g. Ayllon & Haughton, 1962; Hansen, 1979, Van Camp, Lerman, Kelley, Contrucci, & Vorndran, 2000).

Skinner himself (1953; 1968) and many others (e.g. Ayllon & Hughes, 1971; Pitts & Powers, 1971; Schwitzgebel & Kolb, 1974) attempted operationalist descriptions of many different scenarios of human life, holding tightly to the commitment of describing and explaining the psychological events in terms of the operations, both organic and environmental, involved.

The way that Skinner´s (1938) assumptions worked as a major paradigm in psychology has been extensively described by others (Ribes & López, 1985; Carpio, 1992; 1994, 2009), however, this theory entailed several deficiencies and inadequacies that were made clear over the years and contributed to its eventual demise. The first class of these inadequacies was related to conceptual issues, such as the definition of reinforcement or contingency (Bruner, 1991; Ribes, 1991); the second one was the impossibility to create a satisfactory and coherent explanation of a growing body of experimental findings (Cabrer, Daza & Ribes, 1975; Ribes & López, 1985); and the last were methodological difficulties such as those described extensively by Schoenfeld and Cole (1972).

One of the conceptual difficulties most often cited is the very definition of reinforcement. As Ribes (1991) and Carpio (1992) point out, the reinforcer is thought to be the stimulus that, when presented in a contingent manner to the emission of any given operant, has the typical effect of affecting the strength of the operant reflex. The main issue here is that the reinforcer plays a double, and conflicting role as member of the relation and third factor affecting its strength.

On the other hand, Skinner (1938) originally described contingency as a *dependence* relation, i.e. the reinforcer was dependent upon the emission of the response; however, ten years later he published a paper in which he found that the temporally regular presentation of a reinforcer, was enough to observe highly defined changes in the general activity pattern of pigeons, more specifically, the emission rate of some responses (different for each pigeon) increased dramatically, and, response chains of several different topographies were formed

(Skinner, 1948). Interpreting this finding was hard, particularly because it was evident that the dependence relation between response and reinforcer was found to be unnecessary to increase the rate of an operant. According to Bruner (1991), this, among other findings, forced the reduction of the contingency notion to that of temporal contiguity, claiming that dependence was merely one way to obtain and assure such contiguity. At this point, the theoretical system runs an important crumbling risk, because if contingency, a defining trait of the proposed taxonomy, is reduced to temporal contiguity, then we are left with no clear criterion to distinguish between the categories, thus rendering the system obsolete, at least in terms of classification, and opening the doors to the return of old questions like those concerned with the possibility for the existence of only one response mechanism (Konorski & Miller, 1937; Skinner, 1937; Tarpy & Mayer, 1979; Domjan, 2016).

At least two methodological restrictions have been found in the analysis of the behaviorist tradition *a la* Skinner (1938). The first was denounced by Schoenfeld and Cole (1972): In the reinforcement schedules the typical independent variable must be the rate and temporal distribution of reinforcement, while the rate and temporal distribution of response are usually considered to be a dependent variable, however, in many schedules, particularly those that are ratio based, the temporal distribution of reinforcement depends upon the temporal distribution of the response, thus, there is an impossibility to differentiate between dependent and independent variable, a methodologically untenable situation.

The second methodological restraint imposed by the traditional behaviorist framework, is that, understanding behavior as a reflex composed of class of events that covary in time has discouraged the exploration of spatial parameters of stimulation and response (Ribes & López, 1985; Ribes, 1992; Carpio, 1994; 2009). This situation has promoted a strong asymmetry between work devoted to explore temporal parameters and those involved in the exploration of the spatial dimension of behavior[1].

The last group of irregularities that, promoted the demise of the conditioning theory was the inability of the system to give a satisfactory and coherent explanation of the growing body of anomalous data, thus creating *ad hoc* categories and *microtheories* that compromise the evolution of a general, comprehensive theoretical framework about behavior (Cabrer, Daza & Ribes, 1975; Ribes & López, 1985; Bruner, 1991 Carpio, 1992; 1994;). The case of *superstitious behavior* has already been described: a complex pattern of responding appears in a situation where the reinforcer will be delivered regardless of the animal's behavior (Skinner, 1948). Another anomaly was that reported by Brown and Jenkins (1968) who used an arrangement consisting of the paired presentation of food and an illuminated key, and found that after some essays, the pigeons used as subjects would consistently peck the key despite the fact that no response was required to present the food. This finding was, again, interpreted as the emergence of an operant in a non-contingent situation, the rationale was that Brown and Jenkins found a method to automatically shape an operant response, thus the term, *autoshaping*.

This interpretation is problematic because in order to assert that the observed behavior is operant, one has to disregard the original notion of the operant, for it is defined in terms of the contingency system involved, in which the reinforcer is contingent upon the response, an aspect evidently missing in the autoshaping procedure.

The third kind of anomalous datum in conditioning theory is the consistent finding of emergent patterns of behavior in temporally based schedules of reinforcement such as Differential Low Rate (DRL) schedule (Wilson & Keller, 1953; Hodos, Ross & Brady, 1962; Laties *et al,* 1965), or Fixed Interval (FI) schedule (Staddon & Simmelhag, 1971; Roper, 1978; Porter, Brown, & Goldsmith, 1982). These patterns have received a wide number of names such as collateral

---

[1] As will be seen ahead in the paper, most work on the spatial dimension of behavior has come from either cognitive Psychology or Behavioral Ecology.

(Bruner & Revusky, 1961; Glazer & Sing, 1971; Stein, Hoffman & Stitt, 1971), adjunctive (Falk, 1966; Roper, 1978; Porter, Brown, & Goldsmith, 1982) or mediating (Segal-Rechtschaffen, 1963; Laties, Weiss, Clark & Reynolds, 1965; Laties, Weiss & Weiss, 1969) behavior. Some authors (e.g. Ferster & Skinner, 1957 Laties *et al,* 1965; 1969) proposed that these patterns served as "Behavior occurring between two instances of the response under study … which is used by the organism as a control stimulus for subsequent behavior" (Ferster & Skinner, 1957 p. 729)**.** On the other hand, authors like Bruner and Revusky (1961) posited that these patterns emerged incidentally as a by-product of the temporally based schedules due to the effect of the operant reinforcement, thus, increasing the rate and altering the temporal distribution of their components. A different, although somewhat similar case is that reported by Falk (1966) who found that a food deprived animal under a schedule of reinforcement drinks enormous amounts of water during the experimental sessions (up to two times the normal daily consumptions) despite the fact of having *ad lib* access to water. Just like the examples described above, Falk decided to establish a new category for this particular finding, and chose the termed adjunctive behavior in order to bring attention to the fact that these changes were a product of the reinforcement contingencies involved.

The continuous emergence of *ad hoc* categories to explain and describe an extremely narrow set of findings is an undesirable way to proceed, especially when they cannot be adequately included in the system that fostered the research that originated them (Cabrer, Daza & Ribes, 1975).

According to Kuhn (1970), scenarios like this commonly serve as breeding ground to the creation of new ways to conceive the realm of a given discipline or the recovery of long forgotten and discarded assumptions. Psychology has not been the exception, and during the 60's and 70´s, a major strategy was evident and a wide number of researchers were involved in what came to be known as the *Cognitive Revolution* (Miller, 2003).

As expected, the operationalist method was gradually left behind in favor of diverse strategies of research and theorization about the nature of psychological events. One of these, and perhaps the most common, was a return to theories that assigned a major role to processes of hypothetical nature assumed to be necessary for the adjustment of behavior to the environment: *cognition*. Terms such as *perception, memory, retrieval, information, thought and problem solving* are understood as different aspects or stages of cognition (Neisser, 1967).

The definitive abandonment of the operationalist posture carried within the theoretical license to postulate hypothetical entities, processes and phenomena. This promoted an exponential growth of research that involved different phenomena and methodological strategies to understand them. This situation was clearly manifested in at least two approaches to the study of psychological phenomena: revisiting old and unsolved problems for the conditioning theory and trying to use a cognitive vision to solve them; and the exploration and experimentation of situations forgotten by the previous theory.

A clear example of an attempt to reinterpret the data produced under the operationalist tradition has been the development of theories devoted to explore how do organisms adjust their behavior to temporally based contingencies (i.e. the roar of timing theories). On the other hand, a clear example of how did this *new* approach allowed psychologists to learn about the localization of objects within their visual field, and in the environment in which they are immerse, (i.e. spatial learning theories).

The influential position of timing theories reflects the preponderant role assigned to the *time factor* on the study of behavior under both the traditional behaviorist standpoint and the cognitive view. On the other hand, the growing interest on the effects of spatial parameters on behavior has presented a valuable opportunity to expand the scope of psychological research.

THE STUDY OF THE TIME AND PLACE OF BEHAVIOR

Psychologists chose to propose different hypothetical mechanisms in order to explain the observed behavior in the face of the different difficulties that weighted over the conditioning theory. Naturally, this strategy has been kept in the areas of learning about temporal contingencies, and spatial features of the environment.

This way has proven useful not only to re-interpret what is known about different psychological phenomena, but also to generate new methods and theories to understand them, a clear example of this is the research done on the behavior under temporally based contingencies. A very common assumption has been the existence of a learning process responsible for the adjustment of behavior to these situations: Timing.

TIMING: THE ORGANISM THAT MOVES THROUGH TIME

Timing is considered to be one of the most ubiquitous phenomenon in psychology, and it refers to the ability of different species to keep track of the passage of time and make roughly accurate judgments about interval lengths, stimuli duration, etc. (Gibbon, 1977). One of the first papers that showed this ability in animals was the research carried on by Pavlov (1927) on the *temporal conditioning* procedure, which consisted of presenting only the US at regular intervals. Pavlov, using food as US and dogs as subjects, found that they tended to salivate more as the trial progressed reaching the maximum level of response just before the food was presented. This finding suggests that the dogs were somehow keeping track of the time elapsed since the last US presentation.

Some of the challenges entailed by the performance of animals under temporally based schedules of reinforcement were reviewed in the previous section, one of these findings was the pattern described by the temporal distribution of the response under *FI*, which has been described as a *scallop:*

immediately after a reinforcer is delivered, the animal ceases to respond for a period of time, this post-reinforcement pause is followed by a period of responding under a progressively increasing rate that reaches its peak value immediately before the next reinforcer (Ferster & Skinner, 1957; Skinner & Morse, 1957; Morse, 1966; Catania, 1970; Dews, 1962, 1965, 1978).

Another schedule of reinforcement widely used to explore how animals adjust their behavior to temporally based contingencies is the *DRL* (Wilson & Keller, 1953; Hodos, Ross & Brady, 1962; Holz, Azrin & Ulrich, 1963). According to this schedule, just like FI, a reinforcer is delivered for a response emitted once after an interval has elapsed, with the difference that the time marker that starts the clock is the last response emitted, so the subject has to space his responses in time in order to obtain a reinforcer. The typical finding using this schedule is that subjects space their responding, and the mean value of the inter-response time (IRT) is roughly similar to the criterion value, which, again, suggests that the subjects are keeping track of time (Wilson & Keller, 1953; Ferster & Skinner, 1957; Bruner & Revusky, 1961; Hodos, Ross & Brady, 1962).

Additional evidence of the timing abilities of animals is that provided by studies using the *peak procedure* (Catania, 1970; Roberts, 1981). This procedure is quite similar to an FI, with the exception that, interspersed with the typical FI trials there are *peak trials* that last twice or thrice as long as the FI trial and in which the presentation of the reinforcer is omitted. The measure of interest in this procedure is the temporal distribution of response during peak trials. This distribution typically describes a bitonic ascendant-descendent function that reaches its peak around the moment of reinforcer delivery on the FI trials (Roberts, 1981; Hinton & Meck, 2004; Buhusi & Meck, 2007). This finding has been typically interpreted as evidence that the subjects not only keep track of time, but also remember the moment in which reinforcement usually occurs. Kirkpatrick-Steger, Miller, Betti and Wasserman (1996) have produced evidence suggesting that there are fundamentally two sources of control of performance under peak procedures. The first one is learning to start responding around the FI value, and the second one is to stop responding once this value has elapsed and then reset the timing mechanism. Using an interesting modification of the peak procedure, they added peak trials up to 4 times longer than the FI value (4x trials). They found more than one peak on these 4x trials, which suggested that subjects restart their timing when they stop responding.

Another procedure used to test the timing abilities of animals is the *temporal generalization* task (Church & Gibbon, 1982). This method consists of training the animal in a discrimination procedure in which the relevant trait of the stimulus is duration. Interspersed with training sessions, the animals receive probe sessions in which stimulus of several durations are presented including the trained one, and no reinforcer is presented for responses made to any of these. The fundamental measure in these arrangements is usually the proportion of trials in which the animal responds for each duration during the probe sessions. If the subjects are timing the duration of the different stimuli then a generalization gradient should be found, if on the other hand the subjects are guiding their responses by means of any other trait of the stimuli then no such gradient should appear. The most common fining is a generalization gradient that, as expected, has its peak value in the trained duration (Heinemann, 1984; Kristoffferson, 1984; Droit-Volet & Clement, 2001).

Keeping in line with the procedures designed to test the timing abilities for stimuli durations is the *temporal bisection* task. In this procedure, the subject is presented, trial to trial, with a stimulus of one of two durations, and is given opportunity to respond on one of two operanda. Responses on one of them are correct (followed by reinforcement) if the short duration stimulus was presented and responses on the other have this consequence only for trials in which the long duration stimulus was presented. Responses on the incorrect lever have no consequences. Subjects have been shown to master this task, so once this training has been successfully established, probe sessions begin. In them, the subject is presented with stimuli of intermediate durations between the long and the short ones employed during training, and the same response options are presented. The rationale is that the response choice selected by the subject shows whether he reckons that the duration presented is the short or long one. The typical finding is that the proportion of long choices as a function of the duration of the stimulus, describes an ogival pattern, having the lowest point at the shorter durations and the highest point at the longest durations (Church & Deluty, 1977; Siegel, 1986; Allan & Gibbon, 1991).

The attempted explanations for the findings described in the last paragraphs have been many; however, there are three strongly influential theories in the timing field.

The first one is essentially cognitive and has been distinguished for the impact it has upon timing research by providing explanation to a wide range of events, and allowing to generate new methods to explore timing: The Scalar Expectancy Theory (SET).

SET was originally proposed by Gibbon (1977) and the formulation lies critically in one feature of the timing behavior observed in many different situations: the scalar property. This refers to the fact that even though the specific traits of the temporal distribution of behavior are different depending on the values of the schedule involved, the general pattern stays the same. There are two quantitative properties of scalar timing: Superposition of curves and equality of the coefficient of variation. The first one is shown when the temporal distribution of response under different values of the same schedule is plotted in a logarithmic scale and they tend to superimpose. On the other hand, since the timing process is carried in a scalar manner, the error (or variance) produced by such reckoning will tend to be proportional to the duration to be timed, and thus the coefficient of variation will remain roughly constant across different durations (Gibbon, 1977; 1991).

SET proposes a cognitive timing process that has resulted to be quite elegant. The basic idea is that an internal clock that emits pulses at a given rate all the time; under certain conditions (e.g. the onset of a stimulus or the delivery of food) a switch closes and allows the pulses into an accumulator where they are stored as time elapses. The pulses are continuously transferred to the working memory, once there; a comparator mechanism contrasts the current value with a long-term storage containing the value associated with reinforcement. This way the animal’s decision (e.g. choose “long” on temporal bisection, or “respond” on FI) is based on how close these values are. The scalar property in this mechanism lies in the fact that this comparator works based on overall ratios rather than specific values thus, whenever the ratio current/stored approaches 1, regardless of the specific values involved, the animal will make a choice (Gibbon, 1991).

The pacemaker idea has had a deep influence in timing research; the perfect example for this statement is the fact that Killeen and Fetterman’s (1988) Behavioral Theory of Timing (BeT) keeps the idea of an internal pacemaker. In short, BeT suggests that the collateral activity patterns reported to emerge on temporally regular tasks is critical for adequate timing, for it is through the transitions between the different components of these patterns that the animals keep the track of time. However, the endogenous mechanism responsible for these transitions is an oscillator that emits pulses on a given rate, this way, every time a pulse is recorded the animal has a cue to change his behavioral state and this allows him to time intervals and stimuli duration.

Machado (1997) proposed a theory based on BeT: Learning to Time Theory (LeT). Machado also holds the idea that the behavioral states are critical for timing, but removes from his timing mechanism any pacemaker whatsoever. LeT has three major components: A sequence of behavioral states comprised of any given topography of response; associative vectors of different strength among them and with the operant response; and the operant response itself. The rationale is as follows: the activation levels of each of these states changes as time passes, the strength of each vector, which is determined by temporal contiguity, defines which state will be more active at any moment. The fact that each of these states not only has associative links with other states but also with the operant response is important, because this is how LeT explains the temporally precise emission of the operant response: As the states are temporally closer to the operant, the activation level of the operant rises, reaching its maximum following the immediate last state. Once a reinforcer is delivered all the vector links, change their strength, being those closer to the reinforcer the ones which will increase the most.

An interesting recent development is that of Savsatano and Miller (1998), they proposed a time-based theory to account for the data on Pavlovian conditioning, for, the information hypothesis (Rescorla & Wagner, 1972) does not consider temporal relations between the involved stimuli to be crucial for the establishment of conditioning. They described some non-compatible evidence for the information hypothesis and proposed the notion of *temporal map* to account for them. In their own words, this temporal coding hypothesis *"… can be summarized as follows: (1) Temporal contiguity alone is necessary and sufficient for the temporal formation of an association. (2) The temporal relationship between the associated events is automatically encoded as part of the association (i.e. subjects form temporal maps that link events in memory. (3) This temporal information plays a critical role in the nature magnitude and timing of the conditioned response elicited when one of the associates is subsequently presented (4) animals can superimpose maps when elements common to these maps are presented together, even when elements were trained separately*." (Savastano & Miller, 1998, p. 151). The authors later on provide experimental evidence for each of these four defining traits of their theory.

These theories, particularly, SET, BeT, and LeT, have been successfully applied to describe and explain the data thrown by most of the previously described procedures, of course, there are some experimental situations in which dissociate hypotheses can be derived from each of them, however, not one of these theories can be, heretofore, completely ruled out.

So far, in this paper an attempt has been made to show the impact of the cognitive view in an area that deeply troubled Skinnerian behavior analysis: the temporal adjustment of behavior. The basic procedures and dominant theories have been described, but the main idea is that there has been a continuous interest in explaining the timing phenomenon across diverse experimental situations, and the use of cognitive categories is quite common in the description of this kind of psychological event (e.g. Church, 1984). The next section will illustrate a second effect that the paradigm shift in experimental psychology brought: how several aspects worthy of study are recovered and explored.

PLACE LEARNING: THE ORGANISM THAT MOVES IN SPACE

For many reasons, discussed at length in other papers, the systematic exploration of the spatial dimension of stimulation and response was ignored by the experimental analysis of behavior (Ribes, 1992), however, it must be pointed out that, with the paradigmatic shift described pages above, a renewed interest in this kind of study has been quite palpable.

Perhaps one of the first experimentalists interested in the study of the spatial dimension of behavior was Kupalov (1983) who was concerned with the *Situational conditioned reflex*. He coined this term to refer to a procedure employed by him and his colleagues. The task consisted of providing a hungry dog with a piece of food only if it would stand on an arbitrary defined quadrant of the experimental room. The main finding reported by Kupalov is that the dogs tended to spend the majority of the session time in this quadrant, suggesting that they were perfectly capable of keeping track of where they were. Although nowadays this procedure would strike the reader as clearly operant, Kupalov thought he was dealing with a conditioned reflex of the same nature as those of his mentor Pavlov, which is probably why he attempted an explanation based on Pavlov's laws of the conditioned reflex.

The classic procedure designed to study how does an animal moves successfully in its surroundings has been the maze. This procedure was extensively used by many researchers. A notable example of one of them was Edward Tolman (1886-1959), who in his classic paper (Tolman, 1948) used a wide variety of mazes designed to explore how rats learn to move efficiently around the environment in order to obtain food. Tolman found that rats not only could find the food progressively faster, but also were also able to improvise new routes to the food when typical roads were blocked. This suggested to him that, during each trial, the rat was developing a cognitive map of the maze (Tolman, 1948). Ever since Tolman's work, numerous reports of animals adjusting their behavior in a wide variety of mazes have been reported (Gallistel, 1990).

An alternate interpretation of data like those of Tolman was provided by Hull (1943) who claimed that animals did not form mental representations of the maze, but instead, they were learning a more or less specific set of habits to move successfully across it and repeated them, thus, strengthening the habit. Cole, Clipperton and Walt (2007) report that this has been a long historical dispute in the spatial learning area, and there are studies that support the cognitive map view, but there are also data supporting the habit formation view. However, perhaps for representing a more appealing view, the idea that the animals are capable of developing cognitive maps has been quite dominant in this field of research.

Evidence for this claim is provided by the fact that nearly thirty years after Tolman´s (1948) paper was published, O’Keefe and Nadel (1978) published a book reporting data from their own laboratory and other researchers work in which they argue that the animals are capable of forming cognitive representations of their environment, but this time, not only through maze studies, but by means of data obtained through observation of behavior of many different species in natural settings. These authors tried to bring this topic even one step further and presented evidence that the hippocampus is a critical brain structure for the proper development of such maps.

Finally, Gallistel’s (1990) influential work has also supported the notion of the emergence of cognitive representation of the geometrical relations between the different objects in a given surrounding, and took it one step further in trying to analyze two things: How does an animal successfully moves in an environment lacking of such objects (like open seas or the desert), and what strategies are used by the animals in order to adequately employ these maps? Based on an extensive review of studies carried on by many researchers, Gallistel posits that the basic mechanism that answers both questions is the same: *Navigation.*

According to Gallistel (1990), navigation consists of maintaining a heading and a route in space. In order to achieve this, an animal may rely on one of two strategies: *dead reckoning* and *piloting.*

Dead reckoning refers to the ability of several species to compute their current position in space based on their heading, their velocity (directed speed), and the travel time. Gallistel offers evidence that a wide variety of species are capable of such complex computing, for instance, ants have been observed to leave their nests in search for food following a tortuous route while doing so, but, once they found it, they establish their heading towards the nest and return to it following a straight line (Gallistel, 1990). Even more compelling evidence is provided by studies in which an ant is captured 20 feet north from its nest and released in other place; once put down, the ant will walk approximately 20 feet south and then will stop, which suggests that it is searching for its nest. This finding clearly shows how these insects are not randomly moving through space, they are thought to be continuously reckoning where they are, and this information serves to direct their search for food, or their nest.

On the other hand, the piloting mechanism refers to the capacity to use known landmarks to establish and follow a route. A perfect example for the use of this kind of mechanism are birds that use trees, rocks or streams to successfully fly back to their nest after a foraging trip (Gallistel, 1990).

Finally, Gallistel posited that these mechanisms are successfully used only because they are anchored to a cognitive representation of the geometric relations of the objects in the space, (i.e. a cognitive map). Thus, as Bennet (1996) points out, Gallistel's notion of cognitive map is slightly different from Tolman's and O'Keeffe and Nadel's approach because while the latter think the emergence of novel displacement routes as the critical feature of the map, for the former, the successful displacement through space is evidence enough of the existence of this representation.

During this last brief section, a review of the main theoretical frameworks about place learning has been done. The predominance of the cognitive view in this field is evident. Most of the theories about spatial learning involve critical features of a cognitive theory: representations, information processing and behavioral outputs.

So far it has been shown how research has been made on the temporal and the spatial dimension of behavior separately; however, a promising growing body of experimental literature has been attempting to explore the adjustment of the behavior of many different species to contingencies in which food (or any other crucial resource) availability is constrained by both time and space parameters.

TIME-PLACE LEARNING: THE ORGANISM THAT MOVES MOMENT TO MOMENT FROM ONE PLACE TO ANOTHER

So far, the present review has centered upon the theoretical and methodological developments designed to shed light on timing and place learning, however, as many authors point out (Staddon, 1983; Biebach, Gordijn & Krebs, 1989; Gallistel, 1990; Wilkie & Wilson, 1992; Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Hallet & Wilkie, 2007; Thorpe, & Wilkie, 2006 Crystal, 2009) the need to secure resources with a limited spatial and temporal availability is a major pressure for the adequate adjustment of many species to their environment.

A wide number of species have been shown to successfully learn about the temporal and spatial constraints of food (or many other resources) availability. As expected, this fact has prompted many researchers to focus their attention to understand how animals learn about these constraints. According to Wilkie and Wilson (1992) these attempts have come originally from the literature on *foraging* in the Behavioral Ecology field, and it refers to the general ability of animals to find resources and exploit them, it is not surprising then that a good share of the research done about joint spatio-temporal control of behavior involves naturalistic observations (Gallistel, 1990; Wilkie & Wilson, 1992).

The first experimental efforts to understand Time-Place Learning (TPL) have been made somewhat recently; however, the number of studies is enough so that some authors have attempted to classify them in two general types of tasks (e.g. Carr, Tan, Thorpe & Wilkie, 2001; Thorpe & Wilkie, 2006; Thorpe, Hallet & Wilkie, 2007; Crystal, 2009). The first one involves more than one feeding point, and the specific place in which food can be obtained changes in an orderly fashion according to the time of day, thus receiving the name *Daily Time-Place Learning tasks* (Biebach, Gordijn & Krebs, 1989; Krebs & Biebach, 1989; Biebach; Falk & Krebs, 1991; Falk, Biebach & Krebs, 1992; Biebach; Krebs & Falk; 1994 Carr &

Wilkie, 1997; Pizzo & Crystal, 2002). And the second one is the same with the exception that the period of availability is in the order of seconds to minutes, thus receiving the name *Interval Time-Place Learning tasks* (e.g. Wilkie & Wilson, 1992; Wilkie, Saksida, Samson & Lee, 1994; Crystal & Miller, 2002; Pizzo & Crystal, 2004; Thorpe & Wilkie, 2006; Thorpe, Hallet & Wilkie, 2007).

DAILY TPL: THE CONTROL OF MOVEMENT BY TIME OF DAY

The first published paper that approached TPL from an experimental perspective was the study carried on by Biebach, Gordijn and Krebs (1989). They were interested in testing whether garden warblers (*Sylvia Borin*) were able to show TPL. They trained the birds in a Daily TPL task in which there were five rooms, one in the center and one on each of the four sides of the central room. The animal was put on the centre at the start of the session; after 280 seconds the doors of the four rooms were open and the animal was free to choose any of the four rooms, only one of these (i.e. the "correct" room) would contain an active feeder. The particular correct room changed across time in periods of 3h; once every room had served as the correct one, the session ended. Once the animals reached an asymptotic level of correct choices, the contingencies were altered, and during these probe sessions, food could be obtained in any of the four rooms each opportunity. Biebach *et al.* found not only that birds could demonstrably master this task, and visit the correct feeder at the correct times , but that during the probe sessions the pattern of visits remained relatively unaltered, suggesting that, even though they could obtain food in any room, they learned that the spatio-temporal contingencies of training must be followed.

Having demonstrated that garden warblers are capable of showing TPL , Krebs and Biebach (1989) designed an experiment to assess the strategy used by these birds to displace successfully around the experimental chamber, testing two different possibilities: 1) The birds learn a fix route through the rooms; 2)The animals form a map. The training procedure was exactly like the one described in the last paragraph, and once TPL was established the probe phase began. These sessions were like training with the difference that the bird was locked in the central compartment during one of two periods, from 06:00 – 10:00, and 12:00-16:00 (timeout periods), thus precluding the animals to have access to one of the four rooms each session. The rationale is that if the animals learn routes then, once they are free, they should choose the room that would have been active during the timeout period (for this would be the next correct room in the sequence); on the other hand, if some kind of map is created then they should choose the correct room for the moment they are free regardless of the timeout period. The authors found that birds chose the correct feeder for the time they were freed, which suggests that in these tasks the animals do not learn fixed routes or patterns; they learn the association between the place and the time of day where food can be found.

Falk, Biebach and Krebs (1992) reasoned that the ability to learn spatio-temporal regularities of food availability could be strongly tied to the natural feeding habits the particular species involved; for it would be reasonable to suppose that living prey, such as insects, imply narrower windows of availability than that of leaf or grain. They compared the performance on a daily TPL task of an insectivorous bird (*Ploceus bicolor*) against a granivorous one (*Euplectes hordeaceus*). They used training identical to that of Krebs and Biebach (1989), with four feeding sites and periods of availability, that varied along the day, but they used different probe sessions:

1. *Blocking.* From 06:00 to 9:00 food could be obtained by entering the room 1, just like in training sessions. On the other hand, from 9:00 to 13:00 the animal remained locked in the central compartment of the chamber, during the period that room 2 should provide food and one hour into the room 3 period. At 13:00 all feeders were reopen.

2. *Phase Shift.* The normal light-dark (12:12) cycle was altered by shortening the dark period six hours immediately before these probe sessions.

The results of the training phase show that both birds are perfectly capable of showing TPL: A high number of correct choices and a tendency to restrict all entries to the temporally correct room. However strong differences were apparent during the probe sessions. In the blocking phase the insectivorous birds showed a marked tendency to choose room 2, (the next in the sequence); but choices made by the granivorous species seem to be at random. Moreover, during the phase shift condition, the insectivorous birds adjusted, although incompletely their pattern of visiting, switching it by about 2 hours; meanwhile the pattern disappeared for the granivorous birds.

These findings were discussed by the authors in terms of the possible differences imposed by the species typical feeding habits on the ability to display TPL. However, two particular results received special attention; first, the fact that a granivorous species of bird is capable of showing TPL and the second is that none of their subjects adjusted their visits for the six hours of phase shifts. This fact was interpreted by the authors as evidence that the animals are not timing their visits in terms of intervals elapsed between events (such as lights on), and they are rather relying on the phase of a circadian oscillator to guide their choice.

The study by Falk, Biebach and Krebs (1992) had remarkable implications for the nature of the timing mechanism assumed to be involved in Daily TPL. Their data suggested that birds were not timing intervals but rather relying on a circadian oscillator in order to guide their room choice. Biebach, Falk and Krebs (1991) reported an experiment explicitly designed to test the timing mechanism involved in Daly TPL. After the typical training procedure, they used one of two phase shifts for each subject: forwarding the cycle by six hours, or delaying it by the same amount. If birds were using an interval based timing mechanism, they should adjust the visiting pattern (forward or backwards) completely; if, on the other hand the mechanism lies on circadian rhythms, then no such adjustment should be observed. They found the latter possibility to be true, for none of their birds forwarded or delayed the pattern of room visits. These findings point to a circadian oscillator as a dominant timing system in these tasks.

Biebach, Falk and Krebs (1994) found a methodological deficiency in the former studies: the rate of food deliveries remained constant throughout the entire availability period; this situation does not mimic the fact that food typically runs out as the animal eats it in natural settings, therefore, TPL could be deeply affected by local changes in the rate of food delivery in a TPL task. They made some modifications to the traditional training method; the key difference is that they divided each availability period in three identical intervals. During the first one the rate of food deliveries was increased monotonically, during the second interval the final rate reached at the first one was maintained constant, and during the final part of the period the rate was progressively taken to zero. Having completed this training they carried three probe conditions. The first one was making food available on every room every trial with one of three rates of delivery: low, medium and high. The second condition consisted on delaying or forwarding the availability periods for one or two hours and the third condition was to conduct training sessions with the pattern of food availability forwarded by one hour.

The results of the training phase reflected that, even under changing rate of food deliveries, the animals were capable of displaying TPL, as shown by the increase in the correct choices as training progressed. Moreover, the visiting pattern learned during training persisted during the "all feeders active" phase, although differences were observed between performances in each of the rate conditions: as the rate decreases, the alternations between rooms increase. Finally, forwarding by one hour the pattern of rate delivery was accompanied by a one-hour forwarding of the visiting pattern for the same room.

These findings shows that local changes in food delivery rate can alter the feeding patterns of the subjects, of particular interest was the finding that a minor rate of food delivery is accompanied by more alternation between feeding choices. On the other hand, the fact that subjects adjusted their pattern as a product of the change in the rate progression suggests that, at least partially, an interval based timing mechanism should be involved, and it must operate in coordination with the circadian based mechanism to determine the time based behavior of these subjects.

An additional study in which the effects of different feeding rates in a TPL task can be seen is the experiment by Fetterman and Killeen (1995), who used three keys on which pigeons had to peck in order to obtain food, however, only one of these keys was operational for a given period of time. The authors varied the duration of availability intervals in each of these keys and the proportion of reinforced trials (feed rate). They found proportional changes in the temporal distribution of response as a result of changes in the periods of availability, and, as Biebach, Falk and Krebs (1994); they also found changes in the response patterns as a result of changes in the feeding rate in each point.

While the work of Biebach and his colleagues was extensive, they have not been the only ones interested in elucidating the nature and reach of daily TPL. Saksida and Wilkie (1994) conducted an experiment to test whether pigeons could also display daily TPL. They exposed 4 pigeons to a design in which pecks on one key provided food according to a Variable Interval (VI) schedule of reinforcement on morning sessions, and pecks on a different key provided food according to the same schedule during afternoon sessions. These birds quickly began responding mostly on the appropriate key for each type of session. Then testing began, one test was to skip either the morning or the afternoon session and record where the pigeon would peck. They found that pigeons would still restrict the majority of their responses to the temporally correct key, despite the obvious fact that no reinforcement was available during these tests. The second test they conducted was to displace the temporal location of the morning and afternoon sessions, either bringing them closer or farther away. The rationale of this test is that if birds are responding according to an ordinal strategy, they should not be affected by this manipulation, for the order remains the same; on the other hand, if they responded according to a circadian or interval strategy (i.e. according to time of day, or time since a given event), then this test would generate a sensitive increase in the error rate of the subjects. They found the latter case to be true.

The third test conducted by Saksida and Wilkie (1994) was to alter the light: dark cycle for the birds. If birds were using an interval strategy entrained to an event such as “Lights on”, then there should be a considerable immediate effect of this cycle change. On the other hand, since circadian timing is said to be self-sustaining, the effect of this manipulation would have to be developed over time, as the oscillator becomes gradually entrained to the new light: dark cycle. The results were quite clear: There was no effect of the cycle change after 6 days of training. Taken together, the results from training and the three different testing suggests that a circadian strategy is the best option to describe the pigeon´s behavior under these circumstances.

So far, several daily TPL studies have been described, and they all share one particular feature: They were carried out with birds. Evidence for TPL on a different *class*, comes from the classic studies by Reebs (1993, 1996, 1999). In his first experiment, Reebs (1993) conducted a series of test of daily TPL with golden Shiners. A group of fishes living in an aquarium faced the following experimental conditions: In experiment 1, the air supply of the aquarium filter was turned off (signal) 1 minute before food would be delivered on one of four corners of the aquarium (always the same corner). This operation was repeated four times through the day: 08:30; 11:30; 14:30 and 17:30. Reebs found that fish could effectively respond to the signal-food association, for, after 10 days, subjects would spend most of the signal – food interval on the target corner. The same basic operation was carried for experiment II with the exception that food was delivered on one corner on morning (08:30 and 11: 30) sessions and on a different corner for afternoon (14:30 and 17:30) sessions. Reebs (1993) established a *time-place learning* criterion: If, after the signal, a fish would spend more time on the temporally correct corner than on any other corner for two consecutive days, then the TPL criterion was met. After 18 days of training, fish would spend most of the signal – food interval (up to 80%) on either the morning or the afternoon corners, which implies that they learned about where food could be obtained. However, the time spent on morning and afternoon corners was not correlated with the morning or afternoon session, thus, fish in experiment II did not met the TPL criterion. Experiment III was the same as experiments I and II with the exception that each session (08:30; 11:30; 14:30 and 17:30), now was associated with a different feeding corner. Under these conditions, Reebs found that there was not a clear preference for the correct corner on each session. After the signal started, fish would rapidly move through the four corners of the aquarium in an apparent search for food instead of going exclusively to the temporally correct corner, again, TPL criterion was not met.

At this point, there is a series of reasons that might have prevented an adequate TPL in the first three experiments: The size of the aquarium, the fact that fishes were tested in groups, and a relatively short training period. Reebs (1993) conducted a fourth experiment in which he used larger aquaria, he tested only solitary fishes (no groups), and he conducted only two sessions per day: morning (10:00) and afternoon (16:00) and he extended the training period to 30 days. He found that even under these conditions, all fish failed to reach the TPL criterion, for; fish would start swimming back and forth two corners of the tank as soon as the signal started.

The failure of Reebs' (1993) subjects to display TPL was interpreted by him as possibly due to three factors: 1) A possibility is that fish, unlike birds, are not able to learn about time-place associations in food availability. 2) Perhaps subjects would have been able to learn the TPL task if the response cost for exploring every possible option was increased, fish could sample all feeding locations before arriving to the temporally correct one and still obtain all possible reinforcers. 3) A final possibility is that the use of a feeding signal overpowered the temporal parameters of the task, thus precluding a time-place-food association, and, since the feeding signal was the same regardless of the time of the session, it would be reasonable to suppose that a stronger signal-food (on any corner) association was formed.

On a later study, Reebs (1996) tested the ability of a different type of fish (golden shiners) to display TPL. On the first experiment he conducted, a group of golden shiners received food on one side of the aquarium on morning sessions and on the diagonally opposed corner of the aquarium on afternoon sessions. Primary data was obtained from test sessions in which food was omitted and the position of the group of fishes was registered. Reebs found that most fishes would be located on the temporally correct corner, which was interpreted by him as evidence of a time-place association controlling the behavior of the subjects. On a second experiment, fishes found food on one corner during morning sessions; a different corner during afternoon sessions, and then on the first corner during a third *evening* session. This two-places/three-times task proved to produce effective TPL in subjects, for, during test sessions, most fishes were located on the temporally correct option according to the time of day. Finally, a third experiment tested TPL when fish had three different session times during which food could be obtained on a different corner of the aquarium. As a product of this three-places/three times procedure there was not a clear evidence for TPL for fish's locations would be random during test sessions. Reebs interpreted the overall findings as evidence that golden shiners readily show TPL when faced with two availability locations and each associated with a different time of day. The lack of TPL under the three-places/three-times task was interpreted as a possible product of the fact that, in nature, golden shiners forage on only two places at different times of day, which would pose an important difficulty to this particular species to perform a three times/three-places task.

Another interesting experiment of daily TPL was also conducted by Reebs (1999), who tested the ability of inangas (*Galaxias Maculatus)* to display TPL under three different circumstances: When food can be obtained at a different place for each of two daily sessions; when a simulated predator can be avoided by being in one of two different places on each of two daily sessions and, finally, when food can be obtained and a predator can be avoided by being in a given place on each of two daily sessions. Reebs found that fish could display TPL when food could be obtained, however, the same was not true for the predation risk, no consistent time-place association was evident for that particular experiment. Finally, predation risk interfered with the time-place-food association. Reebs interpreted his findings as possible evidence that, unlike food, fish could be exposed to a continuous predation risk in natural settings (i.e. predators could be found anywhere at any time), which could entail no evolutionary pressure to learn time-place-predation associations.

Gomez-Laplaza and Morgan (2005) conducted a simmilar test of Time-Place Learning to that of Reebs (1993) with two exceptions: They used a different kind of cichlid fish (angelfish), and they conserved the morning/afternoon structure of the task but removed the feeding signal. Groups of angelfishes were fed at 30 min intervals from 10:00 to 11:00 on one corner of the tank (morning sessions) and again with the same intervals from 18:00 to 19:00 on a diagonally opposed corner of the tank (afternoon sessions). The authors found that a high percentage of fishes spent most of the feeding and pre-feeding times (15 min prior to the start of each session) on the temporally correct option. Although a number of explanatory alternatives were considered in the paper, these findings were interpreted as evidence for TPL on the angelfish.

Carr and Wilkie (1997) conducted an experiment in which rats could obtain food by pressing one lever on morning sessions and another one during afternoon sessions according to a VR 15 schedule of reinforcement. They found that rats restricted the majority of their responses to the temporally correct lever; this would suggest that rats were showing TPL. However, they conducted several tests including skipping either the morning or the afternoon session; conducting interpolated sessions in the time between morning and afternoon sessions, and altering the light-dark cycle by leaving the lights on throughout the day. All of the results obtained with these tests pointed to the facts that rats were not relying on a circadian timing strategy, but rather an ordinal one. This result is rather odd, for many species so far were shown to readily use time-of day as a cue to find and exploit resources.

Carr and Wilkie (1999) conducted an additional study to test the timing strategy used by rats in daily TPL tasks. Since they found before that an ordinal strategy provided a better description of the data found by them (Carr and Wilkie, 1997), they designed an experiment like the one described above: Rats could obtain food for responding in one of two levers, according to a VR 16. The correct lever changed according to the time of day, so that; responses on one lever would produce food during morning sessions and on the other during afternoon sessions. Their designed caused that the order in which feeders are active had a low predictive value. This was accomplished by having three types of experimental days: 1. Morning only sessions. 2. Afternoon only sessions. 3. Morning and afternoon sessions. The three types of sessions were intermixed with one another. Carr and Wilkie (1998) found that, even under these circumstances, rats did not select the lever to press based on the time of day of the session, but rather, on an ordinal fashion. These two studies reveal that an ordinal timer provides a better description for rat's behavior on TPL tasks, even when faced with conditions in which this strategy is not optimal. The apparent reluctance of rats to use circadian information to guide their choice on TPL tasks has caught the interest of many rsearchers. A really important study in this respect was that of Widman, Gordon and Timberlake (2000), who designed a study to assess the effects of response cost on daily TPL performance of rats in a vertical maze. They conducted a series of studies on which they found that, when a low response cost is employed, rats do not rely on time-of-day in order to find and exploit food. However, when response cost is increased, rats start responding according to circadian timing hypotheses.

Also immersed in the discussion of the nature of the timing mechanism responsible for daily TPL was the study conducted by Pizzo and Crystal (2002). They developed a quite clever procedure to differentiate and test the hypotheses derived from the postulation of each of the timing mechanisms so far considered: ordinal, interval, and circadian. They hid food on one of four corners of an experimental box; the food was located in different sites for each of three shifts (A, B, C). A group of rats searched for food twice in the morning and once in the afternoon (Group AB-C), and another group did the same but once in the morning and twice in the afternoon (A-BC). Once they reached a stability criterion during training, they reversed the conditions delaying the “B” shift for the AB-C group and forwarding it for the A-BC group; this way the order remained the same but the intervals between feeding opportunities was changed, as was the specific hour of the B shift. The rationale is that if the rats continue to be effective during this change, then they would have learned to search for food according to an ordinal timing mechanism, on the other hand, if this change was enough to disrupt their searching patterns then the evidence would suggest the use of an interval or circadian based timing device. They found a random pattern of visits during the switched shifts sessions, which clearly suggested to them that the timing mechanism involved, could be based on circadian or interval timing mechanism in daily TPL tasks but not ordinal.

The fact that rat´s behavior under TPL tasks differs from that typically found with other species raises several questions about the nature of TPL for this particular species, moreover, while some studies fail to find circadian timing with rats, others claim to have found the opposite. One explanatory possibility for this apparent controversy, explored by Cain, Ko, Chalmers and Ralph (2004), is that the strain of rat that is used on different TPL experiments, and perhaps that could explain discrepant data about how rats behave on these tasks. They conducted a Conditioned Place Preference (CPP) experiment in which they carried out each session at the same time-of day. Long Evans and Wistar rats could choose to enter a context paired with food or an unpaired context. Both strains of rats readily displayed a marked preference for the food paired context. Then the tests began. These sessions were carried out at different times of day. The rationale is that, if rats are sensitive to a tripartite time-place-event association, then CPP should decrease when the time of day of the session is moved. Their results showed decreased CPP for Wistar rats but not for Long Evans. This led the authors to conclude that there could be differences in timing behavior between rat strains, and to entertain the possibility that Wistar rats might be more sensitive to temporal parameters than Long Evans rats.

As can be seen, there is somewhat controversial evidence as to the strategy that better describes the finding when rats serve as subjects for TPL tasks. Some studies (e.g. Carr & Wilkie, 1997, 1998) have shown it to be difficult to prove circadian timing, while others (e.g. Pizzo & Crystal, 2002; Cain, Ko, Chalmers & Ralph, 2004) provide evidence of the use of circadian timing. This has generated a particular interest for rat’s difficulty to respond according to circadian timing during TPL tasks that has escalated at least in two levels: Some authors believe that this could be generalized to other rodents (Van der Zee, Havekes, Barf, Hut, Nijholt, Jacobs & Gerkema, 2008), and the neural and bio-chemical correlates of circadian timing in rodents are thought to play a crucial part in this sort of non-adjustment to time-of day as the key parameter in daily TPL (Mulder, Gerkema & Van der Zee, 2013).

Finally, daily TPL tasks have been used on the recent years as a methodological tool to explore basic cognitive functions, such as memory. Mulder, Reckman, Gerkema and Van der Zee (2015) conducted an experiment in which they used a TPL task to assess the nature of cognitive decline as a function of aging. They exposed a group of mice to a TPL task in which subjects had to avoid entering one of three arms in a maze. Entries to the "punishment" arm resulted in an electric shock. The punishment arm changed according to the time of day of the session such that entries to one arm delivered shocks on each of three daily sessions. They found that mice could learn and re-learn this task when it was conducted at 4, 7, 12 and 18 months. Moreover when these mice were 22 months old they could still perform adequately on this task. On the other hand, a group of experimentally naïve mice were first exposed to the task at 17 months old and they were unable to perform adequately. They discuss the possible role of hipocampal rigidity on the absecence of memory loss on old mice among many others neural implications of circadian timing and memory.

The studies describe in the present section have shown that the interest for daily TPL has been constant and has yielded interesting data. Many different species have been tested on TPL tasks. For instance, garden warblers (Biebach, Gordijn & Krebs, 1989; Krebs & Biebach, 1989; Biebach, Falk & Krebs, 1991; Biebach Krebs & Falk, 1994) forest weavers (Falk, Biebach & Krebs, 1992), red bishops (Falk, Biebach & Krebs, 1992), cichlid fish (Reebs, 1993), golden shiners (1996), inangas (Reebs, 1999)pigeons (Saksida & Wilkie, 1994), rats (Carr & Wilkie, 1997; Widman, Gordon & Timberlake, 2000; Carr & Wilkie, 1999; Pizzo & Crystal, 2002; Cain, Ko Chalmers & Ralph, 2004) and different types of mice (Van der Zee, Havekes, Barf, Hut, Nijholt, Jacobs, Gerkema, 2008, Mulder, Gerkema & Van der Zee, 2013; Mulder, Reckam, Gerkema & Van der Zee, 2015). Overall, the evidence suggests a series of important highlights that must be made: First of all The majority of species are readily able to learn the spatio-temporal contingencies entailed by a TPL task. Second, performance of the subjects can be described according to an ordinal, interval, or circadian timing mechanism (Carr & Wilkie, 1997b). Considering these possibilities, most studies have found that their subjects performed according to a circadian timing strategy. On the other hand, this is not particularly true of rats; the evidence shows that they use circadian timing only under certain circumstances. Daily TPL tasks have recently started being used as a methodological tool for the exploration of the neural basis of basic behavior processes such as remembering or forgetting.

Now that a panoramic view of the state of the art in daily TPL research has been established, is time to turn to the analysis of the TPL tasks that involve much shorter periods of time and in which the behavior must not adjust to the time of day, but to a series of temporal relations between different events that occur in different places: Interval TPL.

INTERVAL TPL: TIMING SHORT INTERVALS TO DETERMINE WHERE TO GO NEXT

The previous section dealt with papers devoted to explore Daily TPL. In this review, it was evident that a wide variety of species has been show to be able to learn to visit a certain number of places depending on the time of day.

Crystal (2009) distinguished a second type of TPL which is assumed to be different from Daily TPL because the intervals that must be timed are much shorter, which results in the use of a different timing mechanism: Interval TPL. A typical Interval TPL tasks involves the use of more than one feeding option (usually four), the subject can obtain food (or other biologically significant resource) by responding on one particular option according to a specific schedule of reinforcement for a given period of time (the availability period). Once this time elapses, food can be obtained on a different option (Wilkie & Wilson, 1992; Carr & Wilkie, 1998; Crystal & Miller, 2002; Pizzo & Crystal, 2004; Thorpe, Hallet & Wilkie, 2007; García-Gallardo, Aguilar, Armenta & Carpio, 2015).

One of the first interval TPL experiments reports in the literature is the one carried out by Wilkie & Wilson (1992), whose purpose was to assess whether pigeons could show interval TPL. They used three transiluminated keys as availability points, and 30 seconds availability periods for each of these keys. Subjects were required to peck the key according to a Variable Ratio (VR) schedule of reinforcement, and the order in which pecks on each key was rewarded was a monotonic left-to-right function. The second experiment was the same as the first one with the exception that there were four keys, each with a grain-hopper, and the availability periods were 15 minutes long. The authors found, on both experiments that pigeons restricted the majority of their responses to the correct key. Wilkie and Wilson concluded that their results showed that pigeons could demonstrate TPL, and the stressed the need to understand the timing mechanism involved in arrangements employing shorter durations than those of Biebach *et al* (1989); because some studies using daily TPL have found predominance on the circadian timing mechanism (Biebach, Falk & Krebs, 1991; Falk Biebach & Krebs, 1992), and their arrangement did not seem to promote the same type of timing.

After showing that pigeons can show TPL, Wilkie, Saksida, Samson and Lee (1994) attempted to inquire into more specific properties of the spatial and temporal learning mechanisms involved. The first one was to test whether pigeons could learn the spatio-temporal regularities of food availability under situations of a non-monotonical sequence of availability points thus making it different from that involved in previous research (e.g. Biebach, Gordijn & Krebs, 1989; Biebach, Falk & Krebs, 1991; Falk, Biebach, & Krebs, 1992; Wilkie & Wilson, 1992). To accomplish that, they used a 3*3 matrix of keys beneath which a feeder was mounted. Like previous papers, food could be obtained only by pecking on one of the keys during each 15 min. period, but unlike previous research, the availability pattern did not describe a monotonic sequence; it described an eight figure (top-left →bottom-right→bottom-left→top-right). Wilkie *et al.* (1994) recorded the temporal distribution of responses for each key, finding that most responses occurred at the right key at the right time. They interpreted their findings as strong evidence that pigeons are capable of showing TPL even when a more complex pattern of food availability is used.

Wilkie *et al* (1994) also explored the nature of the timing mechanism involved in interval TPL tasks. Biebach *et al* (1991, 1992) had shown that, at least garden warblers were using a circadian phase timing mechanism, which necessarily raises the question whether this is the case with other birds and smaller intervals. To answer this question Wilkie *et al* conducted an experiment in which they placed four illuminated keys and four feeders, one in each wall of a square Plexiglas operant conditioning chamber. Food could be obtained by pecking only one of these keys according to a VR 15 schedule, the correct key changed every 15 min. Interspersed with these baseline sessions they conducted probe sessions of two kinds.

During the first kind of probe sessions, all keys were turned off for the 15 min period during which food would have been available on the second key on training sessions. After this blackout, they turned all keys back on for 5 minutes and no reinforcer was delivered. The interesting measure was which key would the subjects peck after the blackout: The temporally correct key (Key 3) or the next in the sequence before the blackout (Key 2). On the other type of probe sessions, the animal was removed from the experimental chamber for 5 minutes; after which it was put back in and the session restarted. The authors found that, in the first kind of probe sessions, the pigeons would peck on the key that was next in the sequence before the blackout (Key 2), thus suggesting that the timing mechanism had been paused during the blackout period and restarted once it had ended. On the second kind of probe session they found that, once put back in the box, the animals would concentrate their responses on the first temporally correct option (Key 1); this finding suggested that, when taken out of the experimental chamber, birds restarted their timing mechanism. These findings, taken together do not support the assumption that the organisms use circadian phase timing strategies in interval TPL tasks, for their subjects clearly paused, and restarted the clock, which are thought to be exclusive properties of a stopwatch-like mechanism (Wilkie, Saksida, Samson & Lee, 1994).

Once the ability of pigeons to display TPL was established, Wilkie, Carr Galloway, Parker and Yamamoto (1997) conducted a really interesting study in which they assessed whether TPL could be brought under the control of environmental stimuli. On their first experiment, birds could obtain food for responding to one of two feeders according to a Random Ratio (RR) 12 schedule of reinforcement. The correct feeding option changed every 10 min. The particular feature of this experiment is that the sequence in which every option was active depended on the position of a cue-light. On “North” Sessions, this light was located on the north wall of the conditioning chamber, and the sequence of active feeders was 1→2. On “South” sessions, it was the light on the south wall of the chamber that was lit. On these sessions, the sequence to be followed was: 2→1. Their results showed that the visiting patterns developed by their birds were conditional on the light that was turned on. Their second experiment was nearly identical to the first one, with some important exceptions: 1) there were four feeders, although only three of those would be used for each type of session. 2) The sequence in which feeding options served as the temporally correct one now depended on the color (Red or Green) of the light (not the position). On “Red” sessions, the sequence used was 1→2→3. On “Green” sessions, this sequence was “2→1→4”. This second experiment yielded the same general results as the first one: On “Red” sessions, birds would start pecking on option 1, then move to option 2 and then move to option 3. On “Green” sessions, birds would first peck on option 2, then 1, then 4. Wilkie *et al* (1997) concluded that their findings were evidence enough to show that behavior already in control of the spatio-temporal regularities of a TPL task, can be conditional to the position or color of a light (i.e. TPL can be conditional to environmental features).

At this point, there seems to be a general consensus on the field as to the nature of the timing strategy that better describes the findings on interval TPL: It is interval timing, and the *stopwatch* metaphor provides a clear illustration as to how this timing should work. Therefore, little surprise comes from the fact that Scalar Expectancy Theory (SET) proposed by Gibbon (1977) has already been tested on interval TPL situations. Carr and Wilkie (1998) conducted an experiment in which they varied the length of the availability period (4, 6 and 8 min), across three groups of rats. They reasoned that the scalar property that has been widely reported on many different tasks (Gibbon, 1977; Kacelnik & Bruner, 2002; Stubbs, Dreyfus and Fetterman, 1984; Allan, 1998; Menez, 2012) could also be seen on TPL tasks, and that, if this was the case, then SET could provide an adequate explanation for the observed behavior under interval TPL circumstance, which would be even further evidence that some circadian timing is not an adequate explanation for these findings. They succeeded in finding two important indicators of scalar timing: 1. when plotted on a relative time scale, the average temporal distribution of responses of the three groups overlapped (superposition of curves). 2. The width of the temporal distribution of each group was shown to be a constant proportion of the duration of the availability period (proportionality of variation). They thus concluded that time related performance on interval TPL tasks can be adequately described via the scalar property that is based on Weber´s law; therefore, this is further evidence that there are differences on the timing strategy underlying interval and daily TPL.

Having been previously established that rats can display interval TPL, Carr, Tan, Thorpe and Wilkie (2001) carried an experiment with the purpose of assessing the usefulness of a type of probe session not used before on interval TPL tasks and that resembled some features of standard tests of daily TPL. They used an experimental arrangement quite similar to that used by Wilkie *et al* (1994) with two main differences: The first one is that they used rats instead of pigeons; and the second one was that the availability period for each operandum was 4 min. After the training, Carr *et al* carried probe sessions that, according to them, were conceptually similar to the ones made by Biebach, Gordijn & Krebs (1989): They allowed the animal to obtain food for responses on any of the four operanda throughout the entire session, they named these probes *Open Hopper Test* (OHT). As could be expected, rats were perfectly capable of showing TPL during training, as proven by the fact that they restricted the majority of their responses to the correct levers on the correct times; however, while this pattern persisted during the OHT sessions, it was not without change; for an increase in the alternation between levers was found. Carr *et al* (2001) suggested the possibility that this alternation also occurs during training as a mean to correct timing error (i.e. check if the next one already delivers food); but these anticipated alternations are extinguished during training and reinforced during OHT sessions. In short, the authors interpreted their findings as evidence that rats are perfectly capable of showing TPL, and they check for errors in their timing mechanism by alternating between levers.

The nature of the timing mechanism involved on Interval TPL was the main focus of Crystal and Miller´s (2002) research. Like Carr and Wilkie (1998), they were interested in whether SET could offer a satisfactory explanation of the timing behavior of rats under interval TPL Tasks. They developed a procedure consisting of four levers and four feeders. Food could only be obtained by responses made on one of these levers at a time. However, for this experiment an FI schedule of reinforcement was used so that only one reinforcer could be obtained during each availability period. The schedule was 30 seconds for two levers and 60 seconds for the remaining two. Crystal and Miller (2002) took the temporal distribution of responses on each lever as the main measure and found that the rats did tend to respond more on the correct levers, however, the authors were unable to find curve superposition; and the coefficient of variation was different for each FI value. This finding is not predicted by SET (Gibbon, 1977; 1991). Therefore Crystal and Miller proposed that, while the timing mechanism could very well be interval-based; the inability of SET to explain their findings strongly suggested that a different account for timing behavior must be devised when organisms have more than feeding site.

A similar approach was taken by Thorpe and Wilkie (2002). They exposed rats to a modified TPL task in which each of four feeding locations entailed a different duration of the availability period. Lever 1 provided food during 6 min, then Lever 2 for 4 min, Lever 3 for 2 min, and Lever 4 for 8 min. The rationale was the same as that of Carr and Wilkie (1998) and Crystal and Miller (2002): SET predicts a constant coefficient of variation and superposition of curves when plotted on relative time scales. Thorpe and Wilkie (2002) failed to find either of these. They found that the coefficient of variation was a negative function of the duration to be timed, and that, when plotted on relative time-scales, the width of the temporal distribution for each duration increased as the duration increased. Their results extended the generality of TPL, for they showed that rats mastered this unequal interval TPL task, however, they produced further evidence that SET might not be an adequate alternative to explain time-controlled behavior on TPL circumstances. This is in line with the findings by Crystal and Miller (2002), but not with those by Carr and Wilkie (1998).

Pizzo and Crystal (2004) were interested in assessing the effects of spatial complexity on rats performance on an interval TPL task. They used an eight –arm radial maze. Each of these arms served as a feeding site for a 7-min availability period. They measured the amount of pellets consumed, the correct entries (entering a baited arm), and the false entries (entering a non baited arm) for each session. They found that rats obtained progressively more pellets going in and out of the baited arm in a quick fashion; they also found that, as the availability period of any given arm came closer, the false entries on this arm tended to increase, suggesting that they were somehow anticipating when they could obtain food in that particular arm. Additionally, they found that correct entries tended to increase as training progressed, and the reverse happened for the false entries. These findings served Pizzo and Crystal (2004) to claim that, even with eight feeding sites it is possible to reliably show TPL with rats as subjects.

Along the line of assessing how complex can a sequence be for a rat to display TPL, Thorpe and Wilkie (2006) designed a study in which each of four levers provided food for two nonconsecutive periods of time. The “correct” lever changed every 3 min. This provided an eight element sequence, just like Pizzo and Crystal (2004), but in this sequence, each of four locations would be visited twice. They found that rat´s behavior was under the joint control of spatial and temporal parameters of the task, only during the first half of the session, once the second half started (and thus, rats had to revisit previously “deplenished” sites), subjects seem to be able to time the availability periods, but they could not anticipate where would they find food next. This was interpreted by the authors as evidence that the requirement of revisiting options is enough to disrupt the spatial aspect of performance on a TPL task.

Since TPL has been usually described as a form of learning that is crucial for survival under natural conditions, Thorpe and Wilkie (2005) designed a study in which they attempted to replicate in the laboratory what could be a reasonable scenario in natural settings: While there might be a main source of food on a given period of time, different amounts of food could also be available on other places simultaneously. They designed a TPL task in which rats could obtain food according to a VR 8 for responses on one four levers (High density lever), meanwhile, food could also be obtained on the remaining three levers, but according to a VR 35 schedule (Low density lever). The high density lever changed every 5 minutes. They found that, under these circumstances, rats did allocate most of their responses on the high density lever, however, when an OHT was conducted, they did not find persistence of patterns, which suggests that rats were relying on a win/stay-lose/shift strategy to maximize the food obtained throughout the session.

All the studies described so far have been attempts to elucidate whether certain species can display Interval TPL and some of the most relevant determinants of this learning process in non-human animals. The first test of whether humans can display interval TPL came from a study conducted by Thorpe, Hallet, Fitzpatrick, Murphy and Bakhtiar (2012). They exposed Young children (ages 5-10) to an Interval TPL task in which kids had to press a touchscreen to *find* a toy that appeared on the screen according to a VR 6. The screen featured three distinct room (locations), responses on each room would produce the toy for 30 sec (period of availability). After this training, they conducted a probe session similar to an OHT: the toy would appear according to the same VR 6 for pressing any room. They found that children restricted the majority of their responses to the temporally correct room; moreover, the temporal distribution of responses was quite similar during training and the OHT. They concluded that their report was evidence for interval TPL in humans.

On the other hand, García-Gallardo, Aguilar, Armenta and Carpio (2015), reasoned that, while Thorpe *et al* (2012) findings quite remarkably resembled those typically found with other species; in the case of human performance, these findings could be perfectly compatible with counting how many reinforcers are obtained during each period. They conducted two experiments in order to elucidate this possibility. In experiment 1, computer based software was designed in which undergraduate students (ages 18-19) had to choose to enter one of four rooms in an abandoned house search for a zombie every 3 to 15 sec. Each room could be accessed by clicking a door with a label (“Bedroom”, “Kitchen”, “Bathroom”, and “Basement”). Zombies could be found in only one of these rooms every trial, the correct room changed every 3 minutes. After 4 training sessions, participants were exposed to a probe session in which zombies could be found in any room on every trial (OHT). Almost all participants behaved as if they were timing the availability intervals: they anticipated the changes in the location of the zombie and they persisted in their performance patterns during the probe session, however, verbal reports revealed that they were counting the number of trials in each period in order to decide when to switch between rooms. In the second experiment, the task was modified in two ways: First, counting was made harder by using three different intertrial ranges within each session: 2-6 sec, 2-11 sec and 2-16 sec. Second, labels were displaced during the final session to assess whether participants learned to click on a given place or to follow a set of verbal cues. They found that participants did not notice the label changes suggesting that they learned to respond on a place and not to follow a written cue, and that a win/stay-lose shift strategy was clearly used to decide when to switch rooms in the second experiment. They discussed the implications of verbal behavior when assessing time-place learning with humans and the possible differences in this process between humans and other animals.

Important findings on Interval Time-Place Learning were discussed on this section of the dissertation and a number of interesting facts were revealed. During the early 90´s one primary concern was to evaluate whether animals would rely on the same timing strategy for Interval and Daily TPL. Wilkie and Wilson´s (1992) experiment produced important evidence that pigeons could also show interval TPL, however, their results did not test whether the timing strategy involved could be said to be circadian, ordinal or interval based. It was up to Wilkie, Saksida, Samson and Lee (1994) and Carr and Wilkie (1998) to design studies that, among other things, contrasted the predictions of each of these explanatory alternatives. The evidence for interval based timing seemed quite robust for these authors. An interesting discussion however, is whether or not; a very influential timing theory (SET) is able to adequately describe the data generated with TPL tasks. While Carr and Wilkie (1998) concluded that it does, Crystall and Miller (2002) and Thorpe and Wilkie (2002) concluded that it does not. A critical methodological difference between the study of Carr and Wilkie and the remaining two, is that Carr and Wilkie exposed each group of rats to a different duration, therefore, each subject experienced only one duration of the availability period, meanwhile, both Crystall and Miller (2002) and Thorpe and Wilkie (2002) designed tasks in which each particular feeding location was associated with a different duration of availability, therefore requiring their subjects to time different durations on the very same session. Whether or not this difference explains the discrepant results is not yet clear.

On the other hand, special attention has also been given to some spatial parameters of a TPL task. The sequence complexity has drawn special attention, for it is thought to be evidence of the navigational strategy underlying effective TPL performance (Wilkie, Saksida, Samson & Lee, 1994; Thorpe & Wilkie, 2006). On Wilkie *et al´s* (1994) study, they compared performance on a TPL task that required a monotonical transition between options (clockwise movement), to performance on a more complex task in which an eight shaped pattern would be formed if these transitions were to be drawn. They found no differences between these conditions, which suggests that TPL can be shown regardless of the amount of different movements that had to be done for switching options. Pizzo and Crystal shown that rats could effectively demonstrate TPL even when eight places must be visited during a session. So far, these two studies reveal certain flexibility on the adjustment animals can do of their behavior to the spatial parameters of the task, however, Thorpe and Willkie's (2006) findings strongly argue against this, for they found that when the sequence requires revisiting sites, performance suffers an important detrimental effect.

At this point, it can be noticed that, even though several parameters of an interval TPL task have been manipulated, there is an important difference between the amount of species explored with interval and daily TPL. Rats and pigeons have been primarily used as subjects on interval TPL tasks. On the other hand, as far as the author knows, the only TPL tasks that have been conducted with humans have been about interval TPL tasks. There is a special discrepancy about humans' ability to respond to spatiotemporal regularities without verbal behavior overpowering them. While Thorpe, Hallet, Fitzpatrick, Murphy and Bakhtiar (2012) concluded that the young children that served as participants to their experiment did show typical TPL findings, García-Gallardo, Aguilar, Armenta and Carpio (2015) produced evidence that these findings are compatible with a counting strategy, and that, when counting is precluded (or at least hindered), human subjects rely on a Win/Stay – Lose/Shift strategy.

Along the lines of this and the previous section, special attention has been given to provide a succinct, but complete methodological description of many TPL studies in order to provide a thorough view of important methods and findings on both daily and interval TPL. It is now time to see some of the most influential theoretical considerations that have evolved over the years to explain behavior under TPL tasks.

TIMING AND SPATIAL LEARNING: THE THEORY BEHIND TIME-PLACE LEARNING

The previous section was devoted to a thorough review of some of the most influential experimental papers on time-place learning. A series of common findings and interpretations can be seen. During this section, a review of the different hypotheses or theories about how are animals able to keep track of time, and learn about the spatial features of the task during TPL, will be conducted.

TIMING IN TIME-PLACE LEARNING

As can be noted from the descriptions done in the previous section, three important findings have been usually considered as evidence that subjects are engaging in Timing processes during TPL tasks:

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, Saksida, Samson & Lee, 1994; Carr, Tan, Thorpe & Wilkie, 2001), and others has a plateau (Thorpe, Petrovic & Wilkie, 2002; Pizzo & Crystal, 2002; Thorpe & Wilkie, 2005; Thorpe, Hallet & Wilkie, 2007) 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 (Vg. Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Floresco, Carr & Wilkie, 2002; Thorpe & 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). The widely reported finding during these tests is that the temporal distribution of responses remains roughly similar during both training and OHT. (Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Floresco, Carr & Wilkie, 2002; Thorpe & Wilkie, 2006).

These three findings have strongly pointed to the possibility that animals are timing while engaged in a TPL task, and the natural question has been: How are they doing it? Many of the reviewed studies (e.g. Biebach, Falk & Krebs, 1991; Wilkie, Saksida, Samson & Lee, 1994; Carr, & Wilkie, 1997a; Crystal & Miller, 2002; Thorpe & Wilkie, 2002; Pizzo & Crystal, 2002), had the purpose of testing hypotheses derived from different timing mechanisms as those identified by Carr and Wilkie (1997b):

1. **Ordinal.** The behavior of the organism is under the control of the *order* in which the different events occur. Therefore, subjects are capable of tracking which feeder will be the next in the sequence. This timing mechanism is not sensitive to interval durations as long as the order is preserved.

2. **Circadian. –** The organism responds to environmental or organismical regularities associated with the time of day. Circadian timing typically involves some kind of oscillator entrained to these daily based regular events.

3. **Interval. -** The organism is capable of time the intervals elapsed between different events, such as, the beginning of the session, the last reinforcer, etc. Two different kinds of interval timing systems have been described and tested. An hourglass mechanism that times intervals of one fixed duration and cannot be paused, stopped or reset. And a stopwatch-like mechanism that helps timing intervals of many different durations and can be stopped, paused, and reset by the organism.

There appears to be a general consensus in that the specific timing device used by the animals changes depending on many characteristics of the task and, of course, the species used as subjects. For instance, there is evidence that pigeons and warblers use circadian phase timing mechanisms to perform effectively in daily TPL tasks (Biebach, Krebs & Falk, 1991; Falk, Biebach & Krebs, 1992; Saksida & Wilkie, 1994). However, there is also evidence that rats tend to rely on an ordinal strategy unless high response costs are involved (Carr & Wilkie, 1997a; 1999; Widman, Gordon & Timberlake, 2000).

On the other hand, studies involving interval TPL tasks have allowed researchers to practically rule out the circadian and ordinal possibilities, for it has been evident that neither of these have been capable of explaining the results obtained like an interval based timing system has. Some properties of such a device have already been explored; the data obtained by Wilkie, Saksida, Samson & Lee (1994) suggest that this mechanism has stopwatch-like properties of pausing, reset and restart; much like Gibbon’s (1977) SET; however, some studies have been made with the explicit aim of exploring whether SET can account for the results and the conclusions have been mainly negative (Crystal & Miller, 2002; Thorpe & Wilkie, 2002).

In short, it has been seen that Carr and Willkie’s (1997b) proposed timing systems have overwhelmingly dominated the hypotheses about the nature of the timing mechanism employed by many different species in TPL tasks. It has been found that in daily TPL tasks the organism relies on the use of a circadian phase timer (Biebach, Krebs & Falk, 1991; Falk, Biebach & Krebs, 1992; Pizzo & Crystal, 2002); and during interval TPL tasks they choose to time intervals within and between periods of availability (Wilkie, Saksida, Samson & Lee, 1994; Carr & Wilkie, 1998; Carr Tan, Thorpe & Wilkie, 2001), although an interesting finding is that SET fails to explain how this *internal clock* woks (Crystal & Miler, 2002; Thorpe & Wilkie, 2002).

NAVIGATIONAL STRATEGIES IN TIME-PLACE LEARNING

TPL tasks involve both spatial and temporal restraints in the food availability; therefore, no surprise comes from the fact that animals are perfectly capable to identify, remember, and move between the different feeding sites quite successfully.

Krebs and Biebach (1989) identified two main strategies for doing so, one is to learn a fixed route of visits and stick to it; and other would be to develop some kind of cognitive map that reflects the general characteristics of the experimental room and the time of day at which each feeder will be delivering food. As noted above, the results support the map-based view.

The assumption of a map development implies that there should not be important differences in performances when the sequence is monotonic (i.e. *easy*) and when it is not (i.e. *hard*), for, while there are clear differences between the routes to be learned, the general situation stays the same. This is claim is supported by the data of Wilkie *et al* (1994) and Pizzo and Crystal (2004), for even with harder sequences and more feeding sites, their subjects showed strong evidence for TPL, however, the study reported by Thorpe and Wilkie (2006) does not match this notion of flexibility in the learnable patterns, for they found a lack of spatio-temporal control of behavior under a non-monotonic sequence.

Finally, data provided by Thorpe, Hallet and Wilkie (2007) has produced some evidence on the effect of introducing a certain amount of variability in the sequence or the duration of availability periods in interval TPL tasks. In short, their data suggest that randomizing the sequence has stronger disruptive effects on TPL than randomizing durations. This fact was interpreted by the authors as evidence that the relative weight of spatial and temporal information in a TPL task is asymmetrical, and that the spatial information is surely more relevant than the temporal one.

In summary, the strategy used by subjects to accomplish the spatial feature of TPL tasks has also been explored, finding relatively incompatible evidence, for some studies suggest that a fixed simple sequence is not necessary (e.g. Wilkie, Saksida, Samson & Lee, 1994), while others have argued that increasing the sequence complexity has devastating effects on the TPL performance Thorpe & Wilkie, 2006; Thorpe, Hallet & Wilkie, 2007).

A methodological observation at this point is worth noting: *Complexity of the sequence* is not understood equally among the studies revised. Willkie *et al*. (1994) assume that a sequence is more complex due to the fact that it does not describe a monotonic pattern as in classic studies, however, three fundamental characteristics from these studies are preserve: The sequence comprises four elements; each feeding site is active only once during the session; and the activation pattern is held constant throughout the experiment. On the other hand Thorpe and Wilkie (2006) used an eight element sequence, but they accomplished this by activating each of the four feeding sites twice. Finally, Thorpe *et al.* (2007) returned to a four-element sequence but it was different each session. Therefore it is not surprising that each of these experiments threw different results; however, the fact that *complexity* is understood only as shape of the pattern, or number of elements comprising the sequence, or variability between sessions draws attention, because it is evident that the enormous contribution to the understanding of TPL that could come from assessing the effects of spatial variability *within* the session is being disregarded. This manipulation could allow us to observe how animals adjust their behavior to local immediate changes in the availability of food, which is reasonable to suppose they do.

COMPREHENSIVE MECHANISMS IN TIME-PLACE LEARNING

The theories and hypotheses about the nature of the timing device and the navigational strategies in TPL have been described and discussed in preceding sections of this paper; however, no surprise comes from the fact that some integrative and comprehensive proposal has already been developed; especially because the task itself requires spatio-temporal adjustment of behavior.

The first possibility was, perhaps indirectly, supported by Biebach, Falk & Krebs (1994). They found that as the rate of food delivery decreases on any feeding site; the alternation between sites increased. This finding suggested that animals could be relying on a *win/stay – lose/shift* strategy (Carr, Tan, Thorpe & Wilkie, 2001). A strategy of this sort implies that subjects will continue to respond on one feeding site as long as it provides a determined amount of food and switch when this is not the case. Animals relying on a win/stay – lose/shift strategy would not learn about the time-place association entailed on a TPL task, but would rather respond to the immediate availability of a resource in a given option at a particular time.

Results from many studies involving OHT sessions find that subjects tend to switch sites event when food is still delivered on their current location throughout the session (Carr, Tan, Thorpe & Wilkie, 2006 Thorpe & Wilkie, 2002, 2005, 2006; Thorpe, Hallet & Wilkie, 2007).

Another widely cited formulation is that of Gallistel (1990), and later developed by Wilkie (1995). Gallistel posited that whenever a biologically relevant event occurs, such as finding food, a memory code containing the time, the place, and the nature of the event is created. This tripartite time-place-event memory code is perfected throughout training in TPL tasks, and the reaching of asymptotic levels of learning is prove that this code has been successfully created and is being adequately used. One example of an attempt to study whether this is a viable explanation is the study by Thorpe, Hallet and Wilkie (2007) in which the temporal or spatial component of an interval TPL task was varied so that the tripartite code record could not be developed; and they found evidence for TPL even under these circumstances, which suggests that no such code is needed (Thorpe & Wilkie, 2006b).

In short, spatio-temporal mechanisms have been proposed to attempt an adequate explanation of the findings in TPL tasks; however, the relative lack of attention to them suggests that the dominant belief is that two separate and relatively independent mechanisms operate in conjunction. One would allow animals to keep track of time, and the other to navigate successfully between the feeding points, so that the animal simultaneously forms a map and times accurately the regular intervals involved in the task.

TIMING, PLACE LEARNING AND TIME-PLACE LEARNING: METHODS, DATA, THEORIES AND OPPORTUNITIES

The introductory section of the present dissertation had the purpose of conducting a review of the main procedures, findings and theoretical accounts of Time-Place Learning (TPL). A brief introduction covering the beginnings of the use of experimental methods in psychology was deemed convenient, for it provided a general overview of the experimental tradition in which work about TPL is inserted. Later on the two great areas of research that have served as methodological and theoretical foundations of the research on TPL were described: Timing and spatial learning; the typical experimental arrangements and the dominant theories on each of them have been described.

In the timing case, the general findings of experimental tasks as FI (Ferster & Skinner, 1957; Skinner & Morse, 1957; Catania, 1970 Dews, 1962, 1965, 1978), peak procedure (Roberts, 1981; Hinton & Meck, 2004; Buhusi & Meck, 2007) temporal bisection (Church & Deluty, 1977; Siegel, 1986; Allan & Gibbon, 1991) temporal conditioning (Pavlov, 1927), avoidance (Sidman, 1953, 1955), and temporal generalization (Church & Gibbon, 1982) were discussed. The three dominant timing theories were also described. SET (Gibbon, 1977, 1991; Church, 1984) relies critically on the adequate functioning of an internal clock that serves the animal to keep track of time. On the other hand, BeT (Killeen & Fetterman, 1988) also considers that some sort of pacemaker aids the animal in the track of time, however, it assigns a much more important role to the pattern of general activity usually developed under temporally based contingencies. Finally LeT (Machado, 1997) removes the idea of a pacemakers and, advancing along the line set forth by Killeen & Fetterman (1988), considers that the behavioral states alone are the key cue for animal timing.

The same strategy was used to describe and discuss Spatial Learning. The classical and most common experimental arrangements involve the use of some sort of maze, such as the T (Tolman, 1948) and the radial maze (Olton, Collison & Werz, 1957; Olton, 1979; Gobety & Schenk, 1992; Dubreuil, Tixier, Dutrieux, Edeline, 2003; Cabrera, 2009), furthermore the naturalistic observation of the foraging habits of many different species was briefly revised (Gallistel, 1990). The historically most influential theories developed to explain the findings have included a map (Tolman, 1948; O'Keeffe & Nadel, 1978; Gallistel, 1990), although the possibility for the formation of displacement habits (Hull, 1943) should not be absolutely disregarded yet (Cole, Clipperton & Walt, 2007). One of the most influential systems in this area: Gallistel's (1990) *the organization of Learning* was described at length. The navigational strategies of dead reckoning and piloting were described as well as studies showing a wide variety of animals making use of them.

Finally, particular studies, general arrangements, and explanatory attempts for TPL were described and discussed. The studies were divided into three groups. The first one comprises all those procedures designed to explore the nature and functioning of the timing mechanism involved (Biebach, Falk & Krebs, 1991; Wilkie, Saksida, Samson & Lee, 1994; Carr & Wilkie, 1997a; Crystal & Miller, 2002; Thorpe & Wilkie, 2002; Pizzo & Crystal, 2002). This revision allowed to see that there is still ample controversy around this question; while some studies support the use of a circadian timer (Biebach, Falk & Krebs, 1991); the conclusions drawn by others suggest the dominance of an ordinal timer (Carr & Wilkie, 1997a); and many others led to the belief that an interval based mechanism is involved (Wilkie, Saksida, Samson & Lee, 1995; Crystal & Miller, 2002; Pizzo & Crystal, 2002 Thorpe & Wilkie, 2002). Of particular interest were the studies in which SET was tested as an explanatory option in TPL findings, because many of them failed to find superposition of curves and a constant coefficient of variation(Crystal & Miller, 2002; Thorpe & Wilkie, 2002; Crystal, 2009), which means that SET does not appear to be a viable choice in explaining TPL findings.

A fact that draws attention is that so far, the general assumption has been that the timing mechanism *must be* of the kind of those identified by Carr & Wilkie (1997b); however, some of the dominant theories of timing do not consider the existence of a clock-like mechanism as a critical feature for timing (Machado, 1997). So, facing the evident lack of agreement about the timing mechanism involved, some form of report about the subject's general activity could prove extremely useful, for it has been shown that regularities in this accompany temporal adjustment of behavior (e.g. Wilson & Keller, 1953; Laties, Weiss, Clark & Reynolds, 1968; Laties, Weiss & Weiss, 1969; Machado, 1997; Aguilar & Carpio, 2014).

The second group of studies reviewed thus far involve experiments regarding the navigational strategies developed by animals in TPL situations, as could be expected, one of the first tests was whether subjects create maps of the situation or if they learn route patterns (Krebs & Biebach, 1989), thus bringing back to life the historical dispute on the explanation of maze learning (Cole, Clipperton & Walt, 2007). Most of the TPL studies of this kind have focused their attention on the restraints imposed by this mechanism (whatever it might be), to the ability of some species to display TPL. The effects of the sequence complexity, understood as the shape drawn by the availability pattern (Wilkie, Saksida, Samson & Lee, 1994); the number of elements that comprise the sequence (Pizzo & Crystal, 2004; Thorpe & Wilkie, 2006) and the variability of the pattern (Thorpe, Hallet & Wilkie, 2007) have yielded dissimilar results.

Finally, the third group of studies reviewed comprised those with the main concern was of exploring and testing hypotheses derived from integral spatio-temporal strategies. Gallistel's tripartite memory code proposal has been tested by Wilkie and his colleagues finding that the tripartite code theory does not appear to explain their results (Thorpe, Hallet & Wilkie, 2007).

Many ideas and conclusions can be drawn based on the present review. The first one is that sticking to the view that there is *one* timing or navigational strategy animals can use in different situations is extremely difficult. The most likely possibility is that many species have evolved different timing mechanisms that allow them to keep track of time along an extremely wide range of values (Sherry & Schachter, 1994).

Another idea motivated by this review is that, the traditional TPL task has proven quite useful to explore many characteristics of the adjustment of animal behavior to spatiotemporal contingencies; however, it does impose some restraint on the experimentation possibilities. One of the most severe appears to be the precluding of the orderly exploration of the effects that variability in the sequence or duration of the availability periods could have on TPL, despite the fact that many authors accept that biologically relevant resources can vary both in time and space. This becomes even more evident in the definition of TPL that Thorpe, Hallet & Wilkie (2007) offer: “The ability of animals to learn the spatiotemporal variability of biologically important event, such as food.” (p.55). The restraint rises from the fact that during a typical TPL task the sequence is conducted only once, thus hindering the possibility of assessing the effects of the within-sessions variability in duration or order of the availability periods.

The second and last restraint is the fact that no attempt has been made so far to consider alternate timing mechanisms to the proposed by Wilkie & Carr (1997); moreover, specific attempts to test SET have been made (Pizzo & Crystal, 2004), but theoretical options that disregard the notion of any internal clock whatsoever have not been ruled out (e.g. Machado, 1997).

The aforementioned issues are severe, and could be attended by the design of a TPL task in which, at least three things are considered: Repeating the sequence in several occasions, thus allowing to create within-sessions variability both in space and time and a keep track of the behavior of subjects during the availability periods, for there is a strong possibility that this behavior could be associated with effective timing performance.

In conclusion, the work done on how are animals capable of finding and exploiting resources whose availability is restrained in terms of space and time has been extensive and noticeably influenced by previously developed theories about timing and spatial learning alone. However, innovative methods have been devised that threw data used to rule out some hypotheses, support others, but, mainly to create controversy, a *sine qua non* element for the scientific progress. Fortunately the current state of the TPL research yields, to date, more questions than answers, therefore, research on this topic continues to be possible, convenient and extremely relevant. It is precisely under these considerations that the following experiments were designed and carried out.

The general purpose of the present set of studies was to assess the effects of within sessions variability on the duration or the sequence followed by the availability periods of a TPL task on a number of indicators of performance in these procedures with pigeons.

Two experiments were conducted in order to accomplish this experimental purpose. The first one assessed the effects of randomizing the sequence of food availability locations on a 16 period time place learning task. For the second study, a random set of availability period durations (1, 2, 3 or 6 min) was employed.

GENERAL METHOD

Subjects

Six experimentally naïve White Carneaux pigeons were used in each of the two experiments. All subjects will be housed in individual home cages and food deprived at 70% plus-minus 10g of their *ad lib* weight.

Apparatus

An experimental chamber 64cm long, 64cm wide and 33 cm tall was used in these experiments. 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 8cm wide and 6 cm tall and was located 10 cm above the chamber floor. Each feeder was equipped with an individual 5W light bulb and an infra-red beam light used to record head-entry responses.

A Lanix 586 computer equipped with Med-PC II software was connected to a MED associates interface cabinet SG- 6000C to control experimental events and record responses.

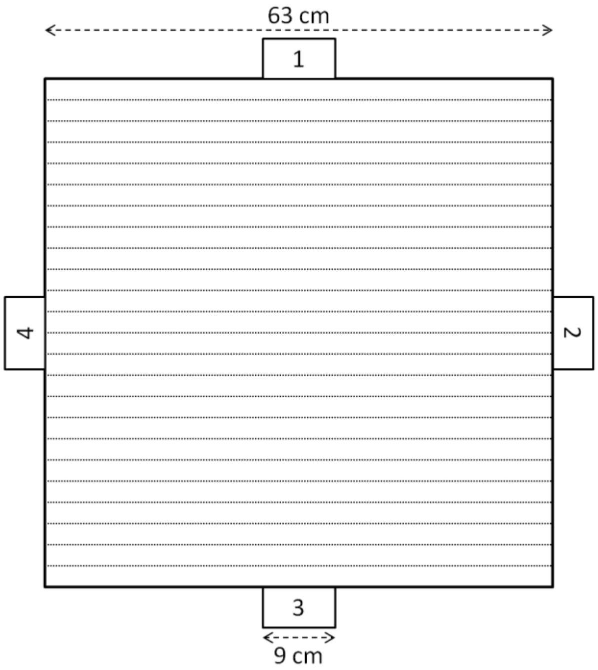


Fig 1. Experimental chamber used in the course of the experiments

Procedure

*Magazine Training and Shaping***.** All Birds were exposed to magazine training sessions in which all four feeders were turned on since the beginning of the session. Once a bird ate from any given feeder, shaping of the head-entry response started on that feeder and the rest of them were turned off. After 5 responses were made on that feeder, reinforcement stopped and the bird had to respond on any other feeder. This phase was concluded once the birds were reliably responding on all four feeders. Birds took between 2 and 6 30 min sessions to reach this criterion.

Continuous Reinforcement (CRF). During this phase, birds were put on a CRF schedule on every feeder. Reinforcement during this and all subsequent phases consisted of 2.5 sec access to food. During these 2.5 sec, the feeder light was turned on and the food tray filled with mixed grain was raised to the feeder brim so that the pigeon could eat. In order to prevent bias to a particular feeder, birds could obtain a maximum of 3 consecutive reinforcements in each feeder.

These sessions were concluded when birds obtained 60 reinforcements (15 per feeder) or 30 min. had elapsed, whichever happened first. This phase was terminated after 3 consecutive sessions in which the bird obtained 60 reinforcers. This took between 3 and 8 sessions for all birds. Once this phase ended, a specific Pretraining for each group began (see specific methods for details).

Experimental conditions

The three experimental conditions that were used on the experiments are:

1. *Spatially and temporally regular*

During this condition, responses were reinforced according to a Random Interval (RI) 25” schedule of reinforcement in one of the four feeders. The specific feeder in which responses were reinforced (i.e. correct feeder) changed every 3 minutes always following the same sequence. This sequence was carried out four times during the sessions, thus having 16 periods of availability during each session, four by feeder.

2. *Spatially irregular and temporally regular*

The same RI 25” Schedule was used, responses on one of the four feeders were reinforced; the correct feeder changed every 3 minutes. However, during this condition, the four sequences that comprised each session were randomized.

3. *Spatially regular and temporally irregular.*

Responses were reinforced according to the same RI 25” in one feeder only. During this condition, the duration of each period of availability was randomly selected out of the following values: 1, 2, 3 or 6 minutes. The correct feeder changed according to a fixed sequence, again, this sequence was repeated 16 times during each session.

Performance of birds under conditions 1 and 2 was compared during experiment 1. And for experiment 2, conditions 1 and 3 were compared.

EXPERIMENT 1: Exploring TPL under variable sequences of food availability

As noted in previous sections of the present dissertation, a highly influential model on the TPL field is Gallistel´s (1990) proposal, who, in summary, proposed a theory about animal learning that 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 (event), the place where it was found (place) and the time when it happened (time). These time-place-event codes are later retrieved to find and exploit these resources. This way, animals can learn about the spatio-temporal regularities involved in TPL tasks.

Considering Gallistel’s model, 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.

During the review about TPL, one experiment was found that explicitly explored the effects of spatial and temporal variability in TPL Tasks: Thorpe, Hallet & Wilkie (2007). They exposed rats to a modified TPL task in which either the temporal or spatial parameters of the task could be variable, thus precluding the animals from forming the tripartite codes proposed by Gallistel (1990), but allowing them to form bipartite time-event or place-event memory codes. 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 and not bipartite ones. Thorpe *et* al (2007) found that rats exposed to a fixed sequence of food locations and a random duration of the availability period were able to solve the task, while rats exposed to a fixed duration and a random sequence were not. They interpreted these results as evidence that tripartite codes might not be necessary for the effective performance under a TPL task, and 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, Hallet & Wilkie, 2007).

Thorpe *et al. (*2007*)* study allows the understanding of what happens when animals are faced with a different sequence of food availability from day to day (between sessions variability). However, since interval TPL is said to depend on learning mechanisms that are regulated by relatively brief events (Wilkie & Wilson, 1992; Wilkie, Saksida, Samson & Lee, 1994; Carr & Wilkie, 1997; Crystal, 2009) it is reasonable to suppose that the exploration of local spatial variability (intra sessions variability) must be explored in order to understand how animals adjust their behavior to variable food availability conditions.

Therefore, the purpose of the present study was 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.

METHOD

Subjects

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

Apparatus

See General methods for details on the experimental chamber and feeders.

Procedure

After magazine training, shaping, and CRF (see general method), birds were put on a Pretraining phase, during which the RI schedule of reinforcement value was increased from 5 to 15 in order to prevent extinction.

Pretraining

Random Interval (RI) 5 Sec. During this phase, all birds could obtain 2.5 sec of access to food for responding according to an RI 5 sec schedule of reinforcement in one of the four feeders (i.e. the “correct feeder”) during 3 minutes. After this period, the correct feeder changed. These sessions ended once each feeder had been active (i.e. Once one sequence was completed), which took 12 minutes. For one group of three birds (Group 1), the sequence of correct feeders was always the same across sessions (Fixed Sequence). For the three birds in the other group (Group 2), sequences were randomized from session to session (Variable Sequence). This phase was in effect for 5 sessions.

RI 15 Sec. This phase was the same as the previous one with two exceptions: 1) Food could be obtained according to an RI 15 sec in the correct feeder. 2) Each feeder was activated two times during the session (i.e. Two sequences were completed); therefore, the duration of these sessions was of 24 minutes. Group 1 birds experienced the same sequence twice during these sessions. On the other hand, Group 2 experienced two randomized sequences of availability. This phase lasted 5 sessions.

Training and Testing

Training. This phase was the same as the previous one with two exceptions: 1) The schedule of reinforcement was an RI 25 sec. 2) Four availability sequences were used throughout the session. The duration of these sessions was 48 min. Birds in Group 1 experienced the same sequence four times during each session. Birds in Group 2 experienced four randomized sequences of availability. This phase was in effect for 50 sessions.

First Open Hopper Test (OHT). During the OHT food could be obtained according to an RI 25 sec for responding on any feeder for 48 minutes.

Reversal Training. During this phase, conditions were reversed for both groups. Birds in the constant Group 1 had now a series of variable sequences and birds in Group 2 had a fixed sequence repeated four times during each session. 50 Reversal Sessions were conducted.

Second OHT. A second OHT identical to the first one was conducted after the reversal training.

RESULTS AND DISCUSSION

One important initial concern is whether birds are able to solve this modified TPL Task. Previous research has found that rats face troubles when complex sequences are employed (Thorpe & Wilkie, 2006).

Figure R1 displays the average percent correct choices in 2 session bins for both groups throughout the experiment. Data for group 1 (Fixed sequence – Variable sequence) is represented by filled circles and the open squares represent data for group 2 (Variable sequence – Fixed sequence). The vertical black continuous line signals the start of the second condition for each group. A number of relevant facts can be seen in this plot. First of all, an increase in the percent correct responses is noticeable for both groups during the first condition. Moreover, there does not seem to be any difference in the acquisition curve between groups during this condition. This impression was confirmed by a mixed effects ANOVA with Session as a within subjects factor and Group as a between subjects factor performed on the percent correct responses from sessions 1 to 50. This test yielded a significant main effect of Session, F (49,196) = 1.90 $p < .05$, but no significant main effect of group nor interaction. Once the reversal was implemented, it had an enormously different effect for each group. An important drop in percent correct responses is noticeable for birds in group 1 but not for group 2. This, somewhat predictable result implies that going from a fixed to a variable sequence poses a much bigger challenge than going from a variable to a fixed sequence. This finding was confirmed by a mixed effects ANOVA with Condition as a within subjects factor and Group as a between subjects factor comparing the last 6 sessions of training in condition 1 against the first 6 sessions of the second condition for each group. This ANOVA showed significant effect of condition, F (1, 34) = 11.41, $p <.05$; of group, F (1, 34) = 17.06, $p < .05$ and a significant group*condition interaction, F (1, 34) = 36.41, $p <.05$.

During the reversal, performance for birds in group 1 improves as the second condition advances, but they never reach levels as high as those attained when their sequence of locations was fixed. On the other hand, birds from group 2 continue to improve early in this condition and then their performance stabilizes around 75% correct responses. A mixed effects ANOVA with Session and Group as factors was performed on the data from session 51 to 100. This test showed a significant main effect of session, F (49, 196) = 3.50, p <.05; and a significant session*group interaction, F (49,196) = 2.01, p < .05, but, again, group was not a significant factor.

The data in this plot shows that birds were able to solve a modified TPL task in which the same sequence is repeated 4 times within a single session (Fixed sequence condition). This finding provides further evidence that some species are capable of learning relatively complex sequences of food availability (Wilkie, Saksida, Samson & Lee, 1994; Pizzo & Crystal, 2004). On the other hand, birds are also able to restrict the majority of their responses to the temporally correct option when a variable sequence is used. This finding could be quite puzzling because it could be misconstrued as evidence that birds show TPL even under spatially variable conditions. However, the reversal has drastically different effects on each group of birds, lowering the percent correct responses for group 1 and leaving this measure unaltered for group 2. This difference hints a strong possibility that, while both group of birds learned to find and exploit food resources during their first condition, they did so by following entirely different strategies.

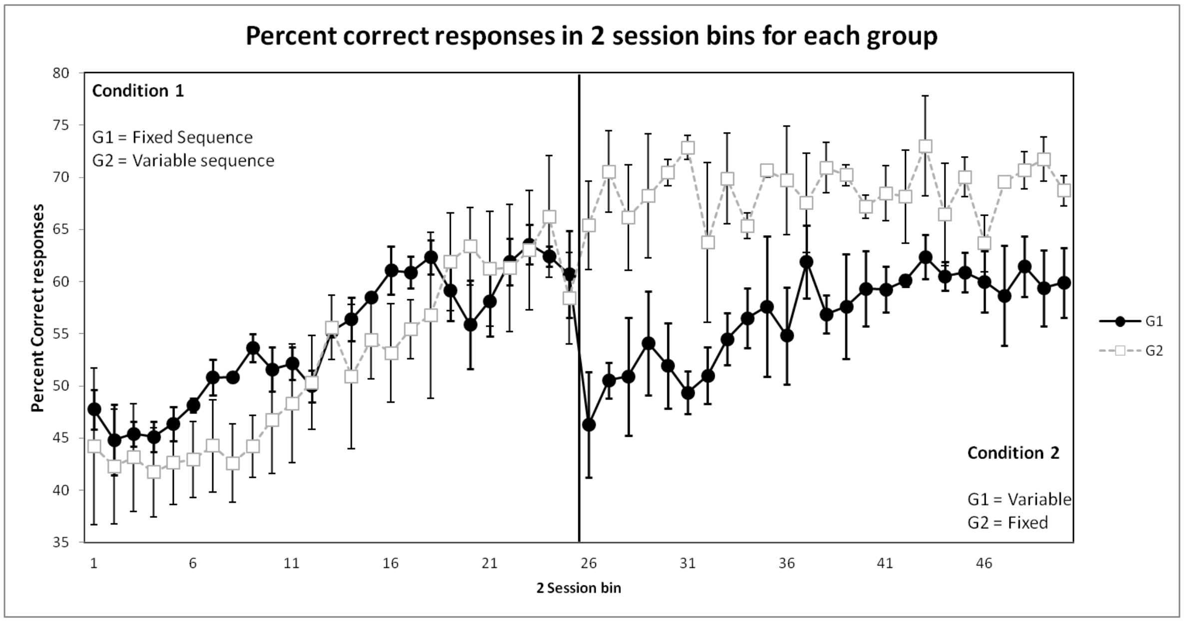


Figure R1. Average percent correct responses in 2 session bins for each group throughout the experiment. Group 1 (Fixed sequence – Variable sequence) is represented in filled circles, and group 2 (Variable sequence – Fixed sequence) in white squares.

The fact that there was no difference between groups in the acquisition curves for the first condition is evidence that both groups of birds were able to restrict the majority of their responses to the temporally correct feeder. However, this fact alone is not enough to judge whether they did so by timing the availability periods or by leaving a feeder until it no longer provided food (i.e. win/stay – lose/shift). Figure R2 was plotted to shed some light into this matter. This figure displays the average normalized response rate for the final 6 days of each condition in 30 sec bins. Data for the Fixed Sequence condition for Group 1 (filled circles) and Group 2 (White squares) are shown in the left panel. Data for the Variable Sequence condition are plotted in the right panel. The vertical dashed lines signal the end of each availability period, and the asterisks signal the correct periods for each option.

Data for the Variable Sequence condition was obtained averaging response rate on each feeder according to their temporal position each day. Therefore, under “Option 1”, there can be responses to any of the four feeders, depending on which was the first temporally correct option from session to session. Moreover, since there is not a fixed sequence that is repeated within the session, the first correct feeder on each sequence during a single session can be different. Therefore, we decided to group as “Option 1”, responses on whichever was the first option on each random sequence used during sessions. This way, we obtained a temporal distribution measure that is directly comparable to that obtained for the fixed sequence condition.

As expected, the majority of responses to each option are made when that option is the temporally correct one under both conditions. There seems to be little difference in the temporal distribution of responses between groups on each condition, however, a marked difference is noticeable between conditions. For the fixed sequence condition, both groups seem to display a standard ascendant – descendent function with its peak around the middle of the availability period which is consistent with anticipation of depletion. However, during the variable sequence condition this is not the case: response rate does not appear to be lower at the end than at the middle of the period.

To further analyze these data, four Analyses of variance were conducted, one for the temporal distribution of responses on each feeder, with Condition as a within subjects factor, and Group as a between subjects factor. These tests yielded the following relevant results (Note that alpha was set at .01 in order to correct for the increased probability of committing the type 1 error associated with conducting multiple statistical analyses on the same data set):

a) For option 1: There was a significant main effect of condition, $F(1,574) = 102.80$, $p < .01$ with no significant main effect of group nor interaction.

b) For option 2: There was a significant group*condition interaction, $F(1,574) = 11.53$, $p < .01$. No main effects were found.

c) For option 3: There was a significant main effect of condition, $F(1,574) = 7.85$, $p < .01$. No other significant effects were found.

d) For option 4: There was a significant main effect of condition, $F(1,574) = 79.04$, $p < .01$; and a significant group*condition interaction, $F(1,574) = 17.40$, $p < .01$.

These analyses reveal a number of interesting facts. First, responding on each feeder is not equally affected by the change of conditions; however, there was a significant main effect of condition on three out of four options. On the other hand, main effects for the group factor were never found, which suggests that there is not a reliable effect associated with the order in which birds experienced the fixed and variable sequences; their final performance in each condition is really alike. Finally, the presence of significant interactions on two feeders suggests that responding on those feeders was not equally affected by the different conditions for both groups. Altogether, these analyses point to the fact that there is a clear impact of the type of sequence used on the temporal distribution of responses, and that the order in which these sequences are experienced does not have such an impact.

The data analyzed so far suggests that birds seem to be able to keep track of the availability period duration during the fixed sequence condition. The replication of the typical ascendant-descendent function is particularly relevant fact, for it provides further evidence that birds are effectively learning about the spatio-temporal regularities of the task even when 16 periods of availability are used, which brings extends the previous findings of TPL literature to a relatively new situation (Wilkie, Saksida, Samson & Lee, 1994; Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Hallet & Wilkie, 2007). On the other hand, these analyses show that birds are not timing the availability periods under the variable sequence condition. This could imply that timing could be affected by the spatial variability in the task.

An interesting question, however, is why would subjects face trouble with timing the availability period on a variable sequence condition even though the availability period duration was kept constant. Of course, one possibility is the need for a tripartite time-place-event memory code. A subsidiary goal of this experiment was to keep record of the general activity patterns of the subjects and see whether these were somehow associated with timing (Laties, Weiss & Weiss, 1969; Killen & Fetterman, 1988; Machado, 1997; Aguilar & Carpio, 2014). The analysis of the general activity of the subjects revealed that from early training, they did not do much more than respond on the different options. The temporal distribution of responses on each option reveals that, towards the end of the fixed condition there is an overall orderly visiting pattern during each period of availability. During each period, early during the period, birds visit the last temporally correct option (lags), as the period advances, responses to the correct option increases, and, towards the end of the period, there is a marked rise in response rate on the next temporally correct option (anticipations). This order is clearly lost during the variable sequence condition; note how response rate on each option does not follow an orderly pattern during their respective incorrect periods.

This finding could be suggestive of a relation between timing and the general activity pattern of the birds, however, there are still some further data to be analyzed in order to be sure whether birds are timing or not the availability periods.

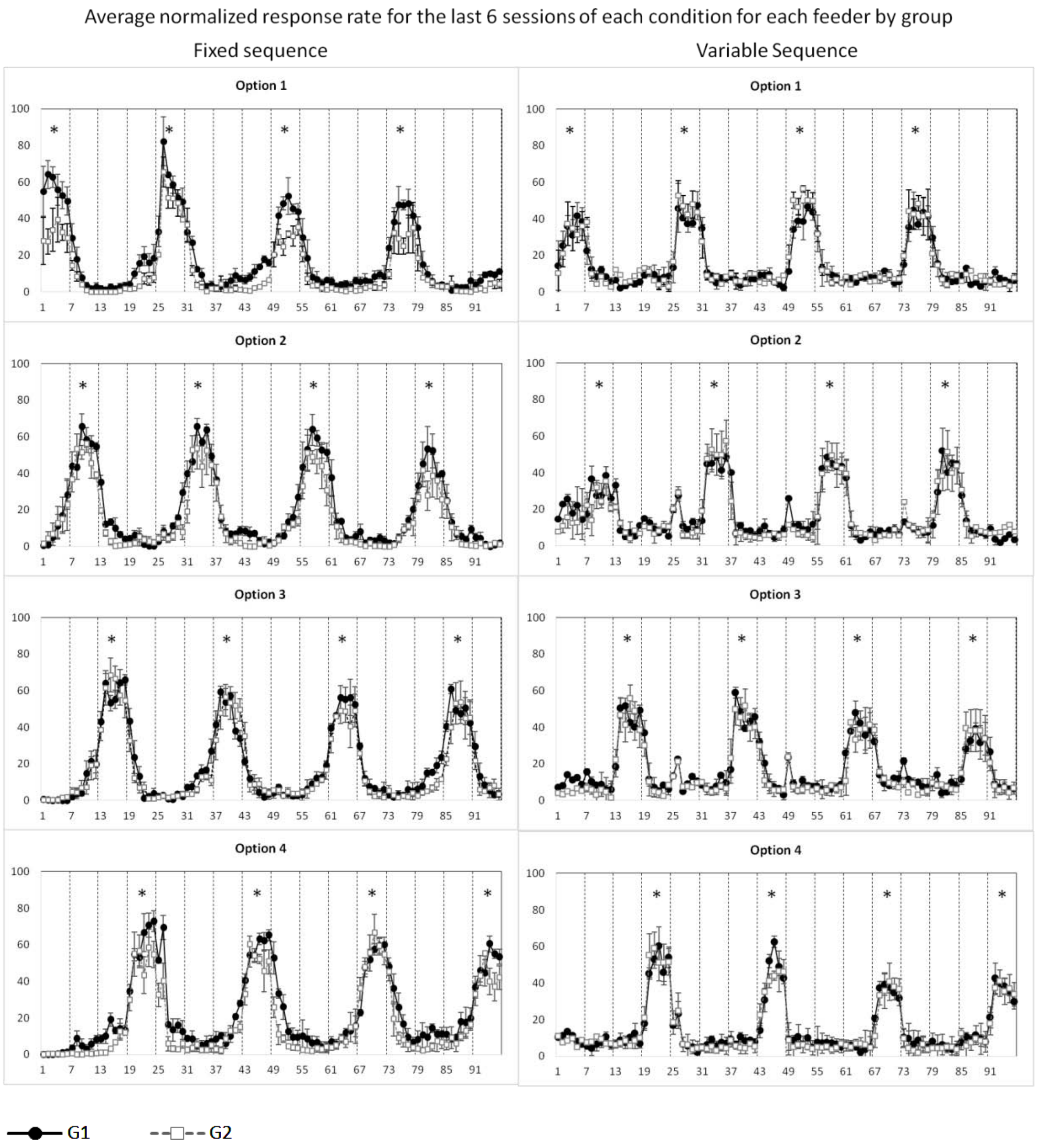


Figure R2. Average normalized response rate for the final 6 days in each condition in 30 sec bins. Left panel shows data for the constant condition for each group on each option. Right panel shows data for the variable condition for each group on each option. Vertical dashed lines signal the end of each availability period. Asterisks show the correct period for each option.

The temporal distribution of responses suggests that anticipation of depletion is greater when a fixed sequence of locations is used than when using a variable sequence. In order to assess this in a more detailed way, the anticipation of depletion difference was obtained and plotted in figure R3. This measure was obtained by subtracting the average response rate during the last minute of the availability period from that obtained during the second minute. Since anticipation of depletion is a decrease of response rate towards the end of the availability period, this difference should be negative when subjects are timing this interval and positive or near zero when they are not.

Figure R3 shows the anticipation of depletion difference for each group in 2 session bins throughout the experiment. Data on the left side of the vertical black continuous line corresponds to condition 1; condition 2 is displayed on the right side of that line. This figure shows that group 1 (filled circles) starts on differences above zero and ends the fixed sequence condition with 10 continuous days below this threshold, which strongly suggests that, by the end of the first condition, these birds were timing the availability periods and, thus, leaving each option before food would stop being available in it. On the other hand, birds on Group 2 do not behave the same way; since this difference never reaches levels lower than zero. However, an analysis of variance with Session as a within subjects factor and Group as a between subjects factor revealed only a significant effect of Session, F (49,196) = 1.55 p <.05. This test suggests that the anticipation of depletion changed across sessions in the same way for both groups, and that there is no significant difference between them during the first condition. On the other hand, a drastic and powerful effect of the reversal can be seen for group 1, from a negative difference, these birds move to a positive difference that hardly ever goes away until the end of the experiment. This finding suggests that these birds were not able to time the availability periods anymore once they were put on a variable sequence of locations. To further analyze the immediate effects of the condition reversal, a mixed effects ANOVA was conducted to compare the last 6 sessions of the first condition against the first 6 sessions of the second condition for each group. This ANOVA showed a significant effect of condition, F (1, 34) = 8.65, p < .05, with a non significant main effect of group and a barely non significant interaction, F (1, 34) = 3.49, p = .07, which suggests that, although there is a difference on how groups are affected by the condition reversal, this difference is not entirely reliable.

The results of condition 2 seem to be somewhat similar to those obtained in the first one: Birds in the fixed sequence (now Group 2) tend to obtain negative differences more frequently than those in the variable sequence. A mixed effects ANOVA with Session and Group as factors confirmed this initial assumption, for there was a main effect of session, F (49,196) = 1.42, p <.05; and of group, F (1, 4) = 12.11, p < .05.

Two important facts about the anticipation of depletion differences plotted in Figure R3 must be highlighted: First, it provides additional evidence that subjects learn to time the availability periods when faced with a fixed sequence of food locations. Second, it supports the initial impression that birds face important difficulties timing the availability period durations once they are put on a variable sequence of food locations. This finding would, overall, agree with Gallistel´s (1990) notion that tripartite codes are necessary for adequate TPL, for, in this experiment, only one of the elements of the code is variable (place), and this variability precludes birds from timing the regular intervals entailed by the task.

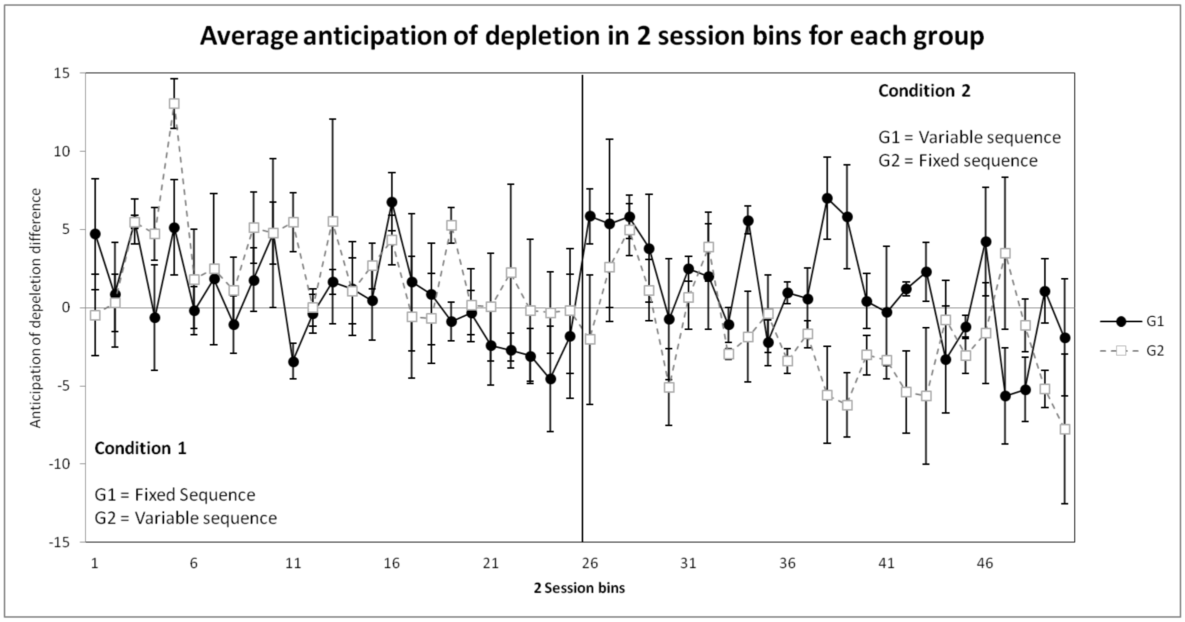


Figure R3. Average anticipation of depletion difference in 2 session bins for each group throughout the experiment. Filled circles represent data for Group 1 and white squares represent data for Group 2.

Further evidence that birds are able to time the availability periods when faced with a fixed sequence of food location comes from the data shown in Figure

R4. This plot shows the average anticipation difference in 2 session bins throughout the experiment. This difference was calculated as the anticipation of depletion difference, except that response rate during the last minute prior to the activation of any given option was subtracted to response rate during the second to last minute prior to this activation. The rationale behind this anticipation difference is that anticipation is said to be reflected on a rise on response rate just before an option becomes the temporally correct one, therefore, a positive difference implies that subjects are able to anticipate when and where food will be available. Note that it is impossible for birds on the variable sequence condition to do this, since the activation sequence is randomized. As can be seen in this plot, both groups quickly rise above zero when they are faced with the fixed sequence condition (Condition 1 four group 1 and Condition 2 for group 2), a clear indication that response rate on every option increases as the temporally correct period for that option approaches. A mixed effects ANOVA with Session and Group as a factors was performed on the anticipation difference for the first 50 sessions (Condition 1). This analysis showed a significant effect of group, F (1, 4) = 15.27, p< .05 with no significant main effect of session nor interaction. A noticeable effect of changing conditions can be seen for both groups. Birds that move from a fixed to a variable sequence are no longer able to anticipate food location, while birds that move from a variable to a fixed condition start doing so. A mixed effects ANOVA with Condition as a within subjects factor and Group as a between subjects factor was conducted to compare anticipation on the last 6 days of training of the first condition and the first six days of training on the second condition. This test confirmed the initial impression: There was a significant main effect of both Condition, F (1, 34) = 21.78, p <.05; and Group, F (1, 34) = 11.05, p <.05; and a significant condition*group interaction, F (1, 34) = 32.72, p <.05. These tests confirm that there is a reliable difference between groups at the end and beginning of each condition, and that the way each group is affected by the switch in condition is different.

An ANOVA was performed on the anticipation differences from sessions 51-100 (Condition 2). This analysis revealed a significant main effect of session, F

(49,196) = 1.45, p <.05 and a marginally nonsignificant main effect of group, F (1, 4) = 6.30 p = .06. Again, no interaction was found. The results obtained with this analysis showed that, when faced with a new condition, there is a reliable effect of training, with an unreliable effect of condition.

Positive anticipation differences imply that birds increase responding on every option as the availability period for each of them becomes closer. On the one hand, this is additional evidence that birds are able to time these periods under a 16 period TPL task. On the other hand, this also shows that birds learned the whole sequence employed, for they are arriving early at each availability location. This finding is consistent with studies that prove that some species are able to learn the spatio-temporal regularities involved in interval TPL tasks when relatively complex sequences are used (Wilkie, Saksida, Samson & Lee, 1994; Pizzo & Crystal, 2004).

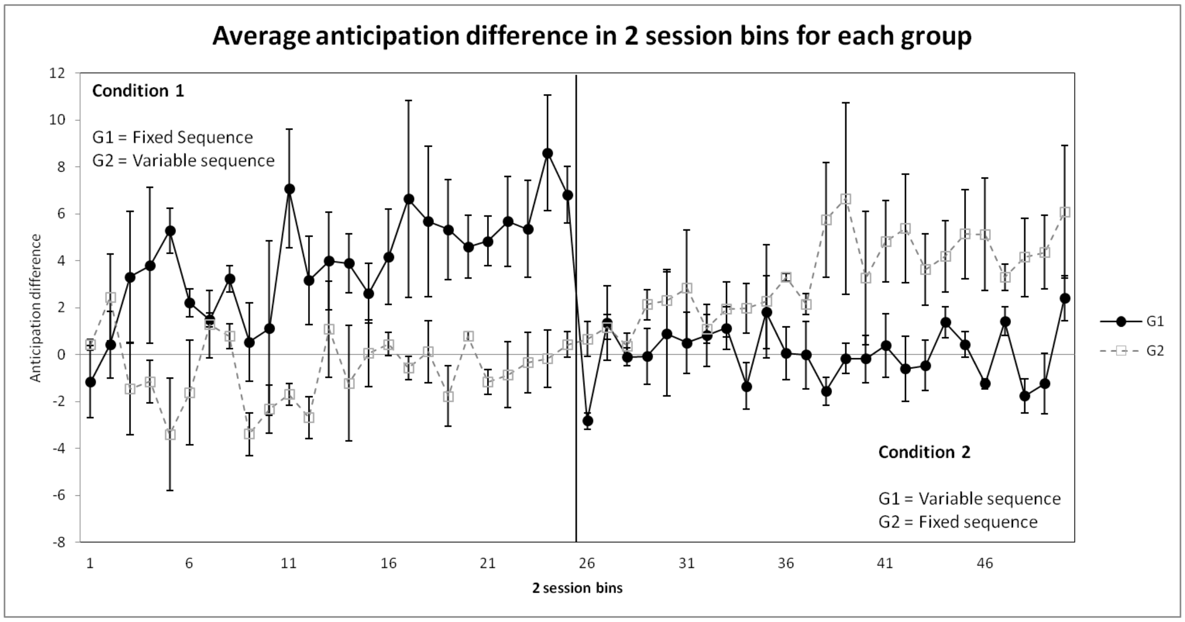


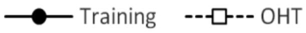
Figure R4. Average anticipation difference in 2 session bins for each group throughout the experiment. Filled circles represent data for Group 1 and white circles represent data for Group 2.

So far, the percent correct responses for both groups under both conditions suggests that birds are ultimately capable of restricting the majority of their responses to the temporally correct option. Further analyses on the temporal distribution of response showed that birds are only anticipating the availability or the depletion of food in each location when faced with a fixed sequence. This last finding strongly suggests that birds use a timing strategy to solve the fixed sequence condition and possibly a *win/stay – lose/shift* strategy to find food under a variable sequence condition. The purpose of conducting an Open Hopper Test (OHT) was to establish more accurately whether these options are true, thus, comparing performance on training on each condition vs their respective OHT ought to be useful to make more accurate guesses on this matter.

Figure R5 was plotted to display the results of the OHT that followed each condition for group 1. This plot shows the average temporal distribution of response in each feeder for the last 6 sessions of training (Filled circles) and the OHT conducted immediately after training (White squares) for group 1. Left panel contains data from the Fixed Sequence condition and the OHT that followed it and the right panel shows data for the Variable Sequence condition and the corresponding OHT.

A few comments on the data shown by this plot must be done prior to describing the findings. The first comment is that this plot shows only data for the first 4 periods of availability. The reason to restrict this analysis is that, just as has been previously found (Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Petrovic & Wilkie, 2002; Thorpe & Wilkie, 2005; Thorpe, Hallet & Wilkie, 2007), even though there is an important resemblance of patterns during training and OHT, variability in the temporal distribution of responses during the OHT is increased as the session elapses, creating somewhat erratic patterns of responding as the session advances. The present experiment was not the exception, therefore, we decided only to present and analyze data for the first 4 periods of availability. The second comment is that, during the variable sequence, any of the options can be the first one in which food can be found, this posed a challenge to the data representation of the temporal distribution during the OHT for: Which feeder is to be coded as the first option? Even though the first temporally correct option is always different from session to session, the pigeon will still start the session responding on one particular feeder, and, if the bird is timing the availability periods, it will move from one feeder to another around the same time as it did during training, therefore, we would be able to see a temporally defined visiting pattern that would resemble that of training. In consequence, we decided to code the feeder in which the highest normalized response rate was observed during the first three minutes (i.e. The time that would have been the first availability period during training) of the OHT was as *Option 1*. The feeder that displayed the highest normalized response rate during the second three minutes of the OHT was as *Option 2* and so on. This method allows keeping track of whether birds are moving from feeder to feeder in the way they would have done during training, thus providing a useful comparison to measure if pigeons were timing the availability periods during training or, if, on the other hand, they were relying on a win/stay – lose/shift strategy to solve the task.

Figure R5 shows a clear difference between conditions: The pattern of responses is quite similar during the final days of fixed sequence training and the OHT. On the other hand, there is a clear difference between patterns of responding of the training on the variable sequence and the corresponding OHT. Even though birds do visit all four feeders during this OHT, it seems clear that they do not move at the times they did during training. The overall high response rate for options 1 and 2 compared with that of 3 and 4 suggests that birds do not move that much from their first and second option of responding, which is more in line with a win/stay – lose/shift strategy than with TPL. Note that responding never seems to stop on the second option they choose.



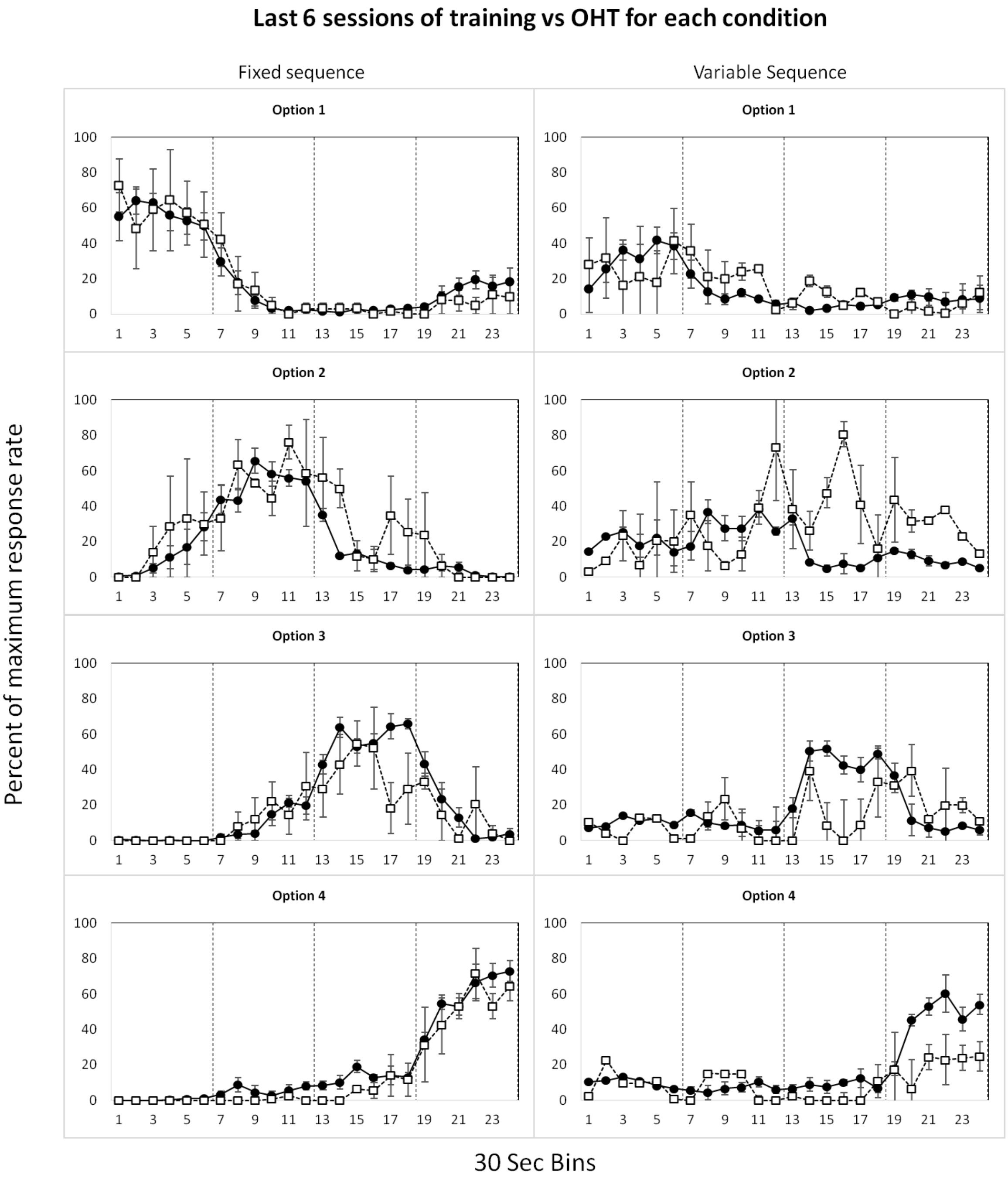


Figure R5. Average normalized response rate in 30 sec bins for the first 4 periods of availability of the last 6 training sessions and the OHT sessions for all birds in group 1 on each option. Left panel shows the comparison between the first training condition (Fixed sequence) and the first OHT, right panel shows the comparison between the second training condition (Variable sequence) and the second OHT.

Figure R6 shows the same data as Figure R5, for group 2. These birds were first exposed to a variable sequence task (Left panel) and to a fixed sequence as a second condition (right panel). This figure shows that, just as for group 1, birds in group 2 show great differences between training in a variable sequence and OHT. They actually never stop responding on the first option they choose during the OHT, additionally, response rate is exceptionally low for the last option they choose, which suggests a win/stay – lose/shift strategy. However, their patterns of responding during the fixed sequence and the corresponding OHT are not so much alike as those obtained for Group 1 (see figure R5 left panel). It appears as if being exposed to a variable sequence prior to the fixed sequence has effects that are not evident during training but are rather shown during the OHT.

A mixed effects ANOVA comparing the effects of Condition (Fixed sequence vs OHT after Fixed sequence) as a within subjects factor and Group as a between subjects factor was separately computed for each option. These analyses yielded the following relevant results:

a) For Option 1: Significant main effect of Condition F (1, 46) = 10.36. p <.01; and a significant Group*Condition Interaction, F (1, 46) = 13.06, p <.01. Subsequent ANOVAs revealed a significant difference between temporal distributions during training and OHT for group 2, F (1, 23) = 15.26, p <.01. But not for Group 1, which is in line with what is seen in figures R5 and R6.

b) For Option 2: Significant Group*Condition interaction, F (1, 46) = 5.80, p <.01 with no statistically significant main effects. Subsequent Analyses of variance showed no significant differences between conditions for either group. This could mean that the significant group*condition interaction could simply imply that there are small differences in responding between training and OHT, but that these differences are not equivalent between groups.

c) For Option 3: No significant effects were found.

d) For Option 4: No significant effects were found.

These analyses provide evidence that a common finding on the TPL literature was replicated in this experiment: Resemblance of patterns (Carr, Tan Thorpe & Wilkie, 2001; Thorpe & Wilkie, 2005; 2006). The temporal distribution of responses is, overall, similar between training in a fixed sequence condition and the OHT that followed it. This finding strengthens the assumption that birds are effectively timing the availability periods during this fixed condition (Crystal, 2009).

On the other hand, the same type of ANOVAs just were carried out in order to compare performance during the Variable Sequence condition with that obtained with the OHT that followed it, one for each feeder. These test yielded the following results:

a) For Option 1: No significant main effects nor interactions.

b) For Option 2: Significant main effect of group, F (1, 46) = 13.36. p < .01. No other significant main effects were found, although the condition factor reached near significance levels, F (1, 46) = 4.99, p = 0.03.

c) For Option 3: Neither significant main effects nor interactions were found. Just as in the case before, there was a marginally significant effect of Condition, F (1,46) = 4.03, p = 0.05

d) For Option 4: There was a significant main effect of condition, F (1, 46) = 18.17, p <.01. With no significant main effect of group, neither a significant group*condition interaction.

The *p* values obtained for the condition effect on options 2 and 3 could be almost taken as significant, however, note that, due to the increased risk of committing the type 1 error when conducting several tests on the same data set, *p* was lowered to .01 for these particular ANOVAs. These ANOVAs altogether show that, even though responding on each feeder is not equally disturbed during the OHT, there is a clear difference between these responses on three out of four feeders. The non significant value of the difference in responding during training and OHT for option 1 something to be expected, since it is the very first option birds choose, it would be easier for them to maintain their response patters, and this would be an increasingly difficult task as the OHT advances. In short, it cannot be definitely stated that birds are relying on a clearcut *win/stay – lose/shift* strategy, for they do move during the OHT (Carr, Tan, Thorpe & Wilkie, 2001). However, there is not a strong resemblance of patterns between training and OHT for any option.

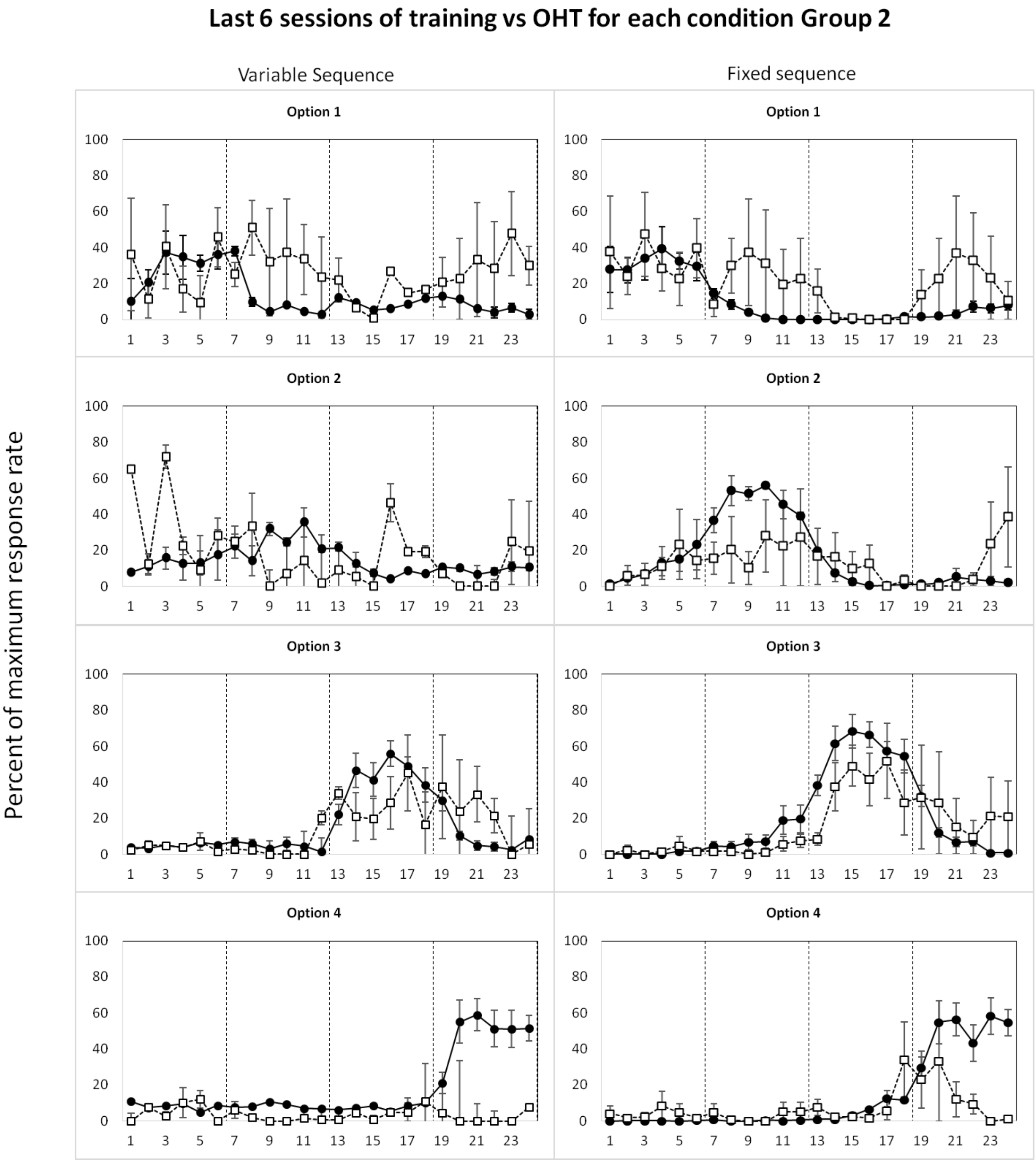


Figure R6. Average normalized response rate in 30 sec bins for the first 4 periods of availability of the last 6 training sessions (Black circles) and the OHT sessions (White squares) for all birds in group 1 on each option. Left panel shows the comparison between the second training condition (Variable sequence) and the second OHT. Right panel shows the comparison between the first training condition (Fixed sequence) and the first OHT.

Overall, all the data suggest that the birds are timing the intervals involved in the availability periods during the fixed sequence (as shown by anticipation,

anticipation of depletion and the persistence of patterns during the OHT). On the other hand, the same data suggest that birds are not able to time these intervals when faced with variable sequences of food location within a session. Of particular interest is the fact that patterns of responding seem to persist during the OHT only when a fixed sequence is the first condition the birds were exposed to (see Figure R5, left panel and Figure R6, right panel).

One of the first highlights of the data reported here is that they extend the widely reported findings that several species are able to learn the spatiotemporal regularities in food availability (Krebs & Biebach, 1989; Biebach, Falk & Krebs, 1991Wilkie & Wilson, 1992; Reebs, 1993, 1996; Saksida & Wilkie, 1994; Schatz, Beugnon & Lachaud, 1994; Wilkie, Saksida, Samson & Lee, 1994; Carr & Wilkie, 1997,1998, 1999; Widman, Gordon & Timberlake, 2000; 1999; Delicio & Barreto, 2008) to TPL situations in which the same sequence is repeated several times during a single session

The data reported here agree with those found by Thorpe, Hallet and Wilkie (2007), who reported that the effects of a variable sequence were highly damaging for TPL performance of rats. And, much in the same way as their findings, the facts described in the above paragraph raise the question about why it could be that birds are unable to keep track of the duration of the availability period when faced with a variable sequence of food locations. After all, this duration was kept constant throughout the entire experiment. Thorpe *et al.* (2007) interpreted their results as evidence 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 temporal.

The same rationale can be applied to the data reported here. When faced with a repetitive fixed sequence of food locations, birds are able to form the tripartite time-place-event memory code that enables them to display TPL, on the other hand, birds faced with a variable sequence of food locations will not be able to form these codes, which would disrupt their entire TPL performance even though the duration of the availability period remains the same. (Wilkie, 1995; Gallistel, 1990). This interpretation would be in line with that offered by Thorpe *et al* (2007), since it would be additional evidence that the spatial regularity of the task is critical for an effective performance on these tasks.

There is, however, an alternate explanation for de poor timing behavior of subjects on the variable sequence condition. Carr and Wilkie (1998) reasoned that, in the absence of a signal associated with the end or start of every availability period, there is a good chance that birds use the first reinforcer they found during each period as a time marker to start their timing process (Carr & Wilkie, 1998). This rationale is really appropriate, especially considering the fact that most timing theories involve some kind of temporal marker that signals the start of the period to be timed (Gibbon, 1977; Killen & Fetterman, 1988; Machado, 1997).

Based on Carr and Willkie's (1998) rationale, a possible interpretation of the data reported here could be that the event that starts the interval timer is the first reinforcement obtained during the availability periods. Therefore, a reasonable assumption (one that Thorpe, Hallet and Wilkie (2007) also entertain) would be that birds facing a fixed sequence task are able to obtain this first reinforcement faster and at more regular times than those faced with a variable sequence because they start responding on any particular option before it becomes the temporally correct one (i.e. they anticipate), while birds with a variable sequence cannot do such a thing. This would mean that birds' ability to time the intervals involved in a TPL task must be related to the time they lose *searching for* the first reinforcement during each period. If the temporal position of each temporal marker (the first reinforcement of each availability period) varies too much, there will be no reliable signal to start timing, leading to inaccurate time judgments. On the other hand, if the temporal marker position entails little variability, this could foster more accurate timing.

Figure R7 was plotted to assess variability in the moment in which the first reinforcer of each period is obtained each session. This figure shows the average standard deviation of the moment of first reinforcement on each period of availability in 2 session bins for group 1 (Filled circles), and group 2 (White squares). If Carr and Willkie's (1998) "temporal marker hypothesis" stands, birds should have obtained low standard deviations under the fixed sequence condition and higher scores of this measure under the variable sequence.

The plot shows that this standard deviation is reduced as training advances for both groups, which reflects no systematic differences in the average standard deviation between groups or conditions. However, just like it happened for the percent correct responses, the condition reversal seems to have a different impact for each group, while group 1 (fixed to variable) returns to its initial levels, there does not seem to be a similar effect in group 2.

A mixed effects ANOVA was conducted on data from this first condition (Sessions 1-50). This ANOVA had session as a within subjects factor and group as a between subjects factor revealed no significant main effects of neither factor nor a significant interaction. On the other hand a similar ANOVA was conducted to compare the last 6 training sessions on the first condition with the first 6 training sessions on the second condition. This Condition*Group Mixed Effects ANOVA yielded a significant main effect of group, F (1, 34) = 20.89 p <.05, and a marginally non significant condition*group interaction, F (1, 34) = 3.87, p = .057. Although, this interaction is, strictly speaking, non significant, it does reflect a difference on how each group is affected by the change of condition. Finally, data for sessions 51-100 were analyzed with the same mixed effects ANOVA as that conducted for the first 50 sessions. Again, neither main effects nor interactions were found with this test.

Overall, these data are somewhat difficult to interpret, for it suggests that birds' ability to keep track of time of the availability period is not necessarily related to the reliability of a temporal marker that signals the start of each period (i.e. the temporal position of the first reinforcement). However, the group difference in the reversal condition does suggest that, towards the end of the first training and the start of the second, there was a reliable difference in the time birds were taking to obtain their first reinforcer, which would be suggestive of a relation between temporal marker and timing behavior. One first possibility is, of course, that the first reinforcement is not the event that marks the start of each period; however, it would seem extremely difficult to pinpoint a different event that could serve this purpose.

Note that the experiment reported here was not explicitly designed to test hypotheses derived from either the temporal marker hypothesis (Carr & Wilkie, 1998) or the tripartite memory code (Gallistel 1990). Therefore, it would not be advisable to rule out the temporal marker hypothesis based on the results reported here alone.

A direct comparison between them could be achieved by arranging a TPL experiment in which different durations of the availability periods are used. All other parameters kept constant, the temporal marker hypothesis would predict that, as the duration of the availability period increases, pigeons should take smaller proportions of this time searching for food, which would increase the likelihood of accurate timing even under variable sequence conditions (García-Gallardo, Aguilar, Armenta & Carpio, 2015). On the other hand, if results like those described here and obtained by Thorpe *et al* (2007) are explained by an impossibility to form tripartite memory codes, then the duration of the availability period should be of no relevance at all, since they would be equally impaired to form the codes regardless of the availability period duration.

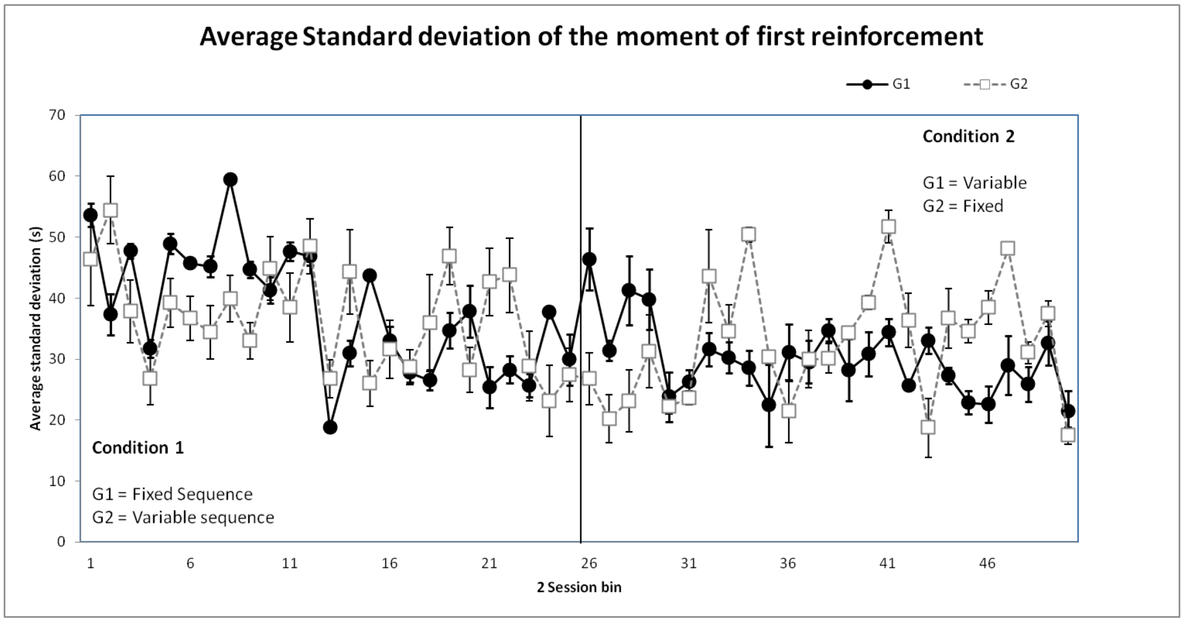


Figure R7. Average standard deviation of the moment of first reinforcement on each period of availability in 2 session bins.

This finding does not support a temporal marker based interpretation of the data reviewed so far. On the other hand, these data do agree with Gallistel´s (1990) tripartite memory code model, for it was found that when one component of the time-place-event code is variable (place), effective TPL performance is not entirely accomplished. This rationale is in line with previous findings about the effects of spatial variability in TPL situations (Thorpe, *et al*, 2007). Thorpe *et* al (2007) pointed out the possibility that the spatial parameters in TPL tasks could be more relevant than the temporal ones. This experiment's results, taken alone, could be considered as an extension of the asymmetrical role played by temporal and spatial parameters of the task to situations in which these vary within sessions.

However, this experiment did not involve the explicit manipulation of the temporal parameters of the task, and this manipulation is extremely desirable for a thorough analysis of the effects of spatial and temporal parameters of a TPL task on performance developed under them.

EXPERIMENT 2: Effects of variable availability period durations under fixed sequences

Experiment 1 ought to determine the effects of variable sequences of food availability locations on a number of performance indicators in a modified TPL task. The exploration of intra-sessions variability on the spatial parameters of the TPL task revealed that birds were ultimately able to solve the task under both conditions (most responses are restricted to the temporally correct option).

Of particular interest was that, overall, findings suggested that birds were unable to adequately time the availability period duration under the variable sequence condition, even though this duration remained constant throughout the experiment. The results agree with Thorpe, Hallet and Willkie's (2007) results in two ways:

1. They show that the spatial parameters of the task play a very important role in the TPL performance, for, just as Thorpe *et al*, we found that a variable sequence precludes subjects from adequately timing the availability periods duration.
2. Even though subjects do respond above chance levels, the highest percent correct choices level is obtained during the fixed sequence level.

These results could be interpreted as evidence that supports Gallistel's (1990) theory that tripartite time-place-event memory codes are needed for typical TPL performance.

On the other hand, Thorpe *et al.* (2007) also explored the effects of varying the duration of the availability period from session to session. They found that timing of the availability period was precluded, which is to be expected since each day a different duration was used. Their rats, however, did learn the spatial parameters of the task: they moved from option to option according to the fixed sequence and obtained higher percent correct responses than rats with a variable sequence and a fixed duration. These results led Thorpe *et al* to two main conclusions about their data:

1. The fact that rats faced with a fixed sequence and variable durations were able to learn the spatial parameters of the task might reflect that the memory codes needed to learn TPL are bipartite and not tripartite.
2. The fact that rats faced with a variable sequence and a fixed duration were not even able to learn about the duration of the availability period might reflect that the place-event memory code is more salient that the time-event code.

These are rather strong conclusions that do not agree with a deeply influential theory about animal learning (Gallistel, 1990), however, they stem from results obtained by assessing the effects of both space and time parameters of the task.

The study reported here has a general purpose of assessing the effects of the same type of changes but in a within-sessions manner for various reasons, therefore, it is quite clear that no valid conclusions about this manipulation can be achieved until the time parameters of the task are also manipulated. For that reason, experiment 2 was conducted.

This second experiment entailed the use of a fixed sequence of food availability throughout the experiment and a variable duration of the period of availability. As noted in the general method section, this period could be 1, 2, 3 or 6 min. long, and it changed within a session.

The experimental purpose is to assess the effects of variable availability period durations on a number of TPL performance indicators in a modified 16 period task with pigeons.

METHOD

Subjects

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

Apparatus

See General methods for details on the experimental chamber and feeders.

Procedure

After magazine training, shaping, and CRF (see general method), birds were put on a Pretraining phase, during which the RI schedule of reinforcement value was increased from 5 to 15 in order to prevent extinction.

Pretraining

Random Interval (RI) 5 Sec. During this phase, all birds could obtain 2.5 sec of access to food for responding according to an RI 5 sec schedule of reinforcement in one of the four feeders (i.e. the "correct feeder") in a fixed sequence. These sessions ended when each feeder had been active once (i.e. Once one sequence was completed), which took 12 minutes for group 3 and between 4 and 16 min for group 4. For one group of three birds (Group 3), the availability period duration remained constant at 3 min throughout the session (Fixed Duration). For Group 4 birds, the availability period duration (i.e. the time each feeder could deliver food according to the RI 5 sec) could be 1, 2, 3 or 6 min. This phase lasted 5 sessions.

RI 15 Sec. This phase was the same as the previous one with two exceptions: 1) Food could be obtained according to an RI 15 sec in the correct feeder. 2) Each feeder was activated two times during the session (i.e. Two sequences were completed). Birds in group 1 experienced the same Fixed Duration as the phase before. Birds in group 2 could experience the same variable availability duration periods as the previous phase with the only restriction that no duration could be repeated on any feeder. This phase lasted 5 sessions.

Training and Testing

Training. This phase was the same as the previous one with two exceptions: 1) The schedule of reinforcement was an RI 25 sec. 2) Four availability sequences were used throughout the session. Birds in group 3 were put in the same Fixed Duration condition. Birds in group 4 experienced the same variable availability period durations with the same restriction: no duration could be repeated on any feeder. This restriction allowed two important controls: 1) All feeders would be active for the same amount of time throughout a single session, thus precluding bias toward a particular feeding location. 2) Since every feeder will go through each duration just once, each value appeared exactly four times during a single session (once per feeder); this allowed matching the availability period and the overall session duration of the Fixed Duration condition:

Possible duration	Times it was used during a session	Aggregate duration
1	4	4
2	4	8
3	4	12
6	4	24

Total session duration = 48 min Average availability period duration = 48/16 = 3

Table E2. Possible durations of the availability period and the number of times they appear during each session. The rightmost column displays the aggregate duration for each possible duration considering the number of time it appears during each session.

First Open Hopper Test (OHT). During the OHT food could be obtained according to an RI 25 sec for responding on any feeder for 48 minutes.

Reversal Training. During this phase, conditions were reversed for both groups. Birds in Group 3 had now a series of variable durations and birds in Group 4 had a fixed duration repeated 16 times during each session. 50 Reversal Sessions were conducted.

Second OHT. A second OHT identical to the first one was conducted after the reversal training.

RESULTS AND DISCUSSION

The first important result to be described is that concerned with the percent correct responses. Figure E2R1 shows this measure for both groups in 2 session bins throughout the experiment. Group 3 (filled circles) faced a fixed duration condition first and then was moved to the variable duration condition. On the other hand, Group 4 (white squares) was exposed to the same conditions but in the reverse order. The black vertical line signals the end of the first condition. The plot shows that the percent correct responses is different for each group since early training. During condition 1, this difference grows as training progresses: while birds in group 1 progressively increase their percent correct responses, birds in group 2 do not. As a product of the condition change, there is a noticeable drop in percent correct responses for group 1, but no such thing can be seen for group 2. The observed difference in percent correct responses between groups was confirmed with a mixed effects ANOVA with Session as a within subjects factor and Group as a between subjects factor. This Analysis showed a significant effect of Session, F (49,196) = 4.08, p<.05; a significant main effect of Group, F (1, 4) = 14.45, p<.05, but no significant session*group interaction. On the other hand, to analyze the immediate effect of the condition reversal, a mixed effects ANOVA comparing the percent correct responses during the last 6 days of the first condition with the first 6 days of the second condition for each group was calculated. This analysis revealed that each group is differentially affected by the condition reversal, as show, by a significant main effect of condition, F (1, 34) = 9.59, p<.05; of group, F (1, 34) = 18.45, p <.05 and a significant group*condition interaction, F (1, 34) = 7.63, p<.05. Two t-tests for paired samples were conducted on the same data in order to determine the effect of the change of condition separately for each group. These tests revealed an important difference in percent correct responses between conditions for Group 1, t (1, 17) = 3.50 p <.05, but not for group 2, t (1, 17) = .30 p>.05. These tests confirmed the initial impression of a major difference on how the condition change affected the percent correct scores for each group.

Once the birds are on the second condition, an interesting thing is that birds in group 1 do increase their percent correct responses when faced with a variable duration, which is something birds in group 2 could not do (see first condition). On the other hand, as was expected, the percent correct responses for birds in group 2 rises when they are faced with a constant duration of the availability period. One important fact that must be noticed is that the difference in percent correct responses between groups was deeply reduced during the second condition. These data were analyzed via a similar mixed effects ANOVA as that for the first condition. This analysis showed a significant main effect of Session, F (49,196) = 2.69 $p < .05$ but no main effect of group nor interaction. This analysis confirms that both groups increase their percent correct responses as training progresses and that the differences between them are not statistically significant.

Altogether, the data provided in figure 1 reveals a number of relevant facts. First, the difference between groups from the start of the experiment shows that, when birds are faced with a TPL task in which time is the variable feature, this poses an important challenge on them (notice that there is not an ascendant function for group 2 in condition 1). This low percent correct responses could be product of one of two strategies: 1). A win/stay-Lose/shift strategy, this strategy could produce low percent correct responses only if we were to assume that birds take too long to notice the absence of reinforcement and then, consequently, the lose/shift part of the strategy could be responsible for the low scores. 2) A faulty timing strategy. Thorpe *et al* (2007) concluded that rats did not rely on any sort of timing when faced with a variable duration, however, they did contemplate the possibility of rats averaging the duration, which, in this case, could be one of many possibilities that explain a low percent correct responses (i.e. birds could switch places at an average duration, which would increase the amount of errors).

On the other hand, the rise in percent correct responses for group 1 is in line with previous findings about 16 period TPL task in which both spatial and temporal parameters of the task are kept constant (see experiment 1).

The effect of the reversal is quite powerful for group 1, but not so for group 2, which is also in line with experiment 1. A possibly puzzling finding is why do birds in group 1 raise their percent correct responses on the variable duration condition while birds in group 2 did not do such a thing? This fact could represent an effect of being first exposed to a fixed duration condition; it is quite possible that, under their first condition, birds learned something about the temporal nature of the task that was helpful once put in their second condition.

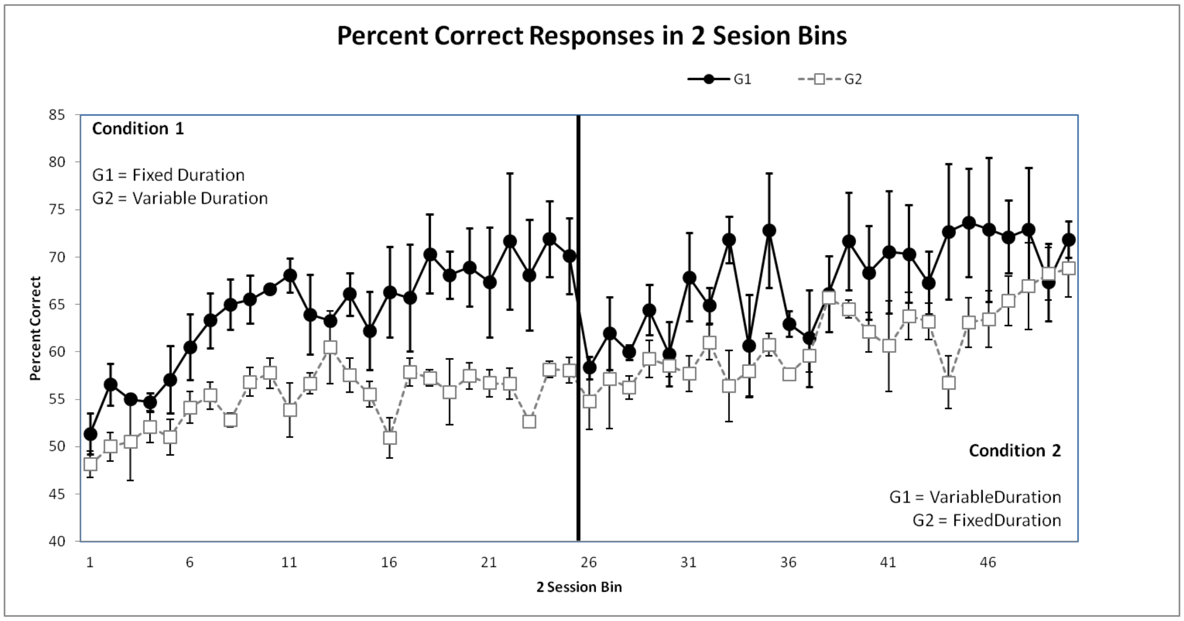


Figure E2R1. Average percent correct responses in 2 session bins for each group

Data presented in figure E2R1 yielded a number of interesting facts that could be interpreted in different ways, however, a critical feature of any interpretation of these data relies heavily on whether or not birds are able to time the availability periods under each condition.

Thorpe, *et al* (2007) entertained the possibility of subjects timing the variable durations used on their experiments in one of three ways: 1. they could time the average duration of the periods. 2. They could time one duration and stick to it throughout the experiment (some sort of temporally defined bias). 3. They could time the first availability period duration and then use that duration as a reference value for the remainder of the session (remember that on their study, the availability period duration was varied from session to session while kept constant within the session). Options 1 and 2 could be true for the present experiment;

however, the third option does not apply to the present situation, for, in this experiment, subjects are faced with variable durations of the availability period within each single session.

The first step that must be taken to shed light on the time-related behavior of birds under these conditions is to analyze the temporal distribution of responses. This poses a challenge to represent averaged data for each group under the variable duration condition, for each availability period can be either 1, 2, 3 or 6 minutes long.

Figure E2R2 presents the average temporal distribution of responses for the last 6 sessions of each condition for each group. Group 1 is represented in filled circles while group 2 by white squares. Data for the fixed duration condition can be seen on the left panel, and the right panel shows data for the variable duration condition. The plot displays the percent maximum rate in bins of 1/6th of the duration of the availability period. That implies that when a 3 minute availability period duration was used, each bin groups data for 30 sec, when for 2 minute availability periods, each bin groups data for 20 sec, when the availability period was 1 minute long, each bin grouped data for 10 sec, and, when it was 6 minutes long, each bin grouped data for 60 sec. This strategy, similar to that used by Thorpe *et al* (2007), allows to express temporal distribution of responses on a relative scale, allowing to average temporal distribution of responses across different values of the availability period duration.

First of all, the plot shows that, under both conditions, birds restrict the majority of their responses to the temporally correct option, as can be seen for the multiple peaks that coincide with the availability period for each option.

The temporal distribution of responses does not seem to be very different between groups on the first condition, both functions overlap most of the time. Moreover, the curve of these functions is quite similar to an ascendant descendant function with a peak around the middle of the period. Two important differences can be observed between conditions for each group of birds. First, there are more responses during *incorrect* times for each option during the variable duration conditions. Notice how this rate is almost always near to zero during the fixed duration condition but not for the variable duration condition. Second, the shape of the curve is also transformed, during the first condition, most peaks appear around the middle of the availability period, which suggests somewhat accurate timing, however, most of the peaks shown on the right panel of the plot (variable duration condition) do not have a clear peak around the middle, but rather some form of *plateau* that does not diminish towards the end of the availability period.

To further analyze these data, four Analyses of variance were conducted, one for the temporal distribution of responses on each feeder, with Condition as a within subjects factor, and Group as a between subjects factor. These tests yielded the following relevant results (Note that alpha was set at .01 in order to correct for the increased probability of committing the type 1 error associated with conducting multiple statistical analyses on the same data set):

a) For option 1: There was a significant group*condition interaction, F (1,574) = 65.28; a significant main effect of condition, F (1,574) = 24.95; both p's < .01 but not a significant main effect of group was found.

b) For option 2: There was a significant main effect of condition, F (1,574) = 59.09; and a significant main effect of group, F (1,574) = 16.24, both p's < .01 but no significant interaction.

c) For option 3: There was a significant group*condition interaction, F (1,574) = 8.14; a main effect of condition, F (1,574) = 61.74, both p´s <.01. No other significant effects were found.

d) For option 4: There was a significant main effect of condition, F (1,574) = 153.75, p<.01; but no significant main effect of group nor interaction.

Overall, these analyses reveal that responding on all feeders is affected by the change of condition; moreover, the presence of a significant effect of group only in option 2 suggests that the temporal distribution of responses for both groups respond is quite similar on each condition. As noted before, the shape of the curve suggests timing on the fixed condition (which is to be expected), but not on the variable duration condition (which was also expected), this impression could be strengthened by the clear effect of condition shown in the ANOVAs, however, the anticipation of depletion difference was obtained for these data in order to obtain a more precise view of timing under each condition.

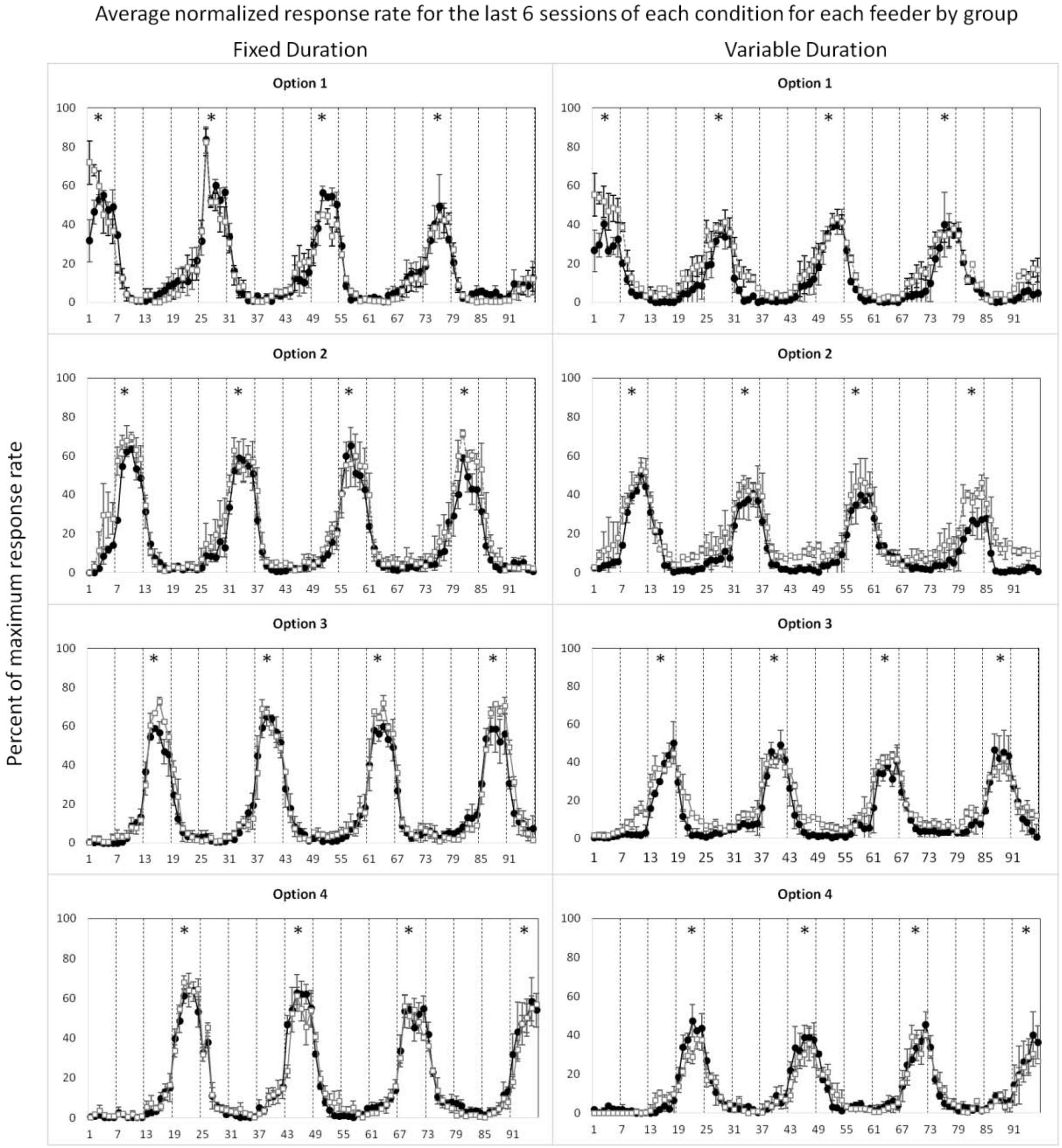


Figure E2R2. Average normalized response rate for the final 6 days in each condition in sixths of the availability period duration bins. Left panel shows data for the constant fixed for each group on each option. Right panel shows data for the variable condition for each group on each option. Vertical dashed lines signal the end of each availability period. Asterisks show the correct period for each option. Note that, for the variable condition, each bin groups data for 10, 20, 30 or 60 seconds.

The anticipation of depletion difference was obtained to get a clearer view of whether subjects are timing the availability period duration under each condition. As before, availability periods were divided in 6 bins. The anticipation of depletion difference was obtained by subtracting the normalized response rate during the last two bins of each period of availability to the normalized response rate during third and fourth bin of each period. Note that bins group data for 1/6th of the availability period duration, which implies that, during the fixed condition, all bins are 30 sec long, however, during the variable duration condition, bins can be either 10, 20, 30 or 60 sec long.

Negative values of this difference imply lower rates of responding towards the end of the availability period (anticipation of depletion), positive or near zero values of this difference imply a flat function of response rate, which would be evidence of lack of anticipation of depletion.

Figure E2R3 shows the anticipation of depletion scores for each group in 2 session bins throughout the experiment. Group 1 is shown in filled circles and group 2 in white squares. The black vertical line shows the end of the first condition and the start of the second. On this figure, a clear difference between groups is evident throughout the first condition, while birds in group 1 start obtaining negative scores around the eight session bin, birds in group 2 do not do so. This difference suggests that the difference in percent correct responses between groups found during the first condition was due to a lack of effective timing of group 2 birds. A mixed effects ANOVA compared performance between groups during the first 50 sessions. This analysis was conducted with Session as a within subjects factor and Group as a between subjects factor, and it revealed a significant main effect of group, F (1, 4) = 86.07, p <.05, but no significant interaction nor main effect of session. The lack of a session effect could be due to the fact that differences start really early in training and, since the 16th session, both functions do not change in an orderly fashion. This ANOVA confirmed an important difference between groups on the anticipation of depletion difference during the first condition. This is highly suggestive of a timing impairment of birds faced with a variable duration of the availability period, which is to be expected.

On the other hand, An important finding shown on figure E2R3 is that, once the conditions are reversed, the difference between groups is immediately vanished, A mixed effects ANOVA comparing the last 6 sessions of the first condition with the first six sessions on the second condition for each group revealed a significant main effect of group, F (1,34) = 4.93, p<.05, and a significant group*condition interaction, F (1,34) = 10.89, p<.05, with no main effect of condition. Two paired samples t-test showed an important difference in anticipation of depletion scores for group 1, t (1, 17) = -3.32, p>.05 but not for group 2, t (1, 17) = 1.35, p>.05. These tests reflect a highly damaging effect of the reversal for the group that is transferred from a fixed duration to a variable condition, but not for the group that goes from a variable to a fixed duration condition.

The difference between groups starts reappearing until the last half of training under the second condition. This suggests that birds in group 1 were no longer able to time the availability periods once put in the variable duration condition (which was expected), but it also suggests that birds in group 2 take longer to start timing these periods when faced with a fixed duration task that did birds in group 1 under the same conditions. This could be understood as a carryover effect. Perhaps having been precluded of performing effective timing for 50 sessions caused them to take longer to start timing once they have an opportunity to do so. A mixed effects (Session*Group) ANOVA like the one conducted for the first condition was carried out for sessions 51-100. This analysis yielded, a significant session*group interaction, F (49, 196) = 1.45, p<.05, and, again, a significant main effect of group, F (1, 4) = 26.27, p<.05 but no main effect of session. This analysis shows that both the average anticipation of depletion difference changes differently for each group throughout the second condition. While birds in group 2 obtain progressively lower values, birds in group 1 do not, moreover, some of the first bins show a negative anticipation of depletion difference (notably bin 30), and these negative values disappear around the 32th bin and never appear again.

Overall, the anticipation of depletion scores shown on figure E2R3 show that both groups of birds are able to time the availability periods when faced with a fixed duration, however, birds on group 2 took longer to do so than birds in group 1. On the other hand, as expected, neither group was able to time these durations when they were variable. So far, these data agree with those presented by Thorpe *et al* (2007) and extend the generality of their conclussions to an interval TPL task in which temporal variability is to manipluated in an intra-sessions fashion.

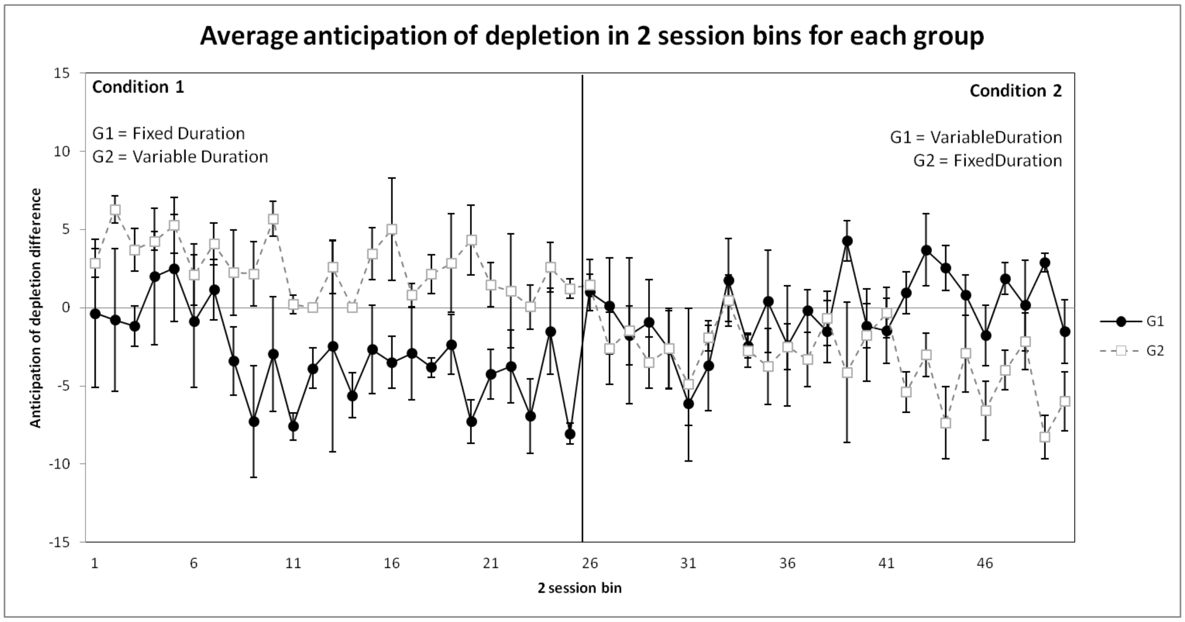


Figure E2R3. Average anticipation of depletion difference in 2 session bins for each group throughout the experiment. Filled circles represent data for Group 1 and white squares represent data for Group 2.

The lack of anticipation of depletion under a variable duration condition is perfectly understandable, since, timing is precluded under these circumstances, on the other hand, there is a strong possibility that birds do learn about the spatial contingencies of the task on both conditions, for the sequence of availability remained fixed throughout this entire experiment. A first glance at this could be obtained by calculating the anticipation scores, for, even when birds do not leave an active option in an orderly fashion (i.e., when no anticipation of depletion is evident), there could still be order in the option they respond on towards the end of an availability period.

Figure E2R4 shows the anticipation difference for each group throughout the experiment. This difference is obtained in the exact same way as the anticipation of depletion difference with the exception that response rate during the last two bins *prior* to the onset of any given option is subtracted to the response rate during the third and fourth bin prior to this onset. This way, positive differences suggest an increase in response rate as the availability on a given option becomes closer, while negative or near zero values suggest lack of anticipation.

An interesting finding is that anticipation difference scores rise above zero for both groups of birds during the first condition. This rise is faster for group 1 (fixed duration) than for group 2. This finding could be somewhat puzzling, since the anticipation of depletion scores suggested that birds in group 2 were not able to time the duration of the availability period, then how are they able to anticipate the arrival of food on a given location? Three important things must be noted about this. First, the anticipation difference is positive bur relatively small, while birds in group 1 reach levels of 10-11, birds in group 2 never surpass 4, which suggests only a slight rise in response rate just before any option becomes the temporally correct one. On the other hand, the fact that birds keep a steady response rate on the temporally correct option does not preclude a simultaneous rise on response rate on the next option. Finally, anticipation of depletion reflects only timing of the availability period, while, on the other hand, anticipation is thought to depend on both timing and place learning, and the low but positive anticipation of depletion scores could be evidence that birds are able to learn the fixed sequence of availability even under variable duration conditions.

A mixed effects ANOVA with Session as a within subjects factor and Group as a between subjects factor revealed no significant main effects or interactions. The lack of a main effect of session was somewhat puzzling, for, the anticipation difference clearly grows as training progress. The nonsignificance of this test could be due to two factors: increased variability and the fact that group 2 shows a really small increase in anticipation scores. To test this, two separate repeated measures

ANOVA were conducted, one for group 1 and another for group 2, these tests yielded a significant effect of Session, F (49,98) = 1.57, p<.05 for group 1, but not for Group 2. These tests confirmed that the lack of a main effect of Session on the mixed effects ANOVA were due to the small size of this effect for group 2.

The analyses conducted on the data presented on the left half of Figure E2R4 suggest that, although birds obtain positive anticipation of depletion differences, only birds in group 1 can be unequivocally said to be able to anticipate food availability on the next temporally correct option. Data for group 2 are harder to interpret, for they do obtain positive anticipation differences, but they are not as big as those obtained by group 1.

On the other hand, there is a clear effect of the reversal for each group, the anticipation difference drops for group 1, who went from a fixed to a variable duration condition, and it rapidly increases for group 2 and reaches levels as high as those attained by group 1 on their first condition. A mixed effects Group*Condition ANOVA was used to compare performance on the last 6 sessions of training in the first condition against the first 6 sessions of training in the second condition for each group. This analysis revealed a significant group*condition interaction, F (1, 34) = 7.27, p<.05 and a significant main effect of condition, F (1, 34) = 4.69, p<.05 and a barely non significant main effect of group, F (1, 34) = 3.98, p = .054. To further analyze the interaction, two paired samples t tests were conducted on the same data, one for each group. These tests revealed a significant difference in the anticipation scores for group 1, t (1, 17) = 3.44, p<.05, but not for group 2, t, (1, 17) = -0.37, p>.05. These test revealed an asymmetrical effect of the condition change. While birds in group 1 seem to stop being able to correctly anticipate the next food location, birds in group 2 do not suffer any immediate change due to the reversal.

Finally, the evolution of anticipation throughout the second condition shows that birds in group 2 progressively learn to anticipate food location, while birds in group 1, seem to suffer a progressive deteriorating effect on this score. A mixed Effects Session*Group ANOVA carried on data from sessions 51-100 showed a significant main effect of Group, F (1, 4) = 8.83 p<.05, but no effect of session nor interactions. The significant effect of group was to be expected from the difference between groups, shown in the plot, however, the lack of a session effect is, again, somewhat puzzling, for the anticipation difference for both groups changes as training advances. The same follow-ups were conducted for these data, two separate ANOVA´s, one for each group, and they yielded a non significant main effect for neither group. This lack of effect could be due to increased variability (particularly for group 2) and the fact that birds in group 2 reach their asymptotic level on the 5th bin of sessions, and, the anticipation difference does not change so much during the other 20 bins. Overall, the plot shows that both groups of birds are able to learn the sequence of food availability under the fixed duration condition. There are two findings that suggest (although not unequivocally) that they are also able to do so under the variable duration condition. First, both groups obtain positive anticipation differences, which are the product of a rise on response rate just before an option becomes the temporally correct one. Second, birds in group 1 reach their asymptotic level around session 22, at it takes nearly half of that for birds in group 2 to accomplish the same, this difference in learning rate strongly suggest that birds in group 2 did learn the spatial regularities of the task during their first condition.

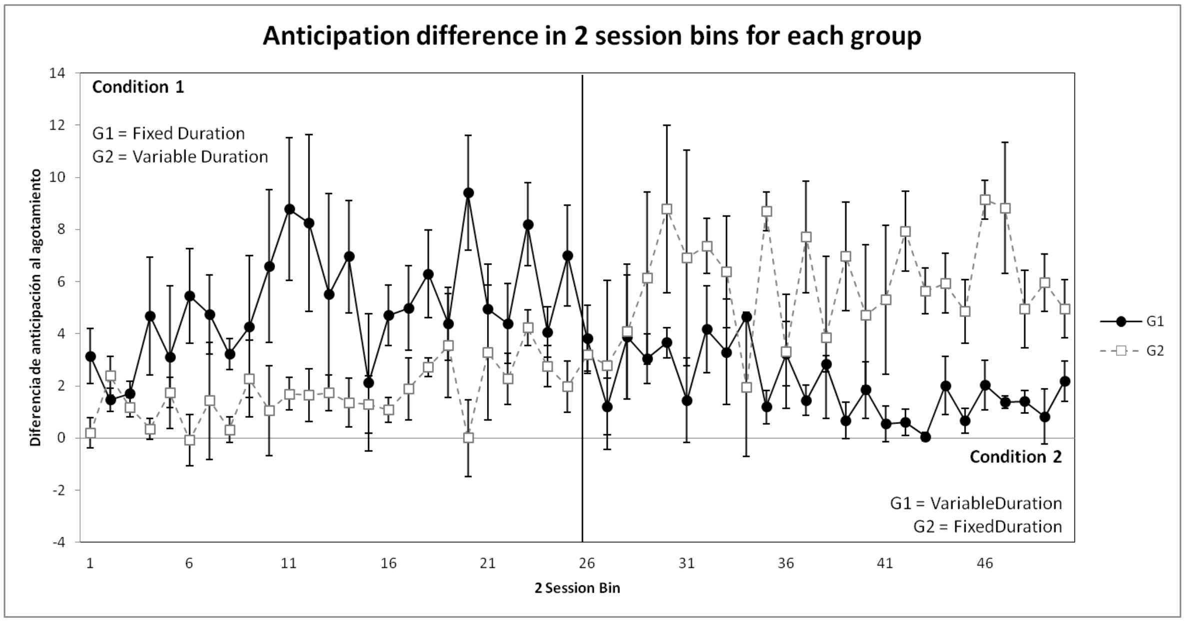


Figure E2R4. Average anticipation difference in 2 session bins for each group throughout the experiment. Filled circles represent data for Group 1 and white circles represent data for Group 2.

The data presented so far shows that birds are ultimately able to solve the task under both conditions. The temporal distribution of responses and the analyses on anticipation and anticipation of depletion suggests that, even though birds do restrict the majority of their responses to the temporally correct option, they do so by using different strategies. An inability to time the availability period duration is perfectly expectable given the fact that this duration is variable; however, anticipation data strongly suggests that birds are able to learn about the sequence of food availability under both conditions. A final comparison that could yield interesting data about the strategy that better describes the birds' performance under each condition is to contrast performance under training and during the OHT that was conducted.

Figure E2R5 shows the average temporal distribution of responses during the first four periods of availability for the final six training sessions each condition (filled circles) and the same data for the OHT that followed each condition (white squares). The left panel shows this comparison for the fixed duration condition while the right panel shows these data for the variable duration condition.

The plot shows that there are differences between training and OHT for both conditions. However, these differences seem greater between variable duration and OHT than between fixed duration and its respective test. In fact, the shape of the temporal distribution curve seems to be quite similar for the fixed duration condition and the OHT that followed it for 3 out of 4 options, the main difference is that all the curves seem shifted rightwards almost for an entire availability period. Analyses of individual data suggested that one of the subjects of this group (S2) is mainly responsible for this curve shift because it spent almost 6 minutes responding primarily on the first option and only then it moved.

On the other hand, the differences between training and OHT during the variable duration condition are much more noticeable. Subjects move around the four options, and they finish their sequence (i.e. reach the fourth option) during the second period of availability. Even tough, a fastening of the completion of the sequence has been previously reported in experiments that used tests similar to these both with daily (Biebach, Gordijn & Krebs, 1989; Falk, Biebach, & Krebs, 1992) and interval TPL (Carr, Tan, Thorpe & Wilkie, 2001; Thorpe & Wilkie, 2005) this case seems to be particular, because subjects reach their highest normalized response rate on option 1 during the first 30 sec bin, on option 2 during the 7th bin, for option 3 during the 8th bin and for option 4 around the 11th bin of the test, this fact reflects a spatially ordered pattern of visits. Additionally, there seem to be clear ascendant-descendant curves for options 1, 2, 3. These data suggest that subjects did not rely entirely on a win/stay-lose/shift strategy, they clearly move throughout the different options (which would not be predicted by this strategy), and, moreover, they do so in the correct order as can be confirmed by the peak location in every option.

The OHT data for group 1 supports the hypothesis that birds faced with a variable duration condition do learn about the fixed sequence of the task, however, the temporal distribution of responses does not suggest an entire lack of timing, for, they do move between options and do so in an orderly fashion.

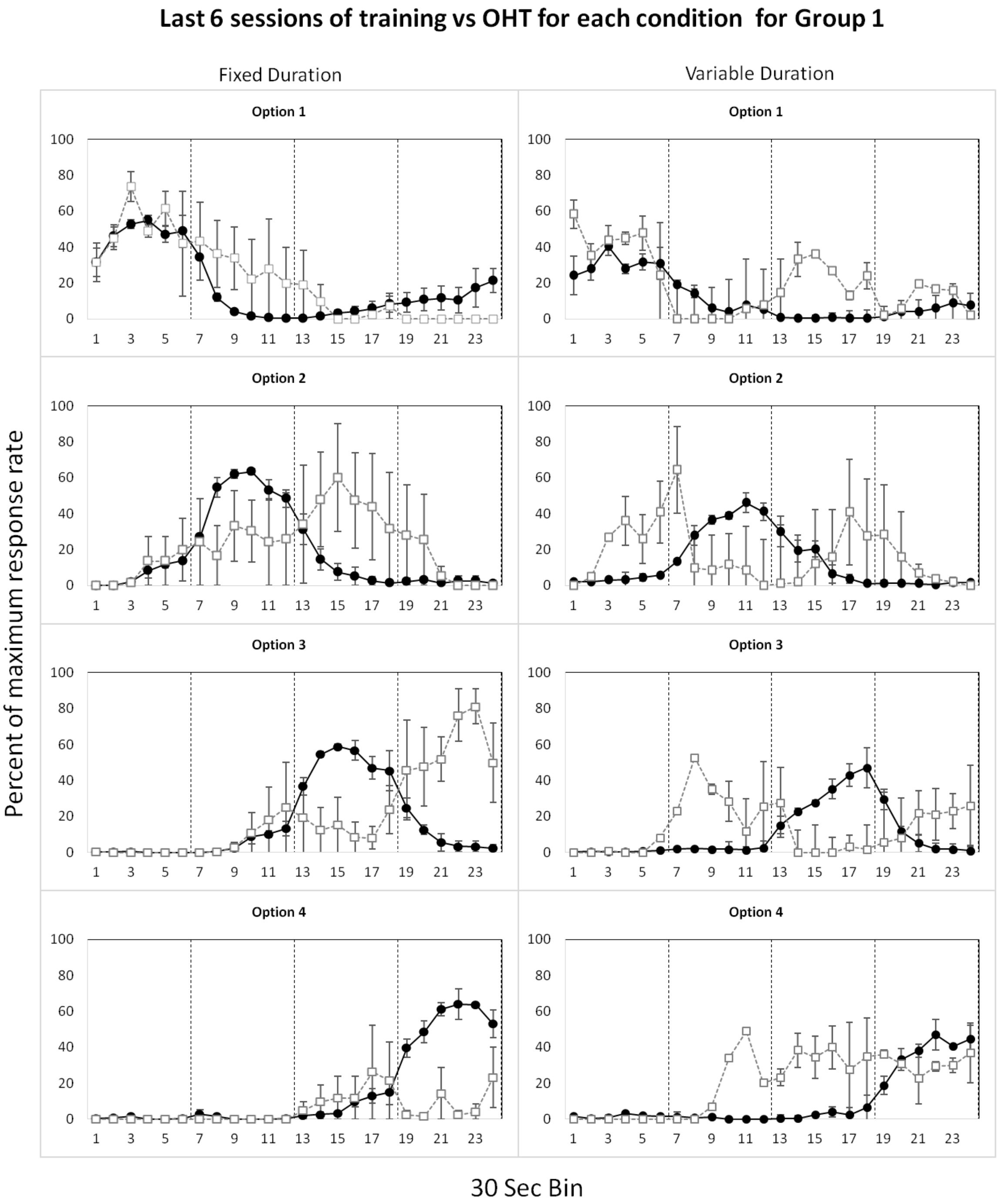


Figure E2R5. Average normalized response rate in 30 sec bins for the first 4 periods of availability of the last 6 training sessions and the OHT sessions for all birds in group 1 on each option. Left panel shows the comparison between the first training condition (Fixed Duration) and the first OHT, right panel shows the comparison between the second training condition (Variable Duration) and the second OHT.

Figure E2R6 shows the same data that last figure but for Group 2. On this plot, the left panel shows training vs OHT for the variable duration condition while the right panel shows the same comparison for the fixed duration condition.

This group of birds shows an even stronger resemblance of patterns between training and OHT than did birds in group 1. There are differences in the temporal distributions that are perfectly expectable (Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Petrovic & Wilkie, 2002; Thorpe & Wilkie, 2005; Thorpe, Hallet & Wilkie, 2007), however, overall, birds show to maintain a very similar visiting pattern during training and OHT for the fixed condition (right panel).

On the other hand, training and OHT during the variable condition produce different temporal distribution of responses, although, these curves are quite more similar than those obtained for group 1. Interestingly, this temporal distribution, again, does not support a win/stay – lose/shift strategy. Birds in group 2 also move around the options and do so in a much more orderly fashion that did birds in group 1.

Four mixed effects ANOVAs (One per option) with group as a between subjects factor and condition (training vs OHT) were conducted to compare differences in responding during the fixed condition and it's respective OHT. None of these analyses revealed significant Main effects or interactions. This negative result suggests that, the temporal distribution of responses is, overall, quite similar during the fixed duration condition and the OHT that followed it. This result was expected given that resemblance of patterns is a widely reported finding in the literature (Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Petrovic & Wilkie, 2002; Thorpe & Wilkie, 2005; Thorpe, Hallet & Wilkie, 2007).

The same analyses were conducted to compare data from the variable duration condition and its OHT. These ANOVA´s yielded the following relevant results:

Option 1: Significant Main effect of Condition, $F(1, 46) = 8.27$, $p<.01$, no significant main effect of group nor interaction were found.

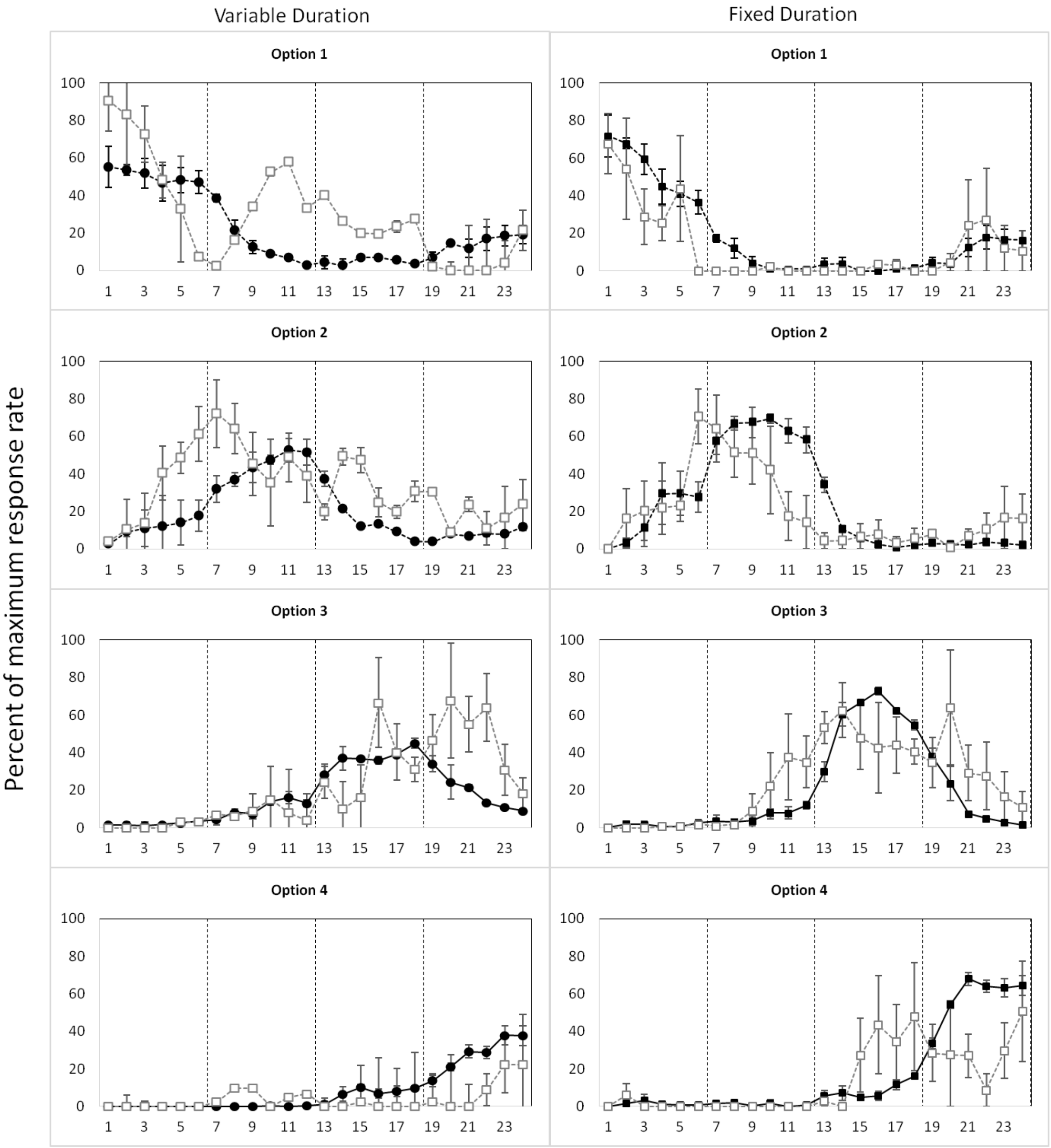
Option2: A barely non significant main effect of Condition, $F(1, 46) = 6.76$, $p =.01$

and a significant main effect of group, F (1, 46) = 9.97, p <.01.

Option 3: No significant Main effects or interactions.

Option 4: A significant group*condition interaction, F (1, 46) = 12.04, and a significant main effect of group, F (1, 46) = 7.77, p <.01.

Last 6 sessions of training vs OHT for each condition for Group 2



Altogether, the data obtained comparing data from training vs OHT suggests that birds tend to maintain a spatially ordered pattern of visits during both conditions. This is additional evidence that birds are able to learn the fixed sequence of availability under both conditions. This fact is particularly interesting because it replicates Thorpe *et al* (2007) finding that variability in the temporal dimension of the task does not preclude an effective adjustment to fixed spatial parameters.

While the difference in percent correct responses between group 1 and 2 during their first condition does reflect an overall better performance under a fixed duration condition, it does not reflect the use of a radically different strategy to solve the task under each condition. The averaged temporal distribution of responses and the anticipation of depletion data suggested that birds were not timing the availability periods under the variable duration condition. However, as the OHT data reveals, there does not seem to be a complete lack of timing, for subjects did move around the options.

One possibility is that, the use of variable durations of availability periods discourages the use of an interval timing strategy in favor of an ordinal one (Carr & Wilkie, 1997). This would mean that birds rely on the order of the events (i.e. the fixed sequence of availability) as the major source of control for time-ordered behavior. An ordinal timing strategy would parsimoniously explain the lack of anticipation of depletion and the absence of a clear win/stay-lose/shift strategy during the OHT.

A different and very interesting possibility was entertained by Thorpe, Hallet and Wilkie (2007) on their interpretation of their data. Maybe subjects do behave according to an interval timing strategy; however, since there are multiple intervals, they could either time the average, or develop bias towards one of these values. Thorpe *et al*, designed a study in which the availability duration period changed from session to session, therefore, they contemplated the possibility that their subjects timed the first period of availability, and then, use this first value throughout the entire session. Even though this would not be an effective timing strategy for the present conditions, there is still the possibility that subjects *checked* whether the availability period had run out by moving from option to option at fixed intervals.

A strong possibility then is that subjects used one of the shorter time values as a time-mark to change options and check if the next option is already available. If this rationale were true, the apparent lack of interval timing suggested by the temporal distribution of responses and the lack of anticipation of depletion could be due to the fact that these measures were obtained averaging sixths of availability period across all values. On the other hand, an *early error checker* could also explain the extreme hastening of the sequence completion during the OHT that followed the variable condition.

Figure E2R7 shows the average normalized response rate for the last 6 training sessions for each duration in 30 sec bins. Circles represent data for the 1 mint periods, diamonds for 2 min periods, squares for 3 min and triangles for 6 min. Top panel displays data for group 1 and the bottom panel displays data for group 2. Data for both groups is quite similar, and it shows that there are no differences in the function of response rate between durations, which suggests that birds respond in the same way as the availability period elapses regardless of the duration of this period. The negatively accelerated curve that is visible for all periods except the first minute, suggests that, once the first minute elapses, birds maintain a somewhat steady response for as long as the availability continues. An interesting fact is that, for the 3 and 6 min durations, there is a slight difference in response rate between the first and second 30 min of each minute, i.e. they respond more at the beginning of each minute than towards the end. This minor difference could be construed as evidence for a one minute *error checker*; however, the size of the difference is quite small.

These temporal distributions of responses suggest that birds do not use any of the values of the availability period duration as a reference value (with the possible although improbable exception of the 1 min value) to move around the options, and that, past the first minute, they rather show a steady response rate towards the end of each duration. These findings are evidence that an ordinal timing strategy is the best option to explain why birds maintain spatially ordered patterns of visiting during the OHT despite the fact that food can be found anywhere at any time.

An ordinal timing interpretation of the OHT data is reasonable, since the order in which food can be found is the only temporal parameter that is kept constant under the variable duration condition. However, this study does not conclusively prove so.

For the present experiment, a special methodological care was given to select the values of availability periods to be used during the variable condition, for the aim was that the average value of this period did not differ from that used during the fixed condition (3 min), and, that only four values were used because. This provided the possibility of matching the number of times each option would be available for each of the duration periods. However, if values of 1, 2, 3, 4, 5, and 6 minutes were to be used, the probability of an availability switch every minute would be higher, and this fact could possibly encourage an interval based timer that checked at the end of every minute whether food has been depleted or not.

One of the main conclusions from this experiment is that the use of a variable duration of the availability period does not entirely preclude timing, and therefore, it does not promote a win/stay- lose/shift strategy.

Overall, the present experiment extended the generality of previous temporal manipulations of the temporal parameters of the task (Thorpe, Hallet & Wilkie, 2007) to situations in which the duration of the availability period can be different within a single session.

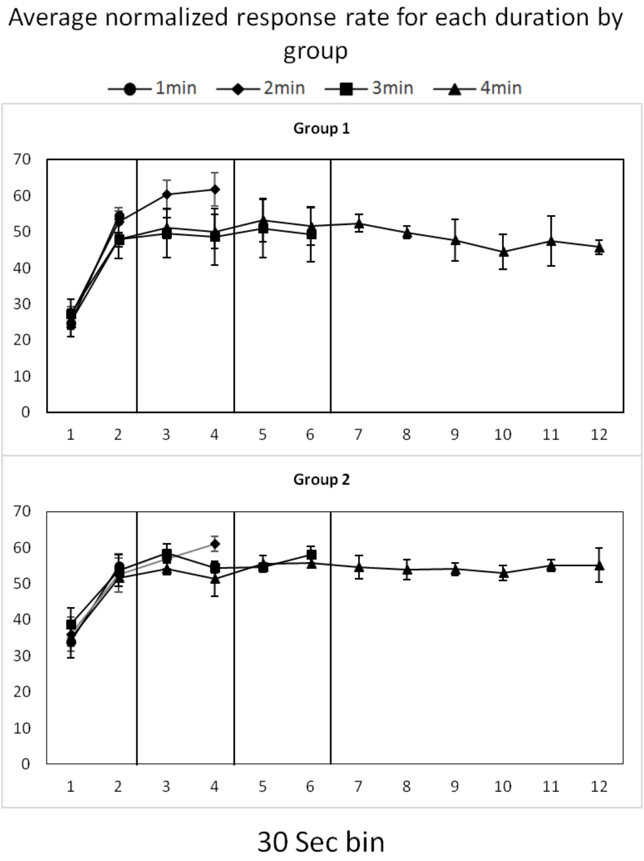


Figure E2R7. Average normalized response rate for each duration of the availability period for the last 6 training sessions in 30 sec bins. The vertical lines signal the end of each availability period duration (1 min, 2 min, 3 min and 6 min).

General Discussion: Time, space, and memory codes

The present study ought to determine the effects of within sessions spatial and temporal variability on the temporal distribution of responses in a TPL task with pigeons.

This general purpose was deemed to be especially relevant in the field for multiple reasons. First, it was thought to be a necessary follow-up to the Thorpe *et al* (2007) study, in which they tested whether Gallistel´s (1990) tripartite code proposition accounted for a daily (between sessions), variability of either the time or place component of the code. Second, since interval TPL is often said to be dependent on an interval timer (Carr and Wilkie, 1998; Carr & Wilkie, 2002; Crystal, 2009; Mulder, Reckman, Gerkema & Van Der Zee, 2015), this poses a special interest in elucidating how do animals (in the present case, pigeons), adjust their behavior to continuous changes in the sequence of food availability or in its duration. Third, this continuous change in immediate food availability could yield insight as to how animals behave under partially predictable patterns of food availability; which faces them with a situation that is reasonable to assume they face in nature. Fourth, including an OHT after both temporal and spatial variability was thought to be a fruitful source of data about what the subjects learned under each of these conditions.

Two experiments were conducted in order to achieve this general goal. First, the effects of spatial variability on a 16 period TPL task were assessed by comparing performance under a variable sequence and a fixed sequence condition while maintaining a fixed duration of the availability period.

As expected, spatial variability precluded the subjects from correctly anticipating where food would be available next, however, of special interest was the fact that this failure extended to *when* food would change availability location. Birds faced with a variable sequence of food availability where unable to show anticipation of depletion and, when put on an OHT, their temporal distribution of responses on every option did not bear any significant resemblance with that shown during training. These findings are highly suggestive of a win/stay-lose/shift strategy. So far, these results agree with those found by Thorpe *et al* (2007), for, varying the spatial dimension of the task had a vastly damaging effect on timing.

While results from the first experiment here and that of Thorpe *et al* (2007) could be interpreted as favoring Gallistel´s (1990) tripartite memory code proposal, a different approach was entertained. A variable sequence of food availability could entail variability in the position of the temporal marker that signals the start of the period to time, this would explain the birds' inability to time the periods of availability. The average standard deviation of the moment in which the first reinforcer of each period was obtained and plotted. The results showed no consistent difference in this standard deviation for the present experiment. This could be interpreted as further evidence favoring Gallistel´s memory based proposal, or as suggestive that the first reinforcement obtained on a given period does not function as a temporal marker and something else does, although it would be unclear what other event could serve this function.

On the other hand, experiment 2 was designed to assess the effects of variability in the duration of the availability period, this was accomplished by comparing performance under a 16 period TPL task in which the duration of the availability period could be either 1, 2, 3, or 6 minutes (variable duration), with that obtained with a similar task in which this duration was kept fixed at 3 minutes. During both of these conditions, birds faced a fixed sequence of availability. This experiment yielded interesting results. As expected, they did not learn to anticipate food depletion; however, these birds did learn to anticipate the next location of food availability, as shown by the positive anticipation differences. Data from the OHT that followed the variable duration condition, revealed a temporally disordered but spatially ordered pattern of visits, i.e., birds responded on all options during the first four periods of this test, while the width of these distributions were variable, the order in which the peaks were located reflected that they maintained the sequence learned during training.

This spatially ordered pattern of responding is not compatible with a win/stay-lose/shift strategy, this suggests that birds are responding to some temporally based regularity involved in the task despite the lack of a fixed duration of the availability period. Two possibilities were contemplated, the first was that an ordinal timer could serve to describe these data; birds faced with a variable duration of the availability period are still faced with a fixed order on the availability locations, which would provide them with a temporally regular phenomenon to lead their behavior. The second possibility is that birds could use one of the lower values of the availability period duration as a reference and then check every 1 or 2 minutes whether food is already available in the next location. The hastening of the sequence completion during the OHT was suggestive of the second possibility, for it would explain why birds switched locations so fast; however, the temporal distribution of responses for each of the availability period durations, did not reveal periodic and significant decreases in response rate (as would be expected if birds would *check* the next option for food availability).

The general data of the second experiment were also in line with the results obtained by Thorpe *et al* (2007), for it is additional evidence that temporal variability does not preclude learning of fixed spatial parameters of the task. Thorpe *et al* concluded that this was proof that the tripartite memory codes are not essential to TPL, however, the finer grain analyses conducted here allow to entertain the possibility that, even with a variable duration of the period, the *time* component of the code is kept constant via an ordinal timer (Carr & Wilkie, 1997b) which would mean that, even under conditions like those reported here and by Thorpe *et al*, a time-place-event memory code can still be formed.

Both experiments comprised a 16 period condition in which the same sequence of availability locations was repeated 4 times within a session maintaining a fixed duration of the availability period. While the results of this fixed duration-fixed sequence condition were not the focus of main interest of the present study, they did reveal a number of interesting results. First of all, this condition produces a significantly higher than chance percent correct responding, temporal distribution of responses very similar to other TPL tasks (Wilkie, Saksida, Samson & Lee, 1994; Carr & Wilkie, 1998; Thorpe & Wilkie, 2002; 2006), which is suggestive of anticipation and anticipation of depletion. When specific scores to test these two indicators were obtained, the results of this fixed condition showed that all birds on the two experiments were correctly anticipating the next location of food availability and food depletion on the temporally correct location. Moreover, when put in an OHT after the fixed condition in both experiments, results showed important similarities between training and testing in the temporal distribution of responses on each option during the first four periods of availability.

A note must be done as to why only the first 16 minutes of the OHT were plotted. It has been previously reported that the resemblance of patterns is almost never perfect, and a common finding is increased variability in the response pattern of the subjects as the OHT advances (Carr, Tan, Thorpe & Wilkie, 2001; Thorpe, Floresco, Carr & Wilkie, 2007; Thorpe, Petrovic & Wilkie, 2002; Thorpe & Wilkie, 2005; Thorpe, Hallet & Wilkie, 2007). This was the case in the present experiment, yielding a high variability in responding that would have hindered interpretation of the data.

An alternate interpretation of the increased variability during OHT could be that it is evidence that subjects were not really timing the availability periods or learning the sequence of food availability under the fixed condition. However, given the robust timing evidence obtained during training, this interpretation seems highly unlikely.

In short, results from the fixed condition carried on both experiments extended the generality of TPL to situations in which the same fixed sequence of availability is repeated 4 times within a single session. This fact suggests a couple of interesting questions about the learning process involved in this task. Namely, are subjects experiencing these sessions as one very complex sequence or as four simple sequences? Are subjects timing only one duration 16 times, or are they timing the 16 periods as only one event? The present experiment was not designed to shed light into these matters, although it would be, of course, really interesting to design future studies to do so.

Along the lines of interesting questions suggested by the data reported here is the replication of a clearly asymmetrical effect of the temporal and the spatial parameters of a TPL task. It must be noted that, unlike in Thorpe, Hallet and Wilkie (2007) study, none of the variable conditions hindered performance on a posterior fixed condition, i.e. learning curves are very similar for the fixed condition regardless of whether it was the first or the second condition experienced by our subjects. However, spatial variability has a powerful and damaging effect on performance, even precluding adequate timing of a fixed duration of the availability period. On the other hand, when a variable duration of the availability period is used, there is not such a clear effect on whether birds learn the fixed sequences of food availability. Simply put, variability on the spatial parameters of the task precludes the birds from adjusting to fixed temporal parameters, but the reverse is not true.

This general finding is perfectly in line with the study of Thorpe *et al* (2007). Their interpretation of their data can be summarized in two major points:

1. The fact that learning occurs under temporally variable conditions suggests that there is no need for a tripartite memory code, and, that a series of bipartite time-event, place-event codes drive adequate TPL.
2. These data are evidence that the spatial information could play a more important role in TPL than temporal information.

Both of these main arguments could apply also to the data of the present experiments, however, the present analyses revealed that this is not the only possible interpretation of the data. An alternate view is to attend the parameters involved in these situations and to reflect on how they affect behavior related to both time and space regularities.

Both facts could be explained by considering that, when the sequence is variable, this can promote changes not only in the spatial dimension of the task, but also on the temporal, for the use of a variable sequence can increase the amount of time the subjects search for food (García-Gallardo, Aguilar, Armenta & Carpio, 2015).

On the other hand, as experiment 2 revealed, there is a strong possibility that varying the duration of the availability period does not preclude temporal order in the task, for, as long as the sequence is kept constant, an ordinal timer could account for the data observed here (Carr & Wilkie, 1997b), and, thus, the need for time-place-event regularity would stand (Gallistel, 1990).

If the above interpretation is true, then these and Thorpe’s data would not reflect an asymmetrical role played by spatial and temporal information on interval TPL task, and they would rather reflect a specific effect of a set of parameters of the task. As a consequence, one of the main contributions of this study would not rest on a replication of a previously reported effect, but on extending the generality of a finding to parametrically different situations, and, therefore, to be used as a stepping stone towards a different course of research in TPL.

One of the obvious problems to test whether a tripartite code is necessary is that there is not apparent way to explore a condition in which time is authentically variable while the sequence remains fixed, for, under these conditions, the ordinal dimension of time will always remain constant, which would therefore preclude a condition in which an authentic bipartite code could be formed.

A different approach, however, would be to vary the *event* component. This way, bipartite time-place codes could still said to be conformed, but no tripartite codes. A modified TPL task in which a different type of reinforcement is randomly available on each choice, would serve this purpose. A tripartite code view would necessarily predict inadequate performance on a TPL task like this (Gallistel, 1990), while a bipartite code would not (Thorpe, Hallet & Wilkie, 2007).

An interesting question that deserves consideration is that of the origin and nature of the memory codes in question. Gallistel (1990) proposed a general theory of animal learning and memory that was recovered by Wilkie (1995) to explain several findings on the TPL Literature. The basic notion is that, whenever an animal encounters a biologically significant event, a record of its occurrence is stored. This record consists of three interdependent parts: The time (which can be extracted either from a phase oscillator or an interval timer), the space (which is extracted from a cognitive map) and the nature of the event. Needless to say, this record will only gain control over behavior if these three parts of the code appear in a regular manner, that is, if the animal finds always the same resource at the same place at the same time. Wilkie (1995) provides an example of how such a memory process is thought to control foraging behavior:

"If, for example, event$_1$ is food availability, a hungry forager can scan memory and find that food has previously occurred several times at place$_1$at time$_1$. The hungry forager can then proceed to this place at the appropriate time and find food. If memory scanning reveals that event$_1$ also happened at place$_3$ at time$_3$, and if time$_3$ is earlier in the day than time$_1$ then the forager may choose to visit place$_3$ rather than place$_1$." (Wilkie, 1995, p.85).

While Wilkie´s example evidently applies to Daily TPL situations, the exact same rationale is followed on interval TPL. Actually, Thorpe, Hallet and Wilkie (2007) designed their study in light of these assumptions, which could explain the apparent *all or nothing* methodological approach, for they were interested in learning whether TPL performance could emerge when the tripartite memory code is precluded via variability on either space or time parameters. Having concluded that these codes might not be strictly necessary, the interesting question becomes if spatial information is really more relevant than temporal information.

While the present study maintained the absolute yes/no approach, the alternate interpretations discussed here suggest a different conceptualization of the processes responsible for TPL under these situations. In Gallistel´s model, the critical assumption is that the animal forms a memory consisting of what, where, and when it found some biologically relevant event. Needless to say, this code will only be truly useful and operational if there is consistency in these three key variables, from this follows that the memory code that is said to control TPL performance depends on environmental regularities, for, in the absence of such regularities, no memory code could be formed.

A very simple and really old argument seems appropriate to the present situation: If the cognitive process that is said to control behavior depends on the environmental properties of the situation, then it would seem appropriate to regard the environmental factors as a cause and not the cognitive process (Watson, 1913, Skinner, 1938; Ribes, 2001; Roca, 2001).

Much could be gained by giving more attention to the parameters involved in the task and their effects on the behavior we can observe rather than in cognitive processes assumed to be responsible for such behavior (Schoenfeld & Cole, 1970; Ribes & Lopez, 1985, Carpio, 1994). For instance, from the cognitive standpoint, the subject either can or cannot form a memory code, however, from a parametrical standpoint, a random and a fixed sequence (or duration) are only the ends of a parametrical continuum of *degrees of variability*. This would yield many more different experimental possibilities.

Another possibility derived from a parametrical standpoint is to elucidate the behavioral or environmental events associated with timing indicators. A well-documented phenomenon is that, under temporally regular conditions, different species including rats (Laties, Weiss, Clark & Reynolds, 1965; Laties, Weiss and Weiss, 1969), pigeons (Skinner, 1948; Staddon & Simmelhag, 1971, Aguilar & Carpio, 2014), and humans (Bruner & Revusky, 1961) develop stereotypical patterns of responding that keep an important relation with the temporal distribution of the operant response under the control of temporally regular contingencies of reinforcement (Killeen and Fetterman, 1984; Machado, 1997; Aguilar & Carpio, 2014).

While this experiment was not explicitly designed to test whether this hypothesis applies to TPL, a detailed observation of the temporal distribution of responses on each feeder yields interesting insights into this matter: Under the fixed condition, there is a temporal regularity that clearly gains control over the animal’s behavior, and, as the temporal distribution of responses on every feeder shows, there is also evident regularity in the general activity of the subjects: Early into the period, they respond on the previously reinforced option, and, towards the end of the period, they move to the next reinforced option. Once put in the variable sequence condition, birds loose this regularity; for, they do not concentrate their responding on one particular option towards the end of the availability period (see Figures R2 and E2R2). This disruption of a temporally regular visiting pattern could be analogous to a disrupted set of *mediating* or *collateral* responding (Laties, Weiss, Clark & Reynolds, 1965; Aguilar & Carpio, 2014), which could be an alternate explanation as to why timing failed even under the same temporally regular conditions.

As noted before, these experiments were not explicitly designed to test a possible role of collateral responding on the temporal regularities in behavior often found in TPL tasks, although the apparent relation between the temporal distribution of responses on all feeders and the ability to anticipate depletion of food does suggest that an interesting and hitherto unanswered question is whether regular patterns of behavior emerge under TPL tasks and if these are associated with timing. An important step towards elucidating this possibility could be to design experiments in which these patterns are disrupted while maintaining the same spatial and temporal parameters.

In short, the present experiment ought to determine the effects of within sessions variability in the sequence of food location or in the duration of the availability period on a number of performance indicators of a TPL task. The results clearly show a more powerful effect of varying the sequence than the availability period duration.

These results are in line with those obtained by Thorpe, Hallet & Wilkie (2007), who conducted a similar experiment with the exception that, in their study, the sequence or duration of the availability period were varied from session to session. This fact, however, does not automatically lead to the exact same conclusions as these authors. They concluded that their finding was evidence that Gallistel's (1990) tripartite memory code model did not pose a necessary condition for TPL, and, they entertain the possibility that temporal and spatial information play asymmetrical roles on tasks like these. This study entailed a number of methodological features that Thorpe *et al*'s study did not, like the OHT after each variable condition, or the reversal in both directions among others. These features allowed analyzing other performance indicators. Altogether, the results obtained in this experiment suggest a number of different possibilities of interpretation. Special attention was given to a parametrical interpretation of the data and the experimental possibilities that can be derived from it to explore TPL.

Research in the TPL field is far from conclusive, and exploring the effects of different degrees of variability on the parameters involved in the task remains a critical question to be answered for it deals with a vital evolutionary function: How can animals learn when and where food can be found, even when there is not a perfectly repetitive pattern of availability? So far, it seems like animals do not move through time as they do through space, however, in time we will learn how animals learn to be in the right place at the right time.

References

Allan (1998) The influence of the scalar timing model on human timing research. *Behavioural Processes.* 44, 101-117.

Allan, L. & Gibbon, J. (1991). Human bisection at the geometric mean. *Learning and motivation*. 22, 39-58.

Anger, D. (1963). The role of temporal discriminations in the reinforcement of Sidman avoidance behavior. *Journal of the Experimental Analysis of Behavior,* 6, 477-506.

Aguilar , F. & Carpio, C. (2014) La función de la conducta adjuntiva en el timing: Un análisis paramétrico de la manipulación espacial. *Revista Electrónica de Psicología Iztacala*. 17, 1580-1596.

Ayllon, T., & Haughton, E. (1962). Control of the behavior of schizophrenic patients by food. *Journal of the Experimental Analysis of Behavior,* 5, 343-352.

Ayllon, T. & Hughes, H. (1971). Behavioural Engineering. En Pitts, C. (Ed). *Operant Conditioning in the classroom: Introductory readings in educational psychology.* New York: Crowell.

Bennet, A. T. (1996) Do animals have cognitive maps? *Journal of experimental biology.* 199, 219-224.

Biebach, H., Krebs, J. & Falk, H. (1994). Time-place learning, food availability and the exploitation of parches in garden warblers, *Sylvia Borin. Animal Behaviour.* 48, 273-284.

Biebach H., Falk, H., Krebs, J.R. (1991). The effect of constant light and phase shifts on a learned time-place association in garden warblers (Sylvia Borin): Hourglass or circadian clock? *Journal of Biological Rhythms.* 6, 353-365.

Biebach, H., Gordijn, M., & Krebs, J. (1989). Time-place learning by garden warblers, *Sylvia Borin. Animal Behaviour.* 37, 353-360.

Bolles, R. C., & Popp, R. J. (1964). Parameters affecting the acquisition of Sidman avoidance. *Journal of the Experimental Analysis of Behavior,* 7, 315-321.

Brown, P. & Jenkins, H. (1968). Auto-shaping of the pigeon's keypeck. *Journal of the Experimental Analysis of Behavior*, *11*, 1-8.

Bruner, A. & Revusky, S. (1961). Collateral behavior in humans. *Journal of the Experimental Analysis of Behavior*, *4*, 349-350.

Bruner, C. A. (1991). El problema de la contingencia en teoría de la conducta. En V. Colotla (Comp.), *La investigación del comportamiento en México* (pp. 153-171). México: AIC, CONACYT, SMAC, UNAM.

Buhusi, C. & Meck, W. (2007). Effect of clozapine on interval timing and working memory for time in the peak-interval procedure with gaps. *Behavioural processes.* 74, 159-167.

Cabrer, F., Daza, C. & Ribes, E. (1975). Teoría de la conducta ¿Nuevos conceptos o nuevos parámetros? *Revista Mexicana de Análisis de la Conducta*, *1*, 191-212.

Cain, Ko, Chalmers and Ralph (2004) Time of day modulation of conditioned place preference in rats depends on the strain of rat used. *Neurobiolgy of Learning and Memory*. 81, 217-220.

Carpio, C. (1992). Transición paradigmática en psicología: Análisis de un caso. *Acta Comportamentalia*, *0*, 85-108.

Carpio, C. (1994). Comportamiento animal y teoría de la conducta. En L. Hayes, E. Ribes & F. López (Coords.), *Psicología Interconductual: contribuciones en honor a J.R. Kantor*. México: Universidad de Guadalajara.

Carpio, C. (2009). Asuntos conceptuales en la investigación del comportamiento animal. En C. Carpio (Coord.) *Investigación, formación y prácticas psicológicas.* México: FES Iztacala.

Carpio, C., Serrano, M. & Camacho, I. (2006). Presence and absence of stimulus control in temporally defined schedules. *European Journal of Behavior Analysis*, *7*, 57-65.

Catania, A. C. (1970). Reinforcement schedules and psychological judgments: A study of some temporal properties of behavior. En W. N. Schoenfeld (Ed.), *The Theory of Reinforcement Schedule* (pp.1-42). New York: Appleton-Century-Crofts.

Carr, J.A.R., & Wilkie, D.M. (1997a). Rats use an ordinal timer in a daily time-place task. *Journal of experimental psychology: Animal Behavior Processes.* 23, 232-247.

Carr, J.A.R., & Wilkie, D.M. (1997b). Ordinal, phase and interval timing. En C.M. Bradshaw & E. Szabaldi (Eds.) *Time and behaviour: Psychological and neurobehavioural analyses*. Amsterdam: Elsevier. Pp 265-237.

Carr, J.A.R., & Wilkie, D.M. (1998). Characterization of the strategy used by rats in an interval time-place learning task. *Journal of experimental psychology: Animal Behavior Processes.* 24, 151-162.

Carr and Wilkie (1999) Rats are reluctant to use circadian timing on a daily Time-Place Learning task. *Behavioural Processes.*44, 287-299.

Carr, J.A.R., Tan, A.O. Thorpe, C.M., & Wilkie, D.M. (2001). Further evidence of joint time-place control of rat's behaviour: Results form an "Open Hopper" test. *Behavioural Processes.* 53, 147-153.

Church, R. (1984). Properties of the internal clock. En J. Gibbon & L. Allan (Eds. del volúmen.), *Timing and time perception: vol. 423. Annals of New York Academy of Science* (pp. 566-582). New York.

Church, R. M., & Deluty, H. Z. (1977). The bisection of temporal intervals. Journal of Experimental Psychology: Animal Behavior Processes, 3, 216-228.

Church, R. M., & Gibbon, J. (1982). Temporal generalization. *Journal of Experimental Psychology: Animal Behavior Processes*, *8*, 165-186.

Cole, M., Clipperton, A. & Walt, C. (2007). Place versus response learning in rats. *Learning and behavior.* 4, 214-224.

Crystal, J.D. (2009). Theoretical and conceptual issues in time-place discrimination. *European journal of neuroscience.* 30, 1756-1766.

Crystal, J.D., & Miller, B. J. (2002). Simultaneous temporal and spatial processing. *Animal Learning and behavior*. 30, 53-65.

Descartes (1637/1973). *Discours de la méthode.* Paris: Le Livre de Poche.

Delicio, H.C. & Barreto, R.E. (2008). Time-Place Learning in food restricted Nile Tilapia. *Behavioural Processes.* 77, 126-130.

Dews, P. (1962). The effect of multiple S^{Δ} periods on responding on a fixed-interval schedule. *Journal of the Experimental Analysis of Behavior*, *5*, 427-435.

Dews, P. (1965). The effect of multiple S^{Δ} periods on responding on a fixed-interval schedule II: In a primate. *Journal of the Experimental Analysis of Behavior.* 8, 53-54.

Dews, P. B. (1978). Studies on responding under fixed-interval schedules of reinforcement: II. The scalloped pattern of the cumulative record. *Journal of the Experimental Analysis of Behavior,* 29, 67-75.

Domjan, M. (2016). Elicited versus emmited behavior. Time to abandon the distinction. *Journal of the Experimental Analysis of Behavior.* 105, 231-254.

Droit-Volet, S. & Clement, A. (2001). Temporal Generalization in 3-8 year-old children. *Journal of Experimental Child Psychology.* 80, 271-288.

Dube, W. V., & McIlvane, W. J. (1997). Reinforcer frequency and restricted stimulus control. *Journal of the Experimental Analysis of Behavior,* 68, 303-316.

Dubreuil, D., Tixier, C., Dutrieux, G., Edeline, J. (2003). Does the radial arm maze necessarily test spatial memory? *Neurobiology of learning and memory.* 79, 109-117.

Falk, J. L. (1966). Motivational properties of schedules induced polydipsia. *Journal of the Experimental Analysis of Behavior*, *9*, 19-25.

Falk, H., Biebach, H. & Krebs, J. (1992). Learning a time-place pattern of food availability: a comparison between an insectivorous and a granivorous weaver species (*Ploceus bicolor* and *Euplectes hordeaceus*). *Behavioral Ecology and Sociobiology.* 31, 9-15.

Farmer, J. & Schoenfeld, W. N. (1966). The effect of a response-contingent stimulus introduced into a fixed-interval schedule at varying temporal placement. *Psychonomic Science*, *6*, 15-16.

Felton, M., & Lyon, D. O. (1966). The post-reinforcement pause. *Journal of the Experimental Analysis of Behavior,* 9, 131-134.

Ferster, C. B. (1953). The use of the free operant in the analysis of behavior. *Psychological Bulletin*, *50*, 263-274.

Ferster, C. B. & Skinner, B. F. (1957). *Schedules of reinforcement*. New York: Apletton-Century-Crofts.

Fetterman, J. G., & Killeen, P. R. (1995). Categorical scaling of time: Implications for clock-counter models. *Journal of Experimental Psychology: Animal Behavior Processes, 21,* 43–63.

Gallistel, C.R. (1990). *The organization of learning.* Cambridge Massachusetts: MIT Press.

García-Gallardo, D. Aguilar, F., Armenta, B. & Carpio, C. (2015). Human strategies for solving a Time-Place Learning Task. The role of counting and following verbal cues. *Behavioural Processes.* 113: 143-151.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, *84*, 279-325.

Gibbon, J. (1991). Origins of scalar timing. *Learning and motivation.* 22, 3-38.

Glazer, H. & Singh, D. (1971). Role of collateral behavior in temporal discrimination performance and learning in rats. *Journal of Experimental Psychology*, *91*, 78-84.

Gobety, M. & Schenk, F. (1992). The influence of spatial irregularity upon radial-maze performance in the rat. *Animal Learning and Behavior.* 4, 393-400.

Gomez-Laplaza, L. and Morgan, E. (2005) Time-Place Learning in the cichlid angelfish *Pterophyllum scalare. Behavioural Processes.* 70, 177-181.

Hansen, G. D. (1979). Enuresis control through fading, escape, and avoidance training. *Journal of Applied Behavior Analysis,* 12, 303-307.

Heinemann, E.G. (1984). A model for temporal generalization and discrimination. En J. Gibbon & L. Allan (Eds. del volúmen.), *Timing and time perception: vol. 423. Annals of New York Academy of Science* (pp. 361-371). New York.

Hinton, S. & Meck, W. (2004). Frontal–striatal circuitry activated by human peak-interval timing in the supra-seconds range. *Cognitive brain research.* 21, 171-182.

Hodos, W., Ross, G. & Brady, J. (1962). Complex response patterns during temporally spaced responding. *Journal Experimental Analysis Behavior*, *5*, 473-479.

Holz, W. C., Azrin, N. H., & Ulrich, R. E. (1963). Punishment of temporally spaced responding. *Journal of the Experimental Analysis of Behavior,* 6, 115-122.

Hull, C. L. (1943). *Principles of Behavior*. New York: Appleton Century-Crofts.

Hume,D. (1772/2004) An enquiry concerning human understanding. New York: Barnes and Noble

Kacelnik, A., & Brunner, D. (2002). Timing and foraging: Gibbon's scalar expectancy theory and optimal patch exploitation. *Learning and Motivation* 33 (1): 177-195.

Keller, F. & Schoenfeld, W. N. (1950). *Principles of Psychology.* New York: Appleton-Century-Crofts.

Killeen, P. & Fetterman, J. (1988). A Behavioral theory of timing. *Psychological Review*, *95*, 274.

Kirkpatrick-Steger, K., Miller, S. S., Betti, C. A., & Wasserman, E. A. (1996). Cyclic responding by pigeons on the peak timing procedure, *Journal of Experimental Psychology: Animal Behavior Processes*, *22*, 447-460.

Kristoffferson (1984). Quantal and dereministic timing in human duration discrimination. En J. Gibbon & L. Allan (Eds. del volúmen.), *Timing and time perception: vol. 423. Annals of New York Academy of Science* (pp. 3-15). New York.

Konorski, J. & Miller, S. (1937). On two types of conditioned reflex. *The Journal of general psychology.* 1, 264-272.

Krebs, J.R. & Biebach, H. (1989). Time-place learning by garden warblers (Sylvia Borin): Route or map? *Ethology.* 83, 248-253.

Kuhn, T. (1970). *La estructura de las revoluciones científicas.* México: Fondo de cultura económica.

Kupalov, P. S. (1983) Situational conditional reflexes. *Pavlovian Journal of Biological Science*, 18, 13-21.

Laties, V., Weiss, B., Clark, R. & Reynolds, M. (1965). Overt “mediating” behavior during temporally spaced responding. *Journal Experimental Analysis Behavior*, 8, 107-116.

Laties, V., Weiss, B., & Weiss, A. (1969). Further observations on overt “mediating” behavior and the discrimination of time. 12, 43-57.

Le Ny, J. F. (1965). *El condicionamiento*. Buenos Aires: Lautaro.

Locke (1690/1956) Ensayo sobre el entendimiento humano. México: Fondo de Cultura Económica.

Machado, A. (1997). Learning the temporal dynamics of behavior. *Psychological Review*, *104*, 241-265.

Mainord, W, (1968). Operant group therapy. En Pitts, C. (Ed). *Operant Conditioning in the classroom: Introductory readings in educational psychology.* New York: Crowell.

Menez, M. (2012) Flexibilidad en la estimación de intervalos. En: P. Guilhardi; M. Menez, & F. López (eds). *Tendencias en el estudio contemporáneo de la estimación temporal*. México:Universidad Nacional Autónoma de México.

Miller, G. A. (2003). The cognitive revolution: a historical perspective. *Trends in cognitive sciences*. 7, 141-144.

Morris, C. J. (1987). The operant conditioning of response variability: Free-operant versus discrete-response procedures. *Journal of the Experimental Analysis of Behavior,* 47, 273-277.

Morse, W. H. (1966). Intermitent reinforcement. En W. K. Honig (Ed.), *Operant Behavior: Areas of Research and Applications*. New York: Appleton-Century Crofts.

Mulder, C.K.; Gerkema M.P.; & Van der Zee, E.A. (2013). Circadian clocks and memory: Time-Place Learning. *Frontiers in molecular neuroscience.* 6, 1-10.

Mulder, C.K.; Reckman, G.A. Gerkema, M.P.; and Van der Zee, E.A. (2015) Time-Place learning over a lifetime: absence of memory loss in trained old mice. *Learning & Memory*. 22, 278-288.

Neisser, U. (1957). *Cognitive psichology.* New York: Appleton Century Crofts.

Pavlov, I. P. (1927). *Conditioned Reflexes.* Oxford: Oxford University Press.

Pavlov. I.P. (1993). Reflejos Condicionados e inhibiciones. México: De Agostini.

Pitts, C. & Powers, M. (1971). Undergraduate performance in an incentive course in educational psychology. En Pitts, C. (Ed). *Operant Conditioning in the classroom: Introductory readings in educational psychology.* New York: Crowell.

Pizzo, M. & Crystall, J. (2002). Representation of time in time-place learning. *Animal Learning and Behavior.* 30, 287-393.

Pizzo, M.J. & Crystal, J.D. (2004). Time-place learning in the eight arm radial maze. *Learning and behavior.* 32, 240-255.

Porter, J., Brown, R. & Goldsmith, P. (1982). Adjunctive behavior in children on fixed interval food reinforcement schedules. *Physiology & Behavior*, *28*, 609-612.

O'Keeffe, J. and Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford: Oxford University Press.

Olton, D. (1979). Mazes, maps and memory. *American Psychologist.* 34, 583-596-

Olton, D., Collison, C., & Werz, M. (1977). Spatial memory and radial arm maze performance in rats. *Learning & Motivation.* 8, 289-314. <u>En texto año 1957</u>

Reebs, S.G. (1993). A test of Time-Place learning on a cichlid fish. *Behavioural Processes.* 30, 273-282.

Reebs, S.G. (1996). Time-Place Learning in golden shiners (Pisces: Cyprinidae). *Behavioural Processes.* 36, 253-262.

Reebs, S.G. (1999). Time-Place learning base don food but not on predation risk in a fish, the inanga (Galaxias maculatus). *Etology*, 105, 361-372.

Reynolds, G.S. (1961). Attention in the pigeon. *Journal of the Experimental Analysis of Behavior*. 4, 203-208.

Rescorla, R.A. & Wagner, A.R. (1972). *A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement*. In: A.H. Black & W.F. Prokasy (Eds). Classical Conditioning II. pp. 64–99. Appleton-Century-Crofts.

Ribes, E. & López, F. (1985). *Teoría de la conducta: Un análisis de campo y paramétrico*. México: Trillas.

Ribes, E. (1990). *Psicología general*. México: Trillas.

Ribes, E. (1991). Skinner y la Psicología: Lo que hizo, lo que no hizo y lo que nos corresponde hacer. *Apuntes de Psicología.* 33, 147-174.

Ribes, E. (1992). Sobre el tiempo y el espacio psicológicos. *Acta Comportamentalia*, *0*, 71-84.

Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavioural Processes*, *7*, 242-268.

Roper, T. J. (1978). Diversity and substitutability of adjunctive activities under fixed-interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior,* 30, 83-96.

Saksida, L.M. & Wilkie, D.M. (1994). Time of day discrimination by pigeons, Columba Livia. *Animal Learning and Behavior.* 22, 143-154.

Savsatano, H.I. & Miller, R.R. (1998). Time as content in Pavlovian conditioning. *Behavioural Processes.* 44, 147-162.

Schatz, B.; Beugnon, J.P. & Lachaud, G. (1994). Time-Place Learning by an invertebrate, the ant, Ectatomma ruidum. *The journal of experimental biology.* 202, 1897-1907.

Schoenfeld, W.N. (1970). *The theory of reinforcement schedules*. New York: Appleton-Century Crofts.

Schoenfeld, W. N. & Cole, B. K. (1972). *Stimulus schedules: The t-tau systems.* New York: Harper & Row.

Schoenfeld, W. N. & Farmer, J. (1970). Reinforcement schedules and the "behavior stream". En W. N. Schoenfeld (Ed.), *the theory of reinforcement schedules*. New York: Appleton-Century Crofts.

Schwartz, B. (1978). *Psychology of learning & behavior*. New York: W. W. Norton & Company, Inc.

Schwitzgebel, R.K., & Kolb, D.A. (1974). *Changing Human Behavior: Principles of planned intervention*. US: McGraw Hill.

Segal-Rechtschaffen, E. (1963). Reinforcement of mediating behavior on a spaced-responding schedule. *Journal of the experimental analysis of behavior.* 6, 39-46.

Sherry, D.F., & Schachter, D.L. (1987). The evolution of multiple memory systems. *Psychological review.* 94, 1-16.

Sidman, M. (1953) Avoidance conditioning with brief shock and no exteroceptive warning signal. *Science*. 118, 157-158.

Sidman, M. (1955). Some properties of the warning stimulus in avoidance behavior. *Journal of comparative and physiological psychology.* 4, 444-450.

Siegel, S. (1986). A test of the similarity rule model on temporal bisection. *Learning and motivation*. 17, 59-75.

Skinner, B.F. (1937). On two types of conditioned reflex: A reply to Konorski and Miller. *The journal of experimental psychology.* 1, 272-279.

Skinner, B. F. (1938). *The behavior of the organisms*. New York: Appleton Century Crofts.

Skinner, B. F. (1948). The "superstition" in the pigeon. *Journal of Experimental Psychology*, *38*, 168-172.

Skinner, B. F. (1953). *Science and human behavior*. New York: McMillan Company

Skinner, B. F. (1968). *The technology of teaching.* New York: Appleton Century Crofts.

Skinner, B.F., & Morse, W.H. (1957). Concurrent activity under fixed interval responding. *Journal of comparative and physiological psychology.* 50, 279-281.

Staddon, J.E.R. (1983). *Adaptive Behavior*. Cambridge: Cambridge University Press.

Staddon, J. & Simmelhag, V. (1971). The “superstition” experiment: A reexamination of its implications for the principles of adaptative behavior. *Psychological Review*, 18, 3-43.

Stein, N. Hoffman, H. & Stitt, C. (1971).Collateral behavior of the pigeon during conditioned suppression during of key pecking. *Journal of the Experimental Analysis of Behavior*, *15*, 83-93.

Stubbs, A. (1968). The discrimination of stimulus duration by pigeons. Journal of the Experimental Analysis of Behavior, 11, 223-238.

Stubbs, D.A. Dreyfus, L.R.; & Fetterman, J.G. (1984). The perception of temporal events. En J. Gibbon & L. Allan (Eds. del volúmen.), *Timing and time perception: vol. 423. Annals of New York Academy of Science* (pp. 3-15). New York.

Tarpy & Mayer (1979). *Readings in learning and memory*. Glenview: Scotts, Foreman & Company.

Terrace, H. S. (1966). Stimulus control. En W. K. Honig (Ed.), *Operant behavior: Areas of research and application* (pp. 271-344). New York: Appleton Century Crofts.

Thorndike, E.L. (1911). *Animal Intelligence.* New York: MacMillan.

Titchener, E. B. (1894). The postulates of a structural psychology. *Philosophical Review*, *7*, 449-465.

Titchener, E. B. (1914). On "Psychology as the behaviorist views it". *Proceedings of the American Philosophical Society*, *53*, 1-17.

Thorndike, E.L. (1911). *Animal Intelligence.* New York: Hafner.

Thorpe, C.M.; Floresco, S.B.; Carr, J.A.R.; & Wilkie, D.M. (2002). Alterations in time-place learning induced by lesions to the rat medial prefrontal cortex. *Behavioural Processes.* 59, 87-100.

Thorpe, C.M. Hallet, D.; Fitzpatrick, C.L.; Murphy, M. and Bakhtiar, A. (2012) Interval Time-Place learning in young children. *Behavioural Processes.* 91, 198-201.

Thorpe, C., Hallet, D. & Wilkie, D. (2007). The role of spatial and temporal information in learning interval-time place tasks. *Behavioural processes.* 75, 55-65.

Thorpe, C. M., Petrovic, V., & Wilkie, D. M. (2002). How rats process spatiotemporal information in the face of distraction. *Behavioural Processes*, 58, 79–90.

Thorpe, C. & Wilkie, D. (2002). Unequal interval-time place. *Behavioural processes.* 58, 157-166.

Thorpe, C. & Wilkie, D. (2005). Interval time-place learning by rats: Varying reinforcement contingencies. *Behavioural Processes*. 70, 156-167.

Thorpe, C. & Wilkie, D. (2006a). Rat's performance on an interval time-place task: Increasing sequence complexity. *Learning and behavior.* 34, 248-254.

Thorpe, C. M., & Wilkie, D. M. (2006b). Properties of time–place learning. In T. R. Zentall & E. A.Wasserman (Eds.), Comparative cognition: Experimental explorations of animal intelligence (pp. 229–245). Oxford: Oxford University Press

Tolman, E.C. (1948). Cognitive maps in rats and men. *The Psychological review.* 55, 189-208.

Van Camp, C. M., Lerman, D. C., Kelley, M. E., Contrucci, S. A., & Vorndran, C. M. (2000). Variable-time reinforcement schedules in the treatment of socially maintained problem behavior. *Journal of Applied Behavior Analysis,* 33, 545-557.

Van der Zee, Havekes, Barf, Hut, Nijholt, Jacobs & Gerkema, (2008) Circadian Time-Place Learning in mice depend on Cry genes. *Current Biology.* 18, 844-848.

Watson, J. B. (1913). Psychology as the behaviourist views it. *Psychological Review*, *20*, 158-177.

Widman, D., Gordon, D. & Timberlake, W. (2000). Response cost and time-place discrimination by rats in maze tasks. *Animal Learning and Behavior. 28,* 298-309.

Wilkie, D. (1995). Time-Place learning. *Current directions in psychological science.* 4, 85-89

Wilkie, Carr Galloway, Parjer and Yamamoto (1997). Conditional Time-Place learning. *Behavioural processes.* 40. 165-170.

Wilkie, D., Saksida, L., Samson, P. & Lee (1994). Properties of time-place learning by pigeons Columba Livia. *Behavioural Processes.* 31, 39-56.

Wilike, D. & Wilson, R. (1992). Time-place learning by pigeons *Columba Livia. Journal of the Experimental Analysis of Behavior.* 57, 145-158.

Wilson, M. P. & Keller, F. S. (1953). Selective reinforcement of spaced responses. *Journal of Comparative and Physiological Psychology*, *46*, 190- 193.