TESIS DOCTORAL

2018

DEVELOPMENT OF SCHEDULE-INDUCED BEHAVIOUR IN TEMPORAL TASKS AND ITS IMPACT ON TIMING

DESARROLLO DE CONDUCTA INDUCIDA POR PROGRAMA EN TAREAS TEMPORALES Y SU IMPACTO EN LA ESTIMACIÓN TEMPORAL

GABRIELA EUGENIA LÓPEZ TOLSA GÓMEZ

Licenciada en Psicología
M. en C. del Comportamiento: Análisis de la Conducta

PROGRAMA DE DOCTORADO EN PSICOLOGÍA DE LA SALUD

Departamento de Psicología Básica I
Facultad de Psicología
Universidad Nacional de Educación a Distancia

Director de la tesis:

Dr. Ricardo Pellón Suárez de Puga

Catedrático de Psicología Básica

TESIS DOCTORAL

2018

DEVELOPMENT OF SCHEDULE-INDUCED BEHAVIOUR IN TEMPORAL TASKS AND ITS IMPACT ON TIMING

DESARROLLO DE CONDUCTA INDUCIDA POR PROGRAMA EN TAREAS TEMPORALES Y SU IMPACTO EN LA ESTIMACIÓN TEMPORAL

GABRIELA EUGENIA LÓPEZ TOLSA GÓMEZ

Licenciada en Psicología
M. en C. del Comportamiento: Análisis de la Conducta

PROGRAMA DE DOCTORADO EN PSICOLOGÍA DE LA SALUD

Departamento de Psicología Básica I
Facultad de Psicología
Universidad Nacional de Educación a Distancia

Director de la tesis:

Dr. Ricardo Pellón Suárez de Puga

Catedrático de Psicología Básica I

"*It's always best to start at the beginning,*

and all you do is follow the yellow brick road"

-Wizard of Oz (1939)

Agradecimientos (Acknowledgments)

Esta tesis es el resultado de cuatro años de recorrer este maravilloso camino de ladrillos amarillos llamado “doctorado”. Tengo la fortuna de haber coincidido con personas maravillosas que me han acompañado en diferentes puntos del camino, a quienes dirijo estas letras.

Mamá, gracias por enseñarme que todos los seres vivos pueden ser sujeto de observación, y la importancia de tratarlos con amor y respeto. Gracias por cada opinión, duda contestada y llamada de auxilio que atendiste durante estos cuatro años. También gracias por tus comentarios y correcciones, es un privilegio tener una mamá conductista que haya revisado mi tesis de doctorado. Gracias por todo tu amor, pero, sobre todo, gracias por impulsarme a seguir el camino amarillo, ¡ya puedo ver la *Ciudad Esmeralda*!

Abue, gracias por inspirarme con tu valentía, por enseñarme que la fórmula de la felicidad incluye ser un poco rebelde, y por todo tu amor, ánimos y cariño. Abuelito, gracias porque me enseñaste que el mundo es grande, y hay que verlo, y la importancia de hacer las cosas *a mi manera*, siempre agradeceré la suerte de haber podido caminar tantos años de tu mano y atesoraré cada recuerdo que compartimos. A mis tías, gracias por la música y el baile, por ser mujeres fuertes que me inspiran con su lucha constante, y por todo el amor y apoyo que me han dado siempre. También agradezco a mis primos: Sebastián, por no darte nunca por vencido, admiro tu capacidad de superar obstáculos, tu fortaleza y resiliencia; Ana Elena, mi princesa, por todo tu amor y cariño, admiro tu ternura, bondad y creatividad; Gabriel, mi chiquito, por tus ocurrencias y amor, admiro tu alegría y capacidad de inventar; y a la sobri-sobri Mar, que llegará con una brisa de aire fresco. Gracias Jesús y Ernesto por ser parte esencial de la familia y cuidar de los Gómez-Autrique. También agradezco a Spoty y

Espinaca, porque a veces tener a quién cuidar es la mejor forma de cuidarse, y así nadie cuidó mejor a mi mamá que ellas.

Ricardo, gracias por apostar por mí desde el primer momento, por la libertad y la confianza que me brindaste en todas las etapas del doctorado. Gracias por guiarme en este camino, por ponerme retos (aunque a veces no te dieras cuenta de que lo eran), por permitirme desarrollarme como investigadora, dándome los ánimos y la autonomía que se necesitan para hacerlo. Gracias por todas las oportunidades que me has brindado y que me has dejado tomar, y por enseñarme que un poquito de *cazurrismo* nunca está de más.

Hugo, gracias por estar siempre cerca y por ser el espejo en el que puedo mirarme cuando necesito un poco de realidad. Porque siempre has encontrado las palabras correctas para hacerme sentir mejor, pero también por saber distinguir cuando sólo necesito que me escuchen y me comprendan. Gracias por acompañarme en los momentos tristes y por celebrar conmigo los momentos felices. Soy la más afortunada del mundo por tenerte en mi vida.

Esmeralda y Pati, gracias porque le dieron sentido a mi primer año de doctorado, por su valiosa amistad, apoyo y cariño durante estos años, y porque cada día me siguen inspirando con su deseo inacabable de aprender y de hacer investigación. Gracias por los viajes, las pelis, los cumples y las *merencenas*; pero también gracias por ayudarme con sus revisiones, sugerencias y comentarios a los borradores de esta tesis y en la recolección de una buena parte de los datos. Gracias especialmente a Esmeralda por la exhaustiva revisión de la tesis, ¡vaya que has *currado* conmigo este verano!

Sergio, gracias por llenar de alegría mi último año de doctorado. Gracias por todas las horas de estrés y agobio que terminaron en risas, por apuntarte (y apuntarme) a todos los planes y por demostrarme lo reforzante que es decir que *sí*. Gracias por estar ahí en las buenas y en las malas, por recordarme con tu pasión por la investigación y el conductismo por qué empecé a recorrer este camino, y por mirar hacia el futuro conmigo.

Antonio, gracias por ser el mejor técnico de laboratorio, por tu amistad y compañerismo. Gracias por mantener el laboratorio funcionado, por las risas y las anécdotas que compartimos, y por cuidar siempre de mis ratitas. No importa a qué laboratorio vaya ahora, sé que siempre harás falta tú. Tu contribución a la ciencia es inconmensurable.

Gracias a Saúl y Natalia, por su ayuda en la recolección de los datos. Su apoyo en las tareas del laboratorio me dio el tiempo que necesitaba para cumplir con todo lo demás.

Gracias a mis demás compañeros del laboratorio: Valeria, por tu cálida bienvenida al laboratorio, por esa primera navidad en Almería, por ofrecerme siempre tu ayuda y amistad; Dania y Raquel, por su amistad, su apoyo y los buenos momentos que hemos compartido, gracias por hacerme partícipe de los momentos importantes en sus vidas; Javier Íbias por animarme a presentar en inglés por primera vez, por tu ayuda con varios detalles de la tesis y por los buenos ratos que hemos pasado juntos; Ana por esas madrugadas con ABA y por tu compañerismo; a Pedro y Leyre por los buenos ratos que pasamos juntos. En especial, a Rocío Donaire, gracias por los increíbles momentos que hemos pasado juntas, y por ofrecerme tu amistad, cariño y apoyo. Soy muy feliz de haberte conocido.

Al Dr. Emilio Ambrosio por estar siempre al pendiente de mí y por ayudarme a sacarle el máximo provecho al doctorado. Gracias especialmente por tu apoyo para realizar la estancia.

Gracias a los profesores del departamento de Psicología Básica I, especialmente a Miguel, Cris y Nuria. También agradezco a Mela por su paciencia y a Silvia Plaza por todo su apoyo con los trámites para asistir a congresos.

Gracias a las demás personas con las que coincidí en el laboratorio, especialmente a Mariano y Telmo, a Nuria y a los chicos de Psicobiología por las conversaciones “de pasillo”.

Also, I want to thank Dr. Armando Machado for welcoming me in his lab in Univeridade do Minho to do the research stay, thank you because you taught me a lot in a

really short period of time. Also, I want to thank Catarina for the conversations we shared and the support you gave me, it's always nice to find someone friendly; and thanks to Carlos Pinto for his assistance in everything I needed. Muito Obrigada!

También quiero agradecer a los Drs. Raúl Ávila, Sarah Cowie y Miguel Miguéns por aceptar ser parte de mi tribunal de tesis; y a los Drs. Cristina Orgaz, Vladimir Orduña y Javier Íbias por aceptar ser parte de mi tribunal de tesis como suplentes. Y los Drs. Antonia Padilla, Jonathan Buriticá, Felipe Cabrera y Felipe Patrón por revisar mi tesis a pesar de la poca anticipación y por preparar los informes sobre la misma. Agradezco también al Dr. Héctor Martínez, por su ayuda en la preparación de los papeles para solicitar la beca; y al Dr. Cristiano dos Santos porque sus enseñanzas durante mi maestría sentaron la base para la realización de esta tesis.

Special thanks to Prof. Peter Killeen for his beautiful letter. I will make my best to live up to his kind words and opinion on my thesis.

También quiero agradecer a mis amigos de *cheer*; en especial a Sisi, gracias por ser mi hermana en España, por los viajes, por cuidarme y entenderme, gracias por estar ahí y sostenerme en momentos difíciles; y a Elena, gracias por tu amistad incondicional, por las conversaciones y los viajes, por los audios interminables que escuchaste pacientemente, por tu ayuda y todos los detalles que has tenido conmigo. Soy muy afortunada de haber coincidido con ustedes.

También agradezco a la Familia Fuentes Verdugo por ser mi familia en España, siempre estaré agradecida por su bondad y cariño hacia conmigo.

Gracias a mis *roomies*: Elena y Bea, por los buenos momentos que compartimos dentro y fuera de casa; a Almu por la paciencia y buena convivencia; y especialmente a Mony, gracias por adoptarme y reírte de mis ocurrencias, por dejarme ser yo misma; gracias por tu apoyo, por consolarme cuando lo necesité y por compartir conmigo este último agosto

escribiendo en casa. A mis caseros, Doña Victoria y Don Pepe, porque nunca se olvidaron de preguntar por “las ratitas”.

Special thanks to Thomas, for answering patiently to my *language* questions and all the challenging and interesting conversations that we shared throughout these years. You have my admiration and gratitude for everything you taught me.

Gracias a mis amigos mexicanos que desde el otro lado del Atlántico han estado ahí para mí. Especialmente a Eddy, gracias por todo tu apoyo en la parte final de la tesis, tu amistad fue una parte crucial para poder terminarla; y a Andrea, gracias porque a pesar de la distancia siempre has estado ahí, por los ánimos y buenos deseos, y por venir a verme y regalarme un genial primer cumple en España. Los quiero mucho.

Gracias a Pepito Lindo, Fidelio y todos mis sujetos, porque el verdadero trabajo de esta tesis se mide en presiones de palanca y lametones; y porque ningún día es malo si puedes abrazar a una ratita.

Y finalmente, gracias a mi México *lindo y querido*, que a través de la beca CONACYT para estudios en el extranjero con el CVU 389663 proveyó el financiamiento para la realización de esta tesis.

Gabriela Eugenia López Tolsa Gómez

Madrid, España, a 26 de septiembre de 2018

Index

List of Figures

CHAPTER 2

CHAPTER 5

List of Tables

Abbreviations, acronyms and symbols

%	Percentage
°C	Celsius degrees
ANOVA	Analysis of variance
BeT	Behavioural Theory of Timing
cm	Centimeter
dB	Decibel
DRL	Reinforcement of low rates
ENW	Experience without water
EW	Experience with water
FI	Fixed interval
FI + Empty bottle	FI with access to an empty bottle
FI + Water	FI with access to water
FR	Fixed ratio
FT	Fixed time
g	Gram
IRI	Inter-reinforcement interval
ITI	Inter-trial intervals
LeT	Learning-to-time
LP	Lever presses
mg	Milligram
min	Minute
n	Sample
ns	Non-significant
NW	No water

PI	Peak intervals
PRP	Post-reinforcement pause
QL	Quarter life
s	Second
S.E.M.	Standard error of the mean
SET	Scalar Expectancy Theory
SID	Schedule-induced drinking
TBT	Temporal bisection task
VI	Variable interval schedule
VT	Variable time
W	Watt
W (group)	Water

Abstract

Organisms develop semi-invariant patterns of schedule-induced and target behaviours during the inter-reinforcement interval when they are exposed to intermittent reinforcement schedules. The sequential property of those patterns has led them to be regarded as a tool for timing, but the role of schedule-induced behaviour in temporal tasks has not been tested thoroughly.

The aim of this thesis was to observe the development of schedule-induced behaviour in different behavioural tasks in order to evaluate its impact on timing. A series of experiments using four different temporals tasks: fixed interval (FI), peak procedure, bisection task and bi-peak procedure were carried out to achieve that goal. In all experiments, rats were divided in to groups, one that had access to water in the experimental chamber (W groups), and therefore could develop schedule-induced drinking (SID), and rats that did not have access to water (NW groups).

The effect of engaging in SID on the performance in FI schedules was evaluated in Chapter 2. Subjects developed a pattern including SID and lever pressing, rats drank in the first part of the interval, and started lever pressing when drinking stopped. Such patterns had different effects in short (FI 15-s and FI 30-s) and long (FI 60-s) intervals. W groups in short intervals showed a better performance than NW groups; whereas W60 group showed a worse performance than NW60 group. Furthermore, rats with previous experience with SID had a lower lever-pressing rate than rats without such experience, but distribution of responses was similar for both groups.

The aim of Chapter 3 was to analyse the distribution and interaction of SID and lever pressing in the peak procedure. The distribution of responses during FI and peak interval (PI)

trials was analysed, comparing groups, subjects and individual trials. Similar to Chapter 2, developing SID had opposite effects for short and long intervals: the peak occurred later for the W15 compared to the NW15 groups and earlier for the W60 compared the NW60 group. Rats with access to water in the FI 15-s developed a more organized behavioural pattern than rats without access to water; there were no differences between FI 60-s groups.

In order to assess the role of schedule-induced behaviours in temporal estimation, the performance of rats with and without access to water in the bisection task was evaluated in Chapter 4. Rats learned to discriminate between 10 and 40-s stimuli and then were tested using intermediate durations. There were no differences in timing measures between groups in Experiment 1, but SID occurred mostly in the ITI. In Experiment 2 subjects were exposed to the same task, but with a shorter ITI. Rats drank during the stimuli, but there were no differences between groups in timing parameters. However, the distribution of responses was different for both groups. Rats with access to water drank during the first 20 s and started head entering after they finished drinking, whereas the distribution of head entries of rats without access to water resembled the distribution of SID.

In Chapter 5 rats were exposed to a bi-peak procedure, which combines elements of FI, peak procedure and bisection task, in order to replicate and merge the findings of previous chapters. Rats learned to discriminate between two levers, one associated with a short FI (20 s) and the other with a long FI (80 s). Trials were randomly alternated and unsignalled. During test phase rats received short and long training trials and non-reinforced peak trials that lasted 150 s. Rats with access to water developed a pattern consisting on a peak of licks, a peak of presses to the short lever and a peak of presses to the long lever; whereas rats without access to water developed a peak of responses to the short lever and then alternated between short and long lever presses until the end of the trial.

Findings in this thesis support the hypothesis that schedule-induced and target behaviours are induced and maintained by the delivery of reinforcement. Reinforcers, then, serve a triple task: select from the available behaviours, maintain them as part of a behavioural pattern and triggering such pattern. In conclusion, timing seems to be a product of the development of sequential patterns of behaviour, shaped by the environment and delimited by temporal parameters.

Resumen y conclusiones

Los organismos desarrollan patrones semi invariables de conductas inducidas por programa y conductas objetivo durante el intervalo entre reforzadores cuando están expuestos a programas intermitentes de reforzamiento. La propiedad secuencial de estos patrones los ha llevado a ser considerados como una herramienta para la estimación temporal, pero el papel de las conductas inducidas por programa en las tareas temporales no se ha evaluado de forma sistemática.

El objetivo de esta tesis fue observar el desarrollo de conductas inducidas por programa en diferentes tareas conductuales para evaluar su impacto en la estimación temporal. Para ello se llevo a cabo una serie de experimentos usando cuatro tareas temporales: intervalo fijo (IF), procedimiento de pico, bisección temporal y procedimiento de bi-pico. En todos los experimentos las ratas se dividieron en dos grupos, uno con acceso a agua en la caja de condicionamiento (grupos W), por lo que podían desarrolla bebida inducida por programa (BIP), y otro en el que las ratas no tenían acceso a agua en la caja de condicionamiento (grupos NW).

En el Capítulo 2 se evaluó el efecto de desarrollar BIP en la ejecución en programas de IF. Los sujetos desarrollaron un patrón que incluía BIP y presión de palanca. Las ratas bebieron en la primera parte del intervalo y comenzaron a presionar la palanca cuando terminaron de beber. Dichos patrones tuvieron efectos diferentes en los intervalos cortos (IF 15-s e IF 30-s) que en el largo (IF 60-s). Los grupos W en los intervalos cortos mostraron una mejor ejecución que los grupos NW, mientras que el grupo W60 mostró un peor desempeño que el grupo NW60. Además, las ratas que tenían experiencia previa con BIP tuvieron una

tasa de presión de palanca menor que las ratas que no tenían dicha experiencia, pero la distribución de las respuestas fue similar en ambos grupos.

El objetivo del Capítulo 3 fue analizar la distribución y la interacción de la BIP y la presión de palanca en el procedimiento de pico. Se analizó la distribución de las respuestas durante los ensayos de IF y de intervalo de pico (IP), comparando grupos, sujetos y ensayos individuales. De forma similar al Capítulo 2, el desarrollo de BIP tuvo efectos contrarios en intervalos cortos y en intervalos largos: el pico ocurrió después para el grupo W15 que para el NW15; y antes para el grupo W60 que para el NW60. Las ratas con acceso a agua en el IF 15-s desarrollaron un patrón de conductas más organizado que las que no tenían acceso a agua. No hubo diferencias en la distribución de presiones de palanca entre los grupos del IF 60-s.

Con el objetivo de estudiar el papel de las conductas inducidas por programa en la estimación temporal, en el Capítulo 4 se evaluó la ejecución de ratas con y sin acceso a agua en la tarea de bisección temporal. Las ratas aprendieron a discriminar entre estímulos de 10 y 40 segundos de duración y después fueron evaluados usando duraciones intermedias del estímulo. No hubo diferencias en las medidas de estimación temporal entre grupos en el Experimento 1, pero la BIP se desarrolló sobre todo en el intervalo entre ensayos (IEE). En el Experimento 2 los sujetos fueron expuestos a la misma tarea, pero con un IEE más corto. Las ratas bebieron durante los estímulos, pero no hubo diferencias entre grupos en los parámetros de estimación temporal. Sin embargo, la distribución de las respuestas fue diferente para ambos grupos. Las ratas que tuvieron acceso al agua bebieron durante los primeros 20 segundos y empezaron a entrar en el comedero cuando terminaron de beber; mientras que la distribución de las entradas al comedero de las ratas sin acceso al agua fue similar a la distribución de la BIP.

En el Capítulo 5 las ratas fueron expuestas a un procedimiento de bi-pico que combina elementos de IF, procedimiento de pico y tarea de bisección, con el objetivo de replicar y combinar los resultados encontrados en los capítulos previos. Las ratas aprendieron a discriminar entre dos palancas, una asociada a un IF corto (20 s) y la otra a un IF largo (80 s). Los ensayos se presentaban alternándose de forma aleatoria y no era señalados. Durante la fase de prueba las ratas recibieron ensayos de entrenamiento cortos y largos, y ensayos de pico no reforzados que duraban 150 s. Las ratas con acceso al agua desarrollaron un patrón que consistía en un pico de lametones, un pico de presiones a la palanca corta y un pico de presiones a la palanca larga; mientras que las ratas sin acceso al agua desarrollaron un pico de respuestas a la palanca corta y luego alternaron entre presionar las palancas corta y larga hasta el final del ensayo.

Los resultados de esta tesis apoyan la hipótesis de que las conductas inducidas por programa y las conductas objetivo son inducidas y mantenidas por la entrega del reforzador, eliminando la necesidad de distinguir entre tipos de conducta (operante *vs*. inducida). Los reforzadores, entonces, tiene una triple función: seleccionar entre las conductas disponibles, mantenerlas como parte de un patrón conductual y desencadenar dicho patrón.

En conclusión, la estimación temporal parece ser un producto del desarrollo de patrones secuenciales de conductas, moldeadas por el ambiente y delimitadas por parámetros temporales. Estos resultados contribuyen para entender las conductas inducidas por programa, en particular; y en general al área del Análisis Experimental de la Conducta. Los investigadores deben aspirar a entender la relación entre los organismos y su ambiente, más allá de la terminología empleada para describirlo. La estimación temporal es un término usado para referirse a conductas que ocurren en procedimientos definidos por parámetros temporales, y el investigador no debe olvidarse del organismo que se está comportando con el

objetivo de explicar procesos que no son directamente observables, pues la conducta es, después de todo, el objeto de estudio del área del Análisis Experimental de la Conducta.

"O tal vez el tiempo no pasa, sino que nosotros pasamos a través del tiempo."

-Isabel Allende (p.215)

CHAPTER 1

GENERAL INTRODUCTION

General Introduction

From adjunctive to schedule-induced behaviours

In 1961, Falk observed that rats exposed to a variable interval (VI) 1-min schedule of food reinforcement developed an excessive amount of drinking in the inter-reinforcement intervals (IRI) when they had access to water in the experimental chamber (Falk, 1961). These observations started a theoretical debate that remains open more than 50 years later and portraits a challenge to the field of the Experimental Analysis of Behaviour: what *is* schedule-induced behaviour?

This phenomenon, initially called "schedule-induced polydipsia" (Falk, 1961; aka schedule-induced drinking, SID), proved to be quite reliable and easily replicable by different authors within the first five years after its first description; at the same time that they proposed different hypothesis to account for its origin, purpose and the mechanisms that sustain it (Clark, 1962; Segal & Holloway, 1963; Segal, Oden & Deadwyler, 1965; Stein, 1964). Schedule-induced drinking appeared to be different from other types of behaviours, although it was similar to collateral or mediating behaviours (Bruner & Revusky, 1961; Ferster & Skinner, 1957), and some authors defended it was acquired adventitiously (Clark, 1962; Segal et al., 1965), its excessiveness and temporal localization at the beginning of the interval led Falk to categorize it as belonging to a different class: adjunctive behaviours (Falk, 1966; Falk 1971).

According to Falk (1971), adjunctive behaviours are those that developed when organisms are deprived of the reinforcer (for example, deprived of food in a food-reinforcement schedule); also, they occur at excessive rates, are usually located in the post-

reinforcement portion of the interval and there is no arranged contingency between them and the delivery of the reinforcer.

Falk (1969) proposed that the term ‘adjunctive’ was appropriate because it implied that those behaviours occurred as an adjunct to other behaviours. The term has been used until recent years (Álvarez, Íbias & Pellón, 2016; Killeen & Pellón, 2013); nevertheless, this kind of behaviours do not always require the development of another one to appear; for example, they have been widely studied using fixed time (FT) schedules (Álvarez et al., 2016; Daniel & King, 1975) in which reinforcers are delivered intermittently but not contingent to any other behaviour. In that sense, the term schedule-induced might be more appropriate. Additionally, Roper (1981) defended the use of the term schedule-induced because it implies that the intermittency of the schedule of reinforcement causes schedule-induced behaviours.

Schedule-induced behaviours include many different activities (Roper, 1978a), depending on the organism and the environment in which it is behaving (Millenson, Allen & Pinker, 1977; Roper, 1978a; Rosellini & Burdette, 1980; Skuban & Richardson, 1975). Some of the schedule-induced behaviours that have been more thoroughly recorded and observed are: wheel running (Levitsky & Collier, 1968); aggression and/or scape (Falk, 1971; Roper, 1981; Knutson & Shrader, 1975)); pica (Falk, 1971; Roper, 1981); air-licking (Falk, 1971); pecking (Miller & Gollub, 1974); paw grooming (Lawler & Cohen, 1992); and smoking (Roper, 1981).

Those activities can develop individually and/or combining two or more of them, depending on the schedule and the availability in the testing environment, competing among them and shaping each other’s distributions during the inter-reinforcement interval (IRI) (Pellón & Killeen, 2015; Roper, 1978a). In a more complex environment, with more

available activities to perform, organisms will develop a wider variety of schedule-induced behaviours (White & Wong, 1982; Lucas, Timberlake & Gawley, 1988).

Schedule-induced drinking: the "star" of schedule-induced behaviours

Although schedule-induced behaviour occurs in different procedures, and can consist on many different activities, most of them are not easy to measure inside regular conditioning chambers, or do not develop consistently among subjects. Nevertheless, schedule-induced drinking (SID) is the most studied schedule-induced behaviour because it develops consistently among most subjects; it has been widely observed under many different schedules of reinforcement and used as a base to draw conclusions about schedule-induced behaviours in general (Clark, 1962; Falk, 1961; 1971; Stein, 1964).

The conditions for developing SID are simple: exposing rats to an intermittent scheduled of reinforcement with food pellets and giving them access to water in the experimental chamber (Falk, 1966). These conditions result in rats developing an excessive amount of drinking that, after some training, concentrates in the first 15-20 s of the IRI (Álvarez et al., 2016); although it also develops if its temporal location is restricted and it cannot occur in the first 20 s of the interval. For example, SID develops even if drinking is permitted only in the first, middle or last portion of an interval (Daniel & King, 1975; Gilbert, 1974; López-Crespo, Rodríguez, Pellón & Flores, 2004) and if other schedule-induced behaviours, like paw grooming or running, are available at the same time (Lawler & Cohen, 1992; Levitsky & Collier, 1968; Segal, 1969b). Furthermore, the temporal localization of SID can change from the beginning to the end of the interval (Flory & O'Boyle, 1972; Segal, 1969bb; Shaeffer & Slazberg, 1967).

What *is* schedule-induced behaviour?

As mentioned at the beginning of this chapter, since it was first described in 1961, the observation of schedule-induced behaviour in many forms and procedures has given place to a theoretical debate about its nature. The dominant view in the early years acknowledged it as being different from operant behaviour, induced by the schedule of reinforcement, but not maintained by it (Falk, 1971; Staddon, 1977).

On the other hand, Timberlake and colleagues (Lucas et al., 1988; Timberlake & Lucas, 1985) consider schedule-induced behaviour to be part of a species-specific behavioural system, mostly related to the consummatory behaviours and elicited with the delivery of reinforcement.

However, the hypothesis that schedule-induced behaviours are adventitiously reinforced, initially proposed by Clark (1962), has been more thoroughly tested in recent years, providing evidence that supports the idea that schedule-induced behaviours are operants (Álvarez et al., 2016; Killeen & Pellón, 2013). On an apparently opposite view, Baum (2012) proposed that all behaviours are induced, and that although they correlate with the delivery of reinforcers, they are not strengthened by them.

Schedule-induced behaviour might be the key to understand the acquisition and maintenance of behaviours, providing a middle point in the operant *vs*. induced debate. Álvarez et al. (2016) exposed rats to a fixed time (FT) 90-s schedule of food reinforcement and varied the contingency between licking and the shortening of the duration of the inter-food interval. They reported that all rats developed SID, but subjects with a higher degree of contingency, developed it faster. They concluded that drinking can be both schedule-induced, which explains its appearance, and strengthened by its consequences.

Killeen and Pellón (2013) analysed the results of different studies and concluded that behavioural patterns include schedule-induced and target behaviours that are developed in the IRIs by means of delayed reinforcement, depending on the proximity (not on the contingency) of each class of behaviour with the delivery of reinforcement. In that sense, schedule-induced behaviour would include all the behaviours that develop on a reinforcement schedule without any arranged contingency with the delivery of reinforcement.

Situations of intermittent reinforcement result in a general increase of the activity level, eliciting different behaviours related to the situation (Killeen, 1975; Levitsky & Collier, 1968), increasing the occurrence of behaviours already present in the situation (Falk, 1971). With progressive training, some behaviours are selected by their temporal proximity (due to contingency or not) with the reinforcement (Killeen, 1975; Skinner 1981).

This view is also consistent with Timberlake and Lucas' (Timberlake & Lucas, 1985; Lucas et al., 1988) approach, because the organization of adaptive reinforcement-related behaviours in sequences in the presence of intermittent stimuli represents an ecological advantage. Behavioural systems would provide the pool of which behaviours are induced and, if fitting for the situation, selected and strengthened by the reinforcer (Lucas et al., 1988).

Taking SID as an example, Clark (1962) proposed that, as part of the normal exploratory behaviour of rats, some licking initially occurs after the consumption of dry pellets, then if the next lever press is followed by a reinforcer the probability of drinking after the next reinforcer will increase, and after a few trials a behavioural pattern including both behaviours will develop (Álvarez et al., 2016; López-Crespo et al., 2004).

The periodic presentation of a reinforcer results in a reorganization of available behaviours, depending on the temporal parameters of the schedule and the complexity of the environment (Lucas et al., 1988). Behaviours occurring in the IRIs compete with each other

and shape each other's distributions into sequential patterns (Pellón & Killeen, 2015). Furthermore, Ruiz, López-Tolsa & Pellón (2016) proposed that schedule-induced patterns are reinforced as a whole.

The existence of patterns that include schedule-induced and target behaviours that compete with each other has been widely documented. Segal et al. (1965) stated that SID is a post-pellet phenomenon because of competition with lever pressing, which, as being contingent to food, would remain close to the time of its delivery. Levitsky & Collier (1968) observed that rats lever pressing for food, with access to a running wheel and a bottle of water in the experimental chamber developed a steady pattern of drinking, running and lever pressing; but when access to the wheel was not permitted, lever pressing increased. In a similar experiment in which lever pressing was also not contingent to the delivery of food, Segal (1969a) observed that when running was not permitted, drinking increased and lever-pressing emerged. Additionally, Gilbert (1974) observed that if water was available during the last 10 s of a FI 60-s schedule, licking increased and, in some cases, lever pressing decreased. Similar results have been observed in the interaction between drinking and paw grooming (Lawler & Cohen, 1992); drinking and wood chewing (Freed & Hymowitz, 1969); and drinking and schedule-induced aggression (Knutson & Shrader, 1975).

The precise topography of schedule-induced behavioural patterns occurring in the IRIs depends on the reinforcement history (López & Menez, 2012; Tang, Williams and Falk, 1988) and state of the organisms (Killeen & Jacobs, 2016); the schedule of reinforcement (Roper, 1978b; Rosellini & Burdette, 1980) and the specific characteristic of the experimental environment (Laties, Weiss & Weiss, 1969; Staddon & Ayres, 1975); but they are usually organized sequentially (although, not necessarily chained) and restricted by the periodic organization of the reinforcer (Harper & Bizo, 2000; Silva & Timberlake, 1998). If the experimental conditions do not change, schedule-induced behavioural patterns are repeated in

a semi-invariant way in most of the IRIs, which has led them to be regarded as a tool for timing.

Behavioural patterns tell time: schedule-induced behaviours and timing

Timing is the adaptation of behaviour of an organism to temporal regularities of relevant events (Church, 2002), without the aid of external stimuli signalling the time to each event (Killeen, Fetterman & Bizo, 1997). There are two main views to account for the mechanisms that enable timing, the cognitive account provided by the Scalar Expectancy Theory (SET; Church, Meck and Gibbon, 1994), and the behavioural account that includes the Behavioural Theory of Timing (BeT; Killeen & Fetterman, 1988) and the Learning to Time (LeT; Machado, 1997) models.

BeT proposes that behaviours in the sequential patterns developed under periodic delivery of reinforcement serve as discriminative stimuli for temporal relevant events (Killeen & Fetterman, 1988); whereas LeT proposes that timing implied the development of patterns of behavioural states that are activated in a sequential way, each of which is coupled with the target response. The target response will follow the behavioural state that it has been stronger coupled to during a specific event (Machado, 1997).

The role of schedule-induced behaviour in temporal tasks is often inferred and has not been tested thoroughly (Lejeune, Cornet, Ferreira & Wearden, 1998; Machado, 1997). There is some evidence that developing schedule-induced behaviours improved performance of subjects on a differential reinforcement of low rates (DRL) schedule (Bruner & Revusky, 1961; et al., 1969; Segal & Holloway, 1963), but it should be considered that engaging in activities other than the target one should improve the performance on a DRL by response competition (if subjects are doing another behaviours they cannot do the target behaviour),

not necessarily by timing processes. Furthermore, Lejeune et al. (1998) observed that subjects develop consistent sequences of behaviours in a task in which they had to stay on a platform for a specific amount of time. Further evidence is needed to account for the impact of schedule-induced behaviour in timing, so it should be tested in different temporal tasks.

López (2012) and Richelle and Lejeune (1980) proposed dividing tasks in those assessing temporal estimation (temporal learning *per se*), and those assessing temporal regulation in which a behavioural adaptation to the temporal regularities in the environment is required. The first category would include tasks like temporal discrimination and the bisection task, in which organisms have to judge the duration of a stimulus and respond accordingly; whereas the second category includes tasks like FI, peak procedure and differential reinforcement of low rates (DRL).

This thesis: schedule-induced drinking and timing

The aim of this thesis was to observe the development of schedule-induced behaviour in different behavioural tasks in order to evaluate its impact on timing. To achieve that, we present the results of a series of experiments comparing the performance of rats when they could or could not develop SID. The effect of developing SID was evaluated in FI schedules in Chapter 2, in the peak procedure in Chapter 3, in the bisection task in Chapter 4 and in the bi-peak procedure in Chapter 5. Finally, a general conclusion is presented in Chapter VI.

CHAPTER 2

THE TIMING PROPERTY OF SCHEDULE-INDUCED BEHAVIOUR DEPENDS ON INTER-REINFORCEMENT INTERVAL LENGTH

Abstract

Organisms develop patterns of schedule-induced and target behaviours that are repeated in the IRIs and have been regarded as a tool for timing due to tis semi-invariance. It has been suggested that schedule-induced behaviours allow organisms to adapt better to temporal regularities of the environment. The main goal of the study presented in this chapter was to observe the effect of engaging in SID on the performance in FI schedules. In Experiment 1 rats were exposed to 30 sessions of a FI 15-, 30- or 60-s schedule, half of them had access to water in the experimental chamber (W groups) and half did not (NW groups). Lever pressing and SID developed during the first few sessions and reached a stable rate. SID occurred in the first 20 s of the interval, regardless of the FI value, and was followed by an increase on lever pressing rate until the end of the interval, which resulted in a better performance on FI 15- and 30-s, but a worse performance on the FI 60-s for the W groups, compared to subjects in the NW groups. In Experiment 2 rats with or without experience with water in another temporal task were exposed to 30 sessions of FI 30-s without access to water in the experimental chamber. After acquisition, rats with previous experience were exposed to the same FI 30-s, but with access to water for 10 sessions and to an empty bottle for another 10 sessions. In general, lever-pressing rate was lower for rats that had experience with water. When the bottle with water was introduced, subjects showed SID, but there were no changes in lever presses. Rats developed the FI scallop, and distribution of lever presses was similar for all groups in the first 2 phases, but rats with previous experience with water started lever pressing earlier in the phase with access to the empty bottle. It is concluded that timing is the temporal organization of available behaviours that leads to a specific behaviour occurring in a specific time which, depending on the value of the schedule, can lead to what researchers interpret as better or worse performance.

The Timing Property of Schedule-induced Behaviours Depends on Inter-reinforcement Interval Length

In 1961 Falk observed that rats exposed to a variable interval schedule (VI) of food reinforcement with water available in the conditioning chamber developed an excessive amount of drinking during the inter-reinforcement interval (IRI). He later classified that phenomenon as *adjunctive behaviour* (a.k.a. schedule-induced behaviour) and distinguished it from operant behaviour (Falk, 1966; 1971). In general terms, schedule-induced behaviours are those that develop at an excessive rate during the IRI in an intermittent reinforcement schedule without having an explicit contingency with the reinforcer. Schedule-induced behaviours have also been identified as collateral (Fetterman, Killeen & Hall, 1998) or mediating behaviours (Ferster & Skinner, 1957).

Although the development of schedule-induced behaviours has been widely documented, there is still no agreement as to *why* they occur and *how* they are maintained. The dominant view in the early years acknowledged schedule-induced behaviours as different from operant behaviours given their excessiveness (Falk, 1961; 1969; 1971), temporal location (Falk, 1971) and lack of explicit contingency between them and the delivery of reinforcement (Falk, 1971). Additionally, Staddon added that schedule-induced interim behaviours are induced by periods of relatively low probability of reinforcement (Staddon, 1977; Staddon & Simmelhag, 1971).

Another view considers that schedule-induced behaviours are part of species-specific behavioural systems that are elicited with the delivery of the reinforcement (Timberlake & Lucas, 1985; see a recent treatment in Killeen, 2014). In the presence of intermittent

reinforcement, organisms would display adaptative organized sequences of behaviours related to feeding and foraging for food (Lucas et al., 1988).

Alternatively, some authors have suggested that schedule-induced behaviours are adventitiously reinforced (Clark, 1962; Cleaveland, Jäger, Röβner & Delius, 2003). More recently, Pellón and colleagues proposed that schedule-induced behaviours are operants, either individually maintained by delayed reinforcement (Killeen & Pellón, 2013; Pellón & Killeen, 2015) or as part of a behavioural pattern that is reinforced as a whole and is repeated on every interval (Ruiz et al., 2016; Segal et al., 1965). This view is also consistent with Skinner's proposal that temporal contiguity between a response and the delivery of a reinforcer is enough for an operant response to be acquired, instead of the classic view of contingency which considers that an operant response needs to *produce* the reinforcer to be acquired (Skinner, 1948).

From an opposite interpretation, Baum (2012) stated that all behaviours are induced, and that reinforcers are events that correlate with responses, but do not strengthen them. Although the operant *vs*. induced mechanisms seem to be opposite explanations, it is quite possible that they both have a role in the development and maintenance of behaviour. Álvarez, et al. (2016) exposed rats to a fixed time (FT) 90-s schedule and established a 100, 50 and 0% contingency between licking and shortening the inter-food interval. They found that all rats developed drinking, but subjects with 100% contingency developed drinking faster and drank more than subjects in the other two groups. Their results show that drinking can be both scheduled-induced and strengthened by its consequences.

There are many examples of schedule-induced behaviours, such as running in a wheel (Levitsky & Collier, 1968), aggression (Knutson & Schrader, 1975), pica (Falk, 1971), air licking (Falk, 1971), wood chewing (Roper, 1981), paw-grooming (Lawler & Cohen, 1992)

and others, but schedule-induced drinking (SID) is the most widely studied, because it develops quickly and consistently with simple experimental conditions.

SID can develop under a wide variety of schedules and with different reinforcers, including dry pellets (Falk, 1967), liquid food (Falk, 1967) and brain stimulation (Cantor & Wilson, 1978). The amount and distribution of SID depends on the schedule, but it usually occurs during the first 10-15 s of every inter-reinforcement interval (IRI) at a steady state, although a few exceptions in which drinking occurred at other times of the interval have been reported (Álvarez et al., 2016; Killeen, 1975; Lawler & Cohen, 1992; López-Crespo et al., 2004). Also, SID can be shifted from the beginning to the end of the interval, replacing target behaviours, both spontaneously (Segal, 1969c; Shaeffer & Slazberg, 1967) or if water is made available only in a specific portion of the interval (Daniel & King, 1975; Flory & O'Boyle, 1972; Gilbert, 1974). Furthermore, López-Crespo et al. (2004) showed that drinking could develop if water was available during the last 15 s of a FT 30-s schedule at a similar rate than if water was available during the first half of the interval.

The amount of SID can vary from interval to interval within an experimental session, including some intervals in which drinking does not occur (Reid, Bacha & Morán, 1993; Staddon & Ayres, 1975), a situation that is not exclusive to schedule-induced behaviours because it is well known that target behaviours like lever presses and key pecks do not occur at the same rate in every trial (Baron & Leinenweber, 1994).

Schedule-induced behaviours interact and compete during IRI (Pellón & Killeen, 2015; Segal et al., 1965). The distribution of behaviours during the IRIs depends on the schedule (Roper, 1978a; Rosellini & Burdette, 1980), the species (Millenson et al., 1977) and the complexity and size of the environment in which the organisms are tested (Skuban & Richardson, 1975; Staddon & Ayres, 1975). Nevertheless, once a specific pattern is developed, it tends to occur in a semi-invariant way during most of the IRIs, if all the

environmental conditions are maintained constant (Cleaveland et al., 2003; Lawler & Cohen, 1992; Segal & Holloway, 1963; Staddon & Ayres, 1975; Staddon & Simmelhag, 1971). If elements in the experimental environment change, for example by giving access to a new element in the experimental chamber (chewing material, running wheel, etc.), subjects will sometimes engage in new behaviours, changing the rate or distribution of the previously-acquired behaviours, or completely replacing them (Freed & Hymowitz, 1969; Knutson & Schrader, 1975; Levitsky & Collier, 1968; Roper, 1978b). Schedule-induced behaviours have been regarded as a tool for timing due to that semi-invariance.

Killeen (1975) proposed that the delivery of reinforcement increases (arouses) the activity level of an organism eliciting different behaviours based on the organism's context and reinforcement history. With progressive training, some of those behaviours will be selected and maintained by contiguity with the reinforcement. Based on that argument, Killeen and Fetterman (1988) proposed the Behavioural Theory of Timing (BeT), which states that timing ability depends on a progression through chains of classes of schedule-induced behaviours that function as a discriminative stimulus of the temporal moment in which they usually occur (like a behavioural clock). Furthermore, Fetterman et al. (1998) argue that 'timing' is the ability of an organism to use natural sequences of stimuli and/or responses in the environment and discriminating their own behaviour to perform appropriately in a temporal-controlled situation. Machado (1997) further elaborated on the BeT model to propose an alternative model that could mathematically explain and predict the learning process in a variety of timing procedures (Learning-to-time, LeT, model).

On the other hand, Lejeune et al. (1998) evaluated the role of schedule-induced behaviours in a temporal task and concluded that schedule-induced behaviours do not mediate timed responses because they do not occur in the same amount in *every* interval,

even though they found evidence of consistent behavioural patterns that included schedule-induced and target responses.

Machado and Keen (1999) exposed pigeons to a temporal discrimination task and observed that each subject developed a behavioural pattern that was consistent across trials and that correlated with their choices in a generalization test. They concluded that behaviours occurring in the IRIs *are* the behavioural clock, not just a representation or expression of an internal clock. In a similar way, Cleaveland et al. (2003) found that budgerigars made choices in a matching to sample task based on the behaviours they were performing at that time in the trial, thus providing evidence of the role of schedule-induced behaviours to solve behavioural tests. Other authors have reported that rats (Laties et al., 1969; Segal & Holloway, 1963) and humans (Bruner & Reyusky, 1961) that developed schedule-induced behaviours showed a better performance on schedules of differential reinforcement of low rates (DRL), which require organisms to not do the target behaviour for a specific amount of time. Further evidence of the effect of schedule-induced behaviours in other temporal learning tasks is needed.

Timing research usually focuses on evaluating behaviour in its steady-state, but to assess the impact of schedule-induced behaviour in temporal learning, research should focus on *how* behaviour is acquired and shaped. López (2012) and Lejeune and Wearden (1991) proposed fixed interval (FI) schedules as a tool to study temporal learning. FI schedules produce a behavioural pattern that consists on a low rate of responses followed by a high rate of responses (break-and-run) that looks like a positively accelerated curve (scallop) when average data is plotted (Baron & Leinenweber, 1994). In contrast to other temporal tasks, FI allows researchers to see the development and changes of the ‘natural’ behavioural pattern in the IRI as it is shaped into the characteristic FI scallop (Lejeune & Wearden, 1991; López, 2012).

López and Menez (2005; 2012) reported that the acquisition of the FI scallop is facilitated when organisms have previous experience in other reinforcement schedules with temporal regularities, but not when they have experience on variable or random time schedules. It is possible that schedule-induced behaviours are part of behavioural patterns that allow organisms to adapt better and faster to temporal regularities of the environment, and that researchers interpret those results as a 'better' performance in temporal tasks. The main goal of this study was to observe the effect of engaging in SID on the performance in FI schedules.

Experiment 1

The aim of Experiment 1 was to compare the development of the FI scallop when rats had or did not have water available in the conditioning chamber. Since it has been established that SID occurs during the first 10-15 s of each interval, the effect of its development on the accuracy of temporal performance should be dependent on the FI length. Three values of FI were chosen: a short one in which SID would occur during most of the interval (FI 15-s); a medium one in which SID would occur only in about half of the interval (FI 30-s); and a long one in which SID would occur only in about the first quarter of the interval (FI 60-s).

Method

Subjects. Subjects were 44[1] experimentally naïve male Wistar rats that were 16 weeks old at the beginning of the experiment. Their weights were progressively reduced for 3 weeks before the start of the experiment and maintained at about 80-85% of their free-feeding weight with an initial average of 319 g (range: 233-451). They were housed individually in

[1] The experiment had originally 55 subjects, but data are presented for just 44 animals, excluding the rats with a lower level of SID.

transparent Plexiglas cages measuring 18 x 32.5 x 20.5 cm in an environmentally-controlled room (22°C and 55% relative humidity) with a 12-hour light-dark cycle (lights on at 8:00 a.m.). Water was always available in the home-cages. Animal care procedures were in accordance with the European Union Council Directive 2010/63, the Spanish Royal Decree 53/2013 and with the authorization of the Community of Madrid with reference PROEX 077/18.

Apparatus. Eight Leticia LI-836 conditioning chambers measuring 29 x 24.5 x 35.5 cm were used. The front panel of each chamber was made of aluminum, the left wall of transparent Plexiglas and the remaining walls of black Plexiglas. The floor consisted on a 16-bar metal grid. In the center of the front wall at a height of 3.7 cm above the floor was located the food tray, at each side of the food tray there was a retractile lever, and above each lever a 3-W round lamp. Only the left lever was used during this experiment, the right one stayed inactive and retracted. Forty-five mg sweet food pellets were dispensed (Bio-Serv, Frenchtown, NJ, USA) into the food tray by a Letica Instruments dispenser. In the right wall, there was a 3.2 x 3.9 cm aperture, situated 20 cm from the front panel and 7 cm from the floor, through which subjects could reach the spout of a water bottle mounted on the exterior of the chamber. The water bottle could be removed if necessary. The spout was placed 2 cm towards the interior of the aperture to allow for licks rather than continuous drinking. Contact between the subject's tongue and the metal spout completed the electric circuit between the floor and the spout that allowed licks registration. Chambers were enclosed in a soundproofed housing equipped with a ventilation system and a small observation window in the left panel. A fan located in the soundproofed housing produced an ambient noise of approximately 60 dB in each chamber to mask any exterior noise. The houselight consisted on an indirect 25-W light mounted in the soundproofed housing. Chambers were controlled using a MED-PC application under a Windows environment.

Procedure. Subjects were divided into 6 groups, considering two variables: having or not having water available (W *vs.* NW) in the conditioning chamber and the value of the FI schedule of food reinforcement (Table 1). Groups W30 and NW30 had an n=6 instead of 8 because 2 subjects in the W30 group did not develop SID, so they were removed from the analyses.

Table 1.

Characteristics of each group.

Group	FI value	Water/No water	n
W15	15 s	Water	8
NW15	15 s	No water	8
W30	30 s	Water	6
NW30	30 s	No water	6
W60	60 s	Water	8
NW60	60 s	No water	8

Note. FI = Fixed Interval; W = Water; NW = No Water; n = sample.

The experiment was conducted 6 days per week (Sunday to Friday), one session per day, and consisted of two phases: pre-training and training. Each session began with the illumination of the houselight and the presentation of the lever. All sessions were the same for all subjects, except that half of the subjects had access to water in the conditioning chambers (W rats) and the other half did not (NW rats).

During pre-training rats were exposed to an autoshaping-like procedure, consisting on a concurrent FT 30-s fixed ratio (FR) 1 food reinforcement schedule. Subjects received one food pellet every 30 s and again after every lever press. Each session in this phase ended

when the subject pressed the lever 50 times or 30 minutes had elapsed. Rats stayed in this condition for 3 to 5 days, until they successfully pressed the lever 50 times in less than 30 min for three consecutive days.

During the training phase rats were exposed to FI 15-, 30- or 60-s food reinforcement schedules during 30 sessions. Each session lasted 60 trials. Depending on the FI schedule, 15, 30 or 60 s after the 60^{th} reinforcer the houselight was turned off, the lever was retracted, and the session ended.

Data analysis. Lever presses and licks were recorded. Data were analyzed using a mixed analysis of variance (ANOVAs) with a repeated measures factor, *sessions* (with 30 levels), and a fixed factor, *group* (with 2, 3 or 6 factors, depending on the analysis). Bonferroni adjustment was used in *post hoc* comparisons. Significance level was established at a minimum $p<.05$. Sphericity principle violations were evaluated with the Mauchly Sphericity test and significant deviations were corrected using Huynh-Feldt to adjust the degree of freedom.

Results

The aim of this experiment was to compare the development of fixed interval patterns when rats had or did not have access to water in the experimental chamber. Figure 1 shows the average response rate for each session and group. Lever-pressing rates (graph A) were similar for all groups, except for W60 rats during the first seven sessions and NW15 from session 9 onwards, differences among groups were not statistically significant, $F_{(5,38)}=.884$, $p=.50$, ns, although there was an effect sessions x group $F_{(30,230)}=1.519$, $p<.05$. Lever-pressing rate slightly increased from the first few sessions and stabilized around session 15 until the end of the experiment.

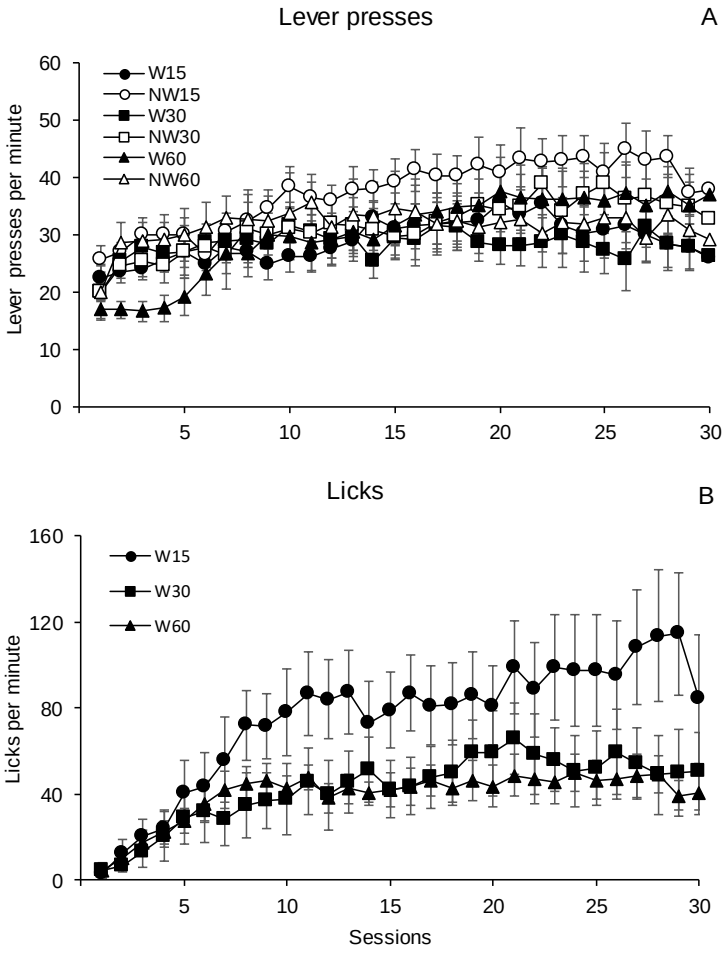

Figure 1. A: mean lever-pressing rate for each session and group throughout the experiment. B: mean licking rate for each group and session. Vertical bars show standard error of the mean (S.E.M.).

Regarding licking rate (Figure 1, graph B), rats in the W30 and W60 group showed similar responding rates, whereas rats in W15 groups showed a higher licking rate, although the differences among groups, $F_{(2,19)}$=2.43, p=.12, ns, were not significant and there was no effect in the interaction sessions x group $F_{(10,69)}$=2.43, p=.11, ns. In contrast to lever pressing, at the beginning of the experiment licking rate was close to zero, but gradually increased during the first 13-15 sessions and stayed at a steady rate until the end of the experiment for W30 and W60 rats, whereas for W15 rats continued to gradually increase until the last

session. The lower point in the last session of W15 group is due to one subject that drank less than usual during that session, but the value was not an outlier, so it was not excluded from the data analysis.

Two timing measures were calculated: post-reinforcement pause (PRP) and quarter life (QL). The PRP is the time elapsed since the beginning of the interval (the delivery of the previous reinforcer) to the first lever press. Figure 2 shows PRP for each group and session. As it was expected, PRP was longer, the longer the interval, and it increased in the first few sessions. Also, rats that had access to water (W15, W30 and W60) had longer PRPs than their homologous that did not have access to water. Differences between W60 and NW60 were larger in sessions 4 to 13 and disappeared towards the last few sessions (graph C); however, differences were larger between W15 and NW15 (graph A) and W30 and NW30 (graph B) towards the end of the experiment. There was a group effect, $F_{(1,14)}=8.808$, $p<.01$ with W15 and NW15 [interaction session x group $F_{(8,117)}=3.08$, $p<.01$], and the *post hoc* test indicated that those differences occurred from session 10 onwards. Nevertheless, differences between groups W30 and NW30, $F_{(1,10)}=0.479$, $p=.3$, ns, and between groups W60 and NW 60, $F_{(1,14)}=0.553$, $p=.5$, ns, were not significant. There was no interaction sessions x group between W30 and NW30 [$F_{(6,64)}=1.71$, $p=.13$, ns] and between W60 and NW60 [$F_{(11,154)}=0.912$, $p=.53$, ns] either.

QL is the time during which the subjects completed the first fourth of the total lever presses emitted in an interval. QL for each group and session is displayed in Figure 3. The same as with PRP, QL was longer the longer the interval and increased during the first sessions. W groups showed a slightly longer QL than NW groups, but differences were not statistically significant between groups of each interval value: FI 15-s: $F_{(1,14)}=2.045$, $p=.2$, ns; FI 30-s: $F_{(1,10)}=1.289$, $p=.3$, ns; FI 60-s: $F_{(1,14)}=1.658$, $p=.22$, ns. Nor were there statistically significant interactions groups x sessions for any of the three analyses.

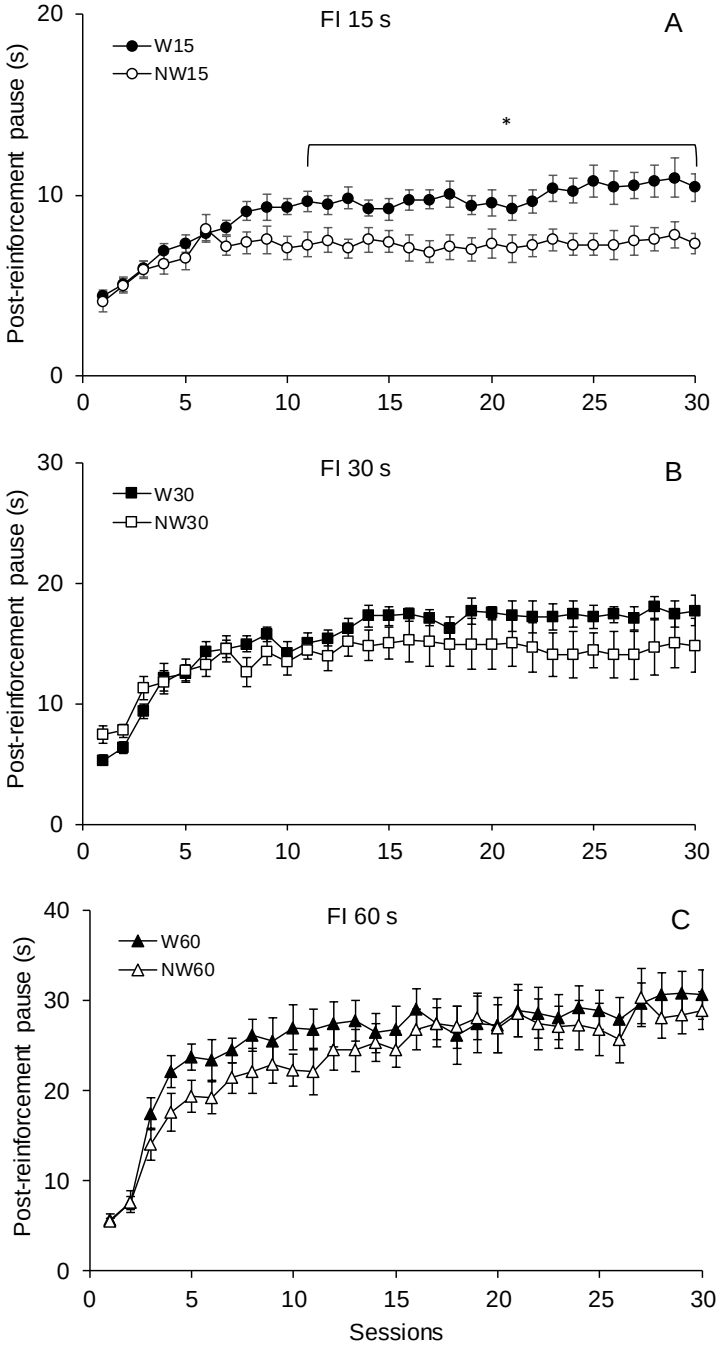

Figure 2. Mean post-reinforcement pause duration for each session and group throughout the experiment. A: W15 and NW 15 groups; B: W30 and NW30 groups; C: W60 and NW60 groups. Vertical bars show S.E.M. Note that y-axis length is different for each graph. * indicates statistically significant differences.

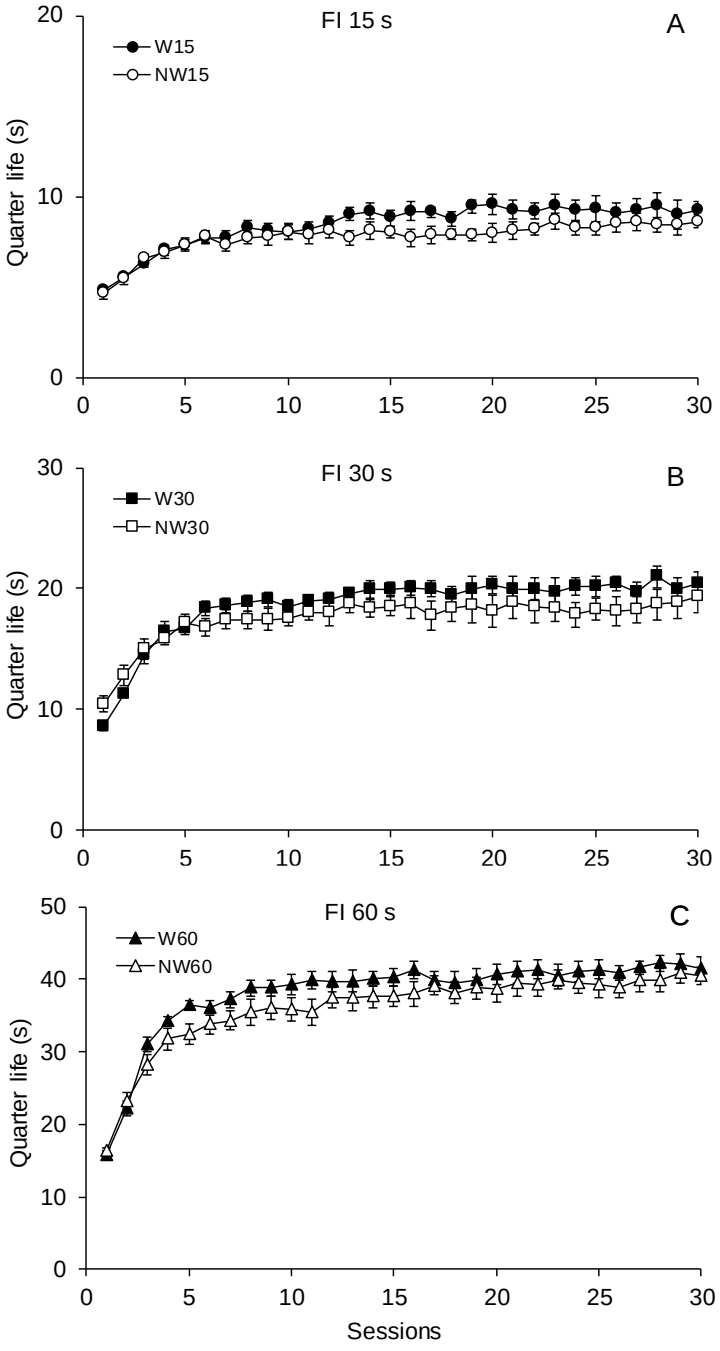

Figure 3. Mean QL duration for each session and group throughout the experiment. A: W15 and NW 15 groups; B: W30 and NW30 groups; C: W60 and NW60 groups. Vertical bars show S.E.M. Note that y-axis length is different for each graph.

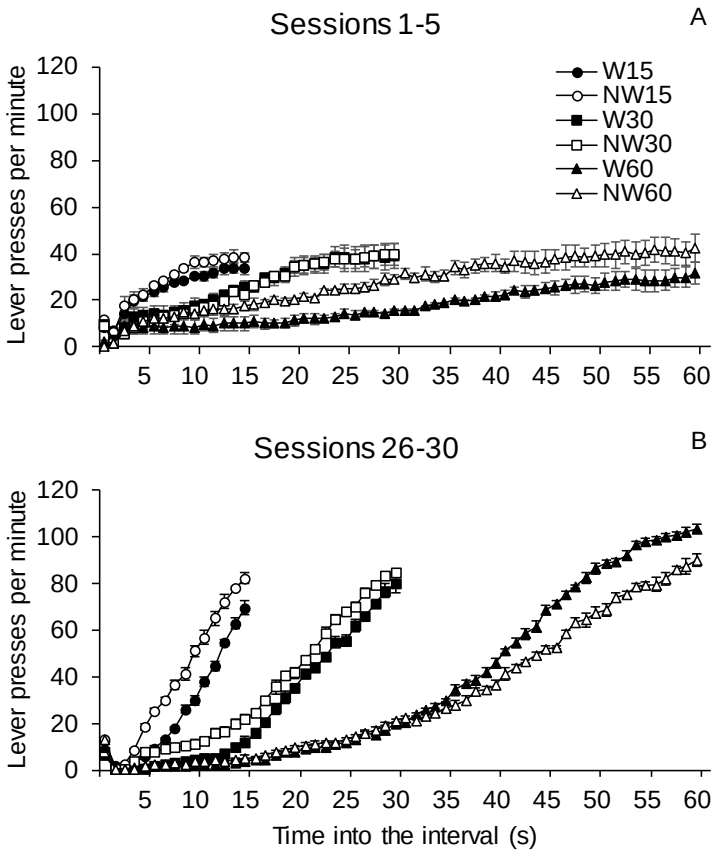

Figure 4. Mean distribution of lever-pressing rate in 1-sec bins along the 15-, 30- or 60-s interval. A: data form the first 5 sessions. B: data from the last 5 sessions. Vertical bars show S.E.M.

Figure 4 shows the temporal distribution of lever presses during the first five sessions (graph A) and the last five sessions (graph B) of the experiment. During the first sessions lever-pressing rate increased gradually during the interval, with a higher rate in NW groups, especially for rats in NW60 group (graph A). At the end of the experiment the FI scallop was visible for all groups: there was little responding at the beginning of the interval and a higher response rate towards the end of the interval. Subjects in groups NW15 and NW30 showed a steeper curve than their homologous W groups, whereas W60 showed a steeper curve than NW60 rats (graph B).

On the other hand, licks (Figure 5) occurred at lower rates during the first experimental sessions but showed similar distributions in the first and last few sessions. The peak of licking rate was different for each group in the first five sessions: second 7, 11 and 13 for groups W15, W30 and W60 respectively (graph A); whereas during the last sessions the peak was 7, 8 and 9 s for groups W15, W30 and W60 respectively (graph B). Although the difference in the peak for W30 and W60 rats differs in only 1 s in the last 5 sessions, W60 rats continued licking until second 30 while W30 rats stopped licking approximately at second 19 of the interval. Conversely, W15 rats continued to lick thorough the interval and abruptly stopped at second 15 without the response rate fading away completely as for the other groups.

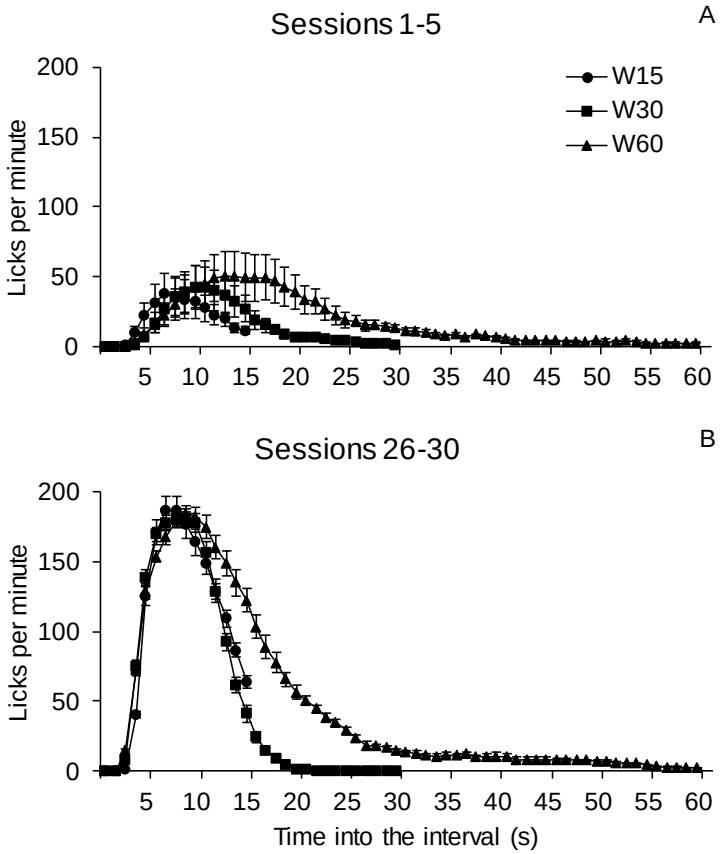

Figure 5. Mean distribution of licking rate in 1-sec bins during the 15, 30 or 60 s interval. A: data from the first 5 sessions. B: data from the last 5 sessions. Vertical bars show S.E.M.

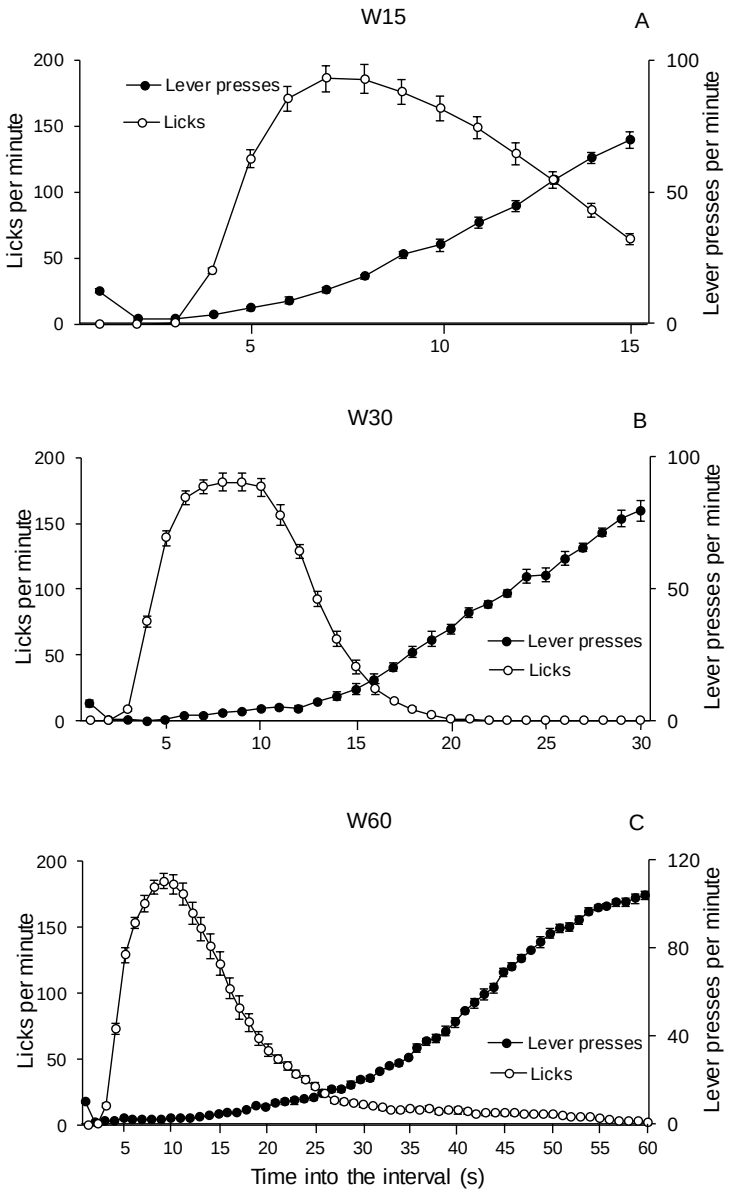

Figure 6. Superposed distributions of licking (y-axis on the left) and lever-pressing (y-axis on the right) mean rates in 1-s bins along inter-reinforcement intervals. Note the x-axis is different for each graph. Data are from the last five sessions of the experiment. A: W15; B: W30; C: W60. Vertical bars show S.E.M.

Figure 6 shows the distribution of licks and lever presses in the last five sessions superposed for each group. These graphs show that lever pressing started after licking stopped for groups W30 and W60. Licking lasted for most of the interval for W15 group

(graph A), but a decrease is observed towards the end of the interval when lever-pressing rate increased, suggesting a behavioural pattern consisting on licking and then lever-pressing. This behavioural pattern resulted in W15 and W30 rats delaying the change from low response rate to high response rate, generating a steeper FI scallop in comparison with NW15 and NW30 groups, as observed in Figure 4. The opposite effect was observed with rats in the W60 group that started responding at a higher rate earlier in the interval than NW60 rats (Figure 4).

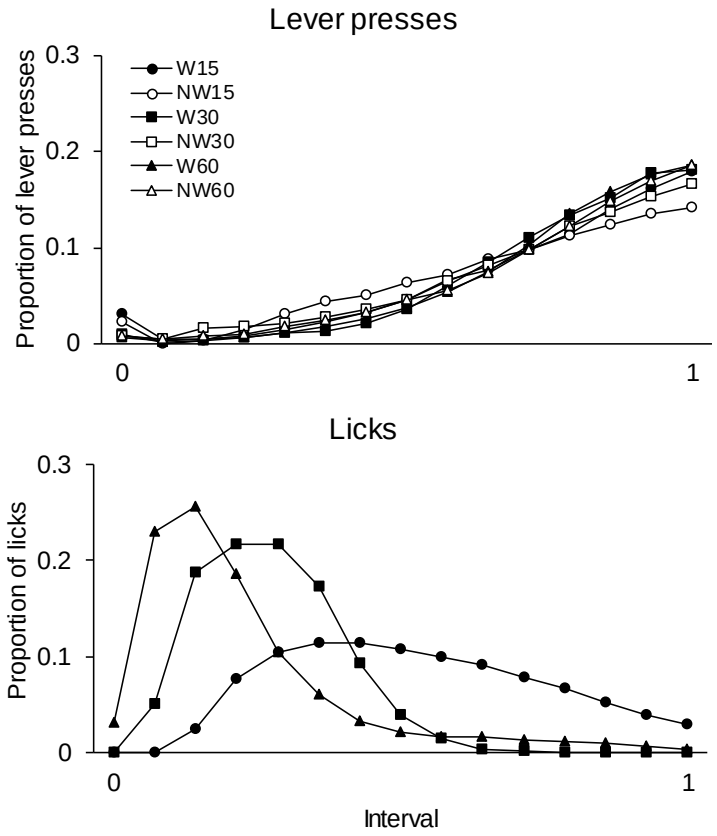

Figure 7. A: proportion of lever presses during the relative length of the inter-reinforcement interval for each group. B: proportion of licks during the relative length of the interval for each water group. Data are from the last 5 sessions of the experiment.

To better compare responding among the three inter-reinforcement interval values, relative distributions for the last five sessions of every group were calculated and are displayed in Figure 7. Relative distributions were calculated by dividing the responses in each unit bin by the total responses in the interval. Each interval was divided in 15 bins of 1, 2 and 3 s for groups W15, W30 and W60 groups, respectively. Lever presses are displayed in graph A and all groups showed the same temporal distribution, except for NW15 that had a flatter distribution than the other groups. On the other hand, the distribution of licks was different for every interval length because licks appear to distribute through most of the interval in FI 15-s, half of the interval for FI 30-s, and the first quarter of the interval in FI 60-s (graph B).

Discussion

Lever pressing and SID developed during the first few sessions until they reached a stable rate, as has been previously reported (Álvarez et al., 2016; Camacho Candia & Cabrera González, 2014; Falk, 1971; López & Menez, 2012). Distribution of behaviours also changed throughout the experiment. During the first five sessions drinking peaked at different times for the three groups, specifically, rats in the W60 group continued drinking at peak levels until second 20, but in the last sessions drinking peaked at seconds 7-9 for the three groups and decreased in a steeper way, showing similar temporal positions (Álvarez et al., 2016). This finding is quite similar to results reported by Pellón and colleagues (Álvarez et al., 2016; Pellón & Killeen, 2015) and suggests that although SID is initially induced, it is reinforced by its occurrence in proximity with the reinforcer in the first sessions, but as organisms adapt to the temporal regularities of the food schedule, it remains at the beginning of the interval, maintained by delayed reinforcement, and is followed by the target behaviours that are more directly reinforced (lever pressing in the present case).

Furthermore, during the first sessions behaviours occurred in a more continued (flat) distribution, probably due to rats alternating between both behaviours a few times across the

interval, while in the last sessions the distributions of both behaviours (lever presses and licks) were more clearly differentiated. These findings are consistent with Killeen's (Killeen, 1975; Killeen & Fetterman, 1988) proposal that the intermittent delivery of reinforcement increases the activity level of organisms and the progressive training selects and shapes a behavioural pattern adequate to the temporal situation. Results reported by Lucas et al.(1988) also support the hypothesis that periodic presentations of food organize available behaviours into repetitive patterns.

Lever presses and licks showed an important difference in their distributions: lever presses showed the scalar property (Church, Meck & Gibbon, 1994), whereas licks occurred for a similar fixed period of the interval regardless of the value of the FI. One of the arguments against schedule-induced behaviours being operants is their temporal location early in reinforced intervals (Falk, 1971; López-Crespo et al., 2004), nevertheless, the individual temporal distribution of each behaviour may not be as relevant as their interaction, as the end of one response may lead to the start of the next response in the behavioural pattern.

Why, then, rats only drink mostly in the first 10-20 s of the interval in a non-scalar way? One possibility is that rats can consume only a limited amount of water per interval, thus they drink *as much as they can*, and spend the rest of the interval pressing the lever. Furthermore, it seems that delivery of reinforcement induces licking, which occurs in the first part of the interval, but is maintained by the delivery of the next reinforcer either by delayed reinforcement (Pellón & Killeen, 2013) and/or as part of a behavioural pattern that includes licking and lever pressing (Ruiz et al., 2016).

PRP and QL are an attempt to summarize quantitatively the performance pattern on FI schedules and have been used to measure time discrimination on FI schedules (Buriticá & dos Santos, 2017). The effect of developing SID over PRP was different depending on the FI

value: knowing that PRP was longer in W groups than in NW groups, difference between them was larger towards the last few sessions when SID had fully developed in FI 15- and 30-s; whereas in FI 60-s the difference was larger during the first few sessions, when drinking occurred for a longer portion of the interval, but differences in the PRP between W60 and NW60 disappeared when drinking stopped earlier in the interval in the last sessions. These findings support the behavioural-pattern hypothesis proposed by Killeen and Fetterman (Fetterman et al., 1998; Killeen & Fetterman, 1988): rats go from one state of behaviour (drinking) to the other (lever pressing), and PRPs reflect the change from SID to lever pressing. Rats in the NW groups probably engaged in other activities that were not measured here.

Furthermore, the lack of differences in QL suggests that rats drank for a specific period of the interval, but once they started lever pressing they did not go back to drinking; this is also consistent with the development of behavioural patterns repeated in every interval (Ruiz et al., 2016).

Killeen (1969) compared the performance of pigeons under a fixed ratio schedule and their yoked subjects that were responding under a "variable interval" schedule (they received a reinforcer after the first response when the lead animal met the ratio criterion). He found that PRP were the same for both groups, meaning that pigeons started to respond at the same time, although the pecks of yoked animals did not have an effect. In the present experiment schedule-induced drinking occurred only during the PRP, thus explaining the lack of statistical differences between groups, and that once rats started lever pressing they did not go back to drinking until they got the next reinforcer.

Lejeune et al. (1998) stated that schedule-induced behaviours do not mediate timed responses and proposed a two-process account for timed behaviour. One process of timing responses with a 'counter' and a second process with an arousal mechanism that relates

activity to reinforcement rate accounting for changes in their number and rate. But what if the first process does not really occur? It is simpler to propose a single process in which available behaviours are simply aroused (induced, see Baum, 2012) and organized by the periodic delivery of reinforcement (Killeen, 1975; Lucas et al., 1988; Ruiz et al., 2016).

In general, data in this experiment supports the hypothesis that the development of SID in a FI food schedule affects the temporal adjustment to the schedule. Nevertheless, the development of SID did not always imply a better adjustment to the schedule, as revealed by the timing measurements and the distribution of responses in the last sessions. It appears that the development of SID only improved the temporal performance of rats exposed to 15- and 30-s intervals, whereas rats exposed to a FI 60-s showed a better performance when they did not have access to water in the experimental chamber. In that sense, these data are better explained by the hypothesis of behavioural patterns consisting on successive states of behaviours maintained by the periodic delivery of reinforcement.

López and Menez (2005; 2012) reported that previous experience can change the speed at which rats learn a FI schedule; more specifically, they suggested that experience under schedules with temporal regularities facilitates the acquisition of the FI scallop. One hypothesis to account for those results is that organisms develop a behavioural pattern that will be maintained until the environmental circumstances change, and even after they have changed, as long as the pattern is not incompatible with the new environmental conditions.

Behavioural patterns developed by organisms seem to include not only the target behaviour (lever press/key pecks), but other usually unmeasured behaviours such as SID. The acquisition of behavioural patterns and its maintenance through time (López-Tolsa, Ardoy & Pellón, *in preparation*) impacts the adaptation of an organism to new environmental conditions. The effect of removing the possibility to engage in one behaviour is not always the same, but rather, it seems to depend on many variables, like the time available to engage

in other behaviours, as seen in Experiment 1. The aim of Experiment 2 was to compare the development of the FI scallop when rats had previously developed SID in another temporal task, but do not have water during the acquisition of the FI schedule.

Experiment 2

Method

Subjects. Subjects were 12 male Wistar rats with previous experience in a temporal bisection task [2] (TBT). Rats were between 41 and 51 weeks old at the beginning of the experiment, because they began the experiment 30 days after finishing the TBT experiment, which occurred at different times for each subject. Their weights were maintained at about 80-85% of their free-feeding weight with an average of 329 g (range: 317-338). Housing conditions were the same as in Experiment 1.

Apparatus. Apparatus were the same as in Experiment 1.

Procedure. Subjects were divided in two groups: half of them had had access to water in the conditioning chamber during the TBT experiment (EW), and the other half did not (ENW). The procedure consisted in three phases: *FI acquisition*, *FI with access to water* and *FI with access to an empty bottle*. It was conducted 6 days per week (Sunday to Friday) at about the same time every day.

Phase 1: FI acquisition. This phase consisted on exposing the subjects to a FI 30-s for 30 sessions, for which the first lever press after 30 s had elapsed since the start of the sessions or the previous reinforcer was followed by a single pellet of food. There were 60 trials per

[2] For more detailed information on the procedure of the TBT experiment, see Experiment 5 in Ruiz et al. (2016).

session. Each session ended 30 s after the 60th reinforcer. During this phase subjects did not have access to the water bottle, emptied or filled, in the experimental chamber.

Phase 2: FI with access to water (FI + Water). During this phase, subjects were exposed to the same FI 30-s food reinforcement schedule for 10 sessions. Only subjects in group EW had access to water during the sessions. ENW rats remained the same as in the previous phase.

Phase 3: FI with access to an empty bottle (FI + Empty bottle). This phase lasted 10 more sessions during which subjects were exposed to the same FI 30-s food reinforcement schedule. Subjects in EW group had access to an empty bottle in the experimental chamber during the sessions, whereas rats in the ENW group remained in the same conditions as in the two previous phases of the experiment.

Data Analysis. Lever presses and licks were recorded. Data were analyzed using a mixed analysis of variance (ANOVAs) with a repeated measures factor, *sessions* (with 30 or 10 levels), and a fixed factor, *group* (with 2 factors). Bonferroni adjustment was used in *post hoc* comparisons. Significance level was established at a minimum $p<.05$. Sphericity principle violations were evaluated with the Mauchly Sphericity test and significant deviations were corrected using Huynh-Feldt to adjust the degree of freedom.

Results

The aim of this experiment was to evaluate the effect of previous experience with SID in the acquisition of the FI scallop. Figure 8 depicts the lever-pressing rate of the two groups in the 3 phases of the experiment and the licking rate of the EW rats in phases 2 and 3. In general, rats in the EW group pressed the lever less than rats in the ENW group. During the 30 sessions of phase 1 lever-pressing rate slightly increased and was higher for the ENW rats, although differences between groups were not significant $F_{(1,10)}=2.59$, $p=.14$, ns [interaction sessions x group $F_{(3,27)}=.437$, $p=.71$, ns]. During phase 2, when water was introduced in the

conditioning chamber for the EW group, lever-pressing rate stayed at a similar level and licking rate increased throughout the sessions. Lever-pressing rate of ENW rats continued slightly increasing throughout phase 2. During phase 3, lever-pressing rate of ENW rats stayed at a similar level while the rate of EW group increased compared to previous phases. There were no significant differences between EW and ENW groups in phase 2, $F_{(1,10)}=2.182$, $p=.17$, ns, but there was an effect sessions x group $F_{(5,46)}=2.88$, $p<.05$; and there were no significant differences in phase 3, $F_{(1,10)}=.856$, $p=.38$, ns [interaction sessions x group $F_{(3,34)}=.870$, $p=.48$, ns]. Licking rate decreased almost to 0 when the water bottle was emptied.

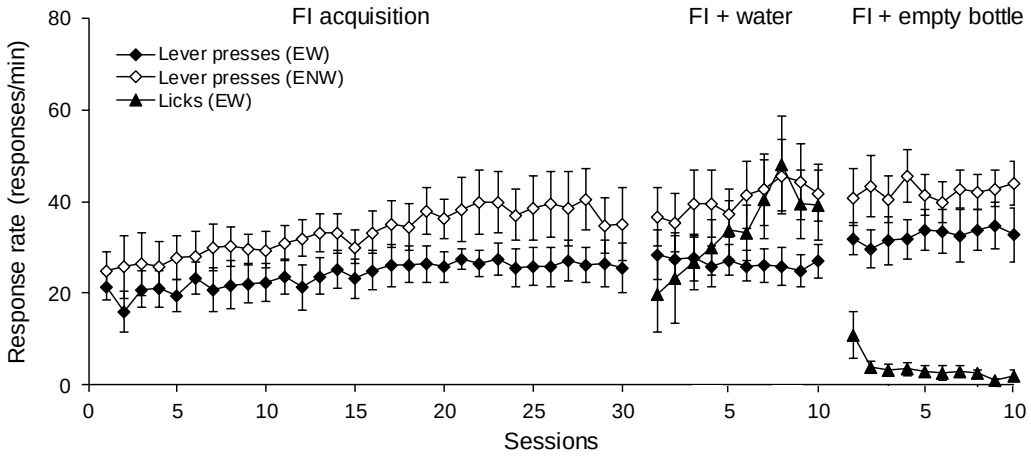

Figure 8. Mean response rate for all groups during each session of the three phases of the experiment: FI acquisition (first 30 sessions); FI + water (middle 10 sessions); and FI + empty bottle (last 10 sessions). Vertical lines show S.E.M.

PRP and QL were calculated as in Experiment 1. Figure 9 shows the mean PRP during each session of the 3 phases of the experiment. PRP increased during the first 12 sessions, and then stayed at similar levels until the end of the experiment. PRPs were higher for the EW group throughout the experiment, however there were not statistically significant

differences between groups: phase 1: $F_{(1,10)}$=2.155, p=.18, ns [interaction groups x sessions $F_{(7,65)}$=.861, p=.53, ns]; phase 2: $F_{(1,10)}$=1.872, p=.21, ns [interaction groups x sessions $F_{(3,30)}$=.96, p=.43, ns]; and phase 3: $F_{(1,10)}$=1.387, p=.27, ns [interaction sessions x group $F_{(6,56)}$=1.61, p=.17, ns]. There were no significant differences in the QL of both groups, either: phase 1: $F_{(1,10)}$=.587, p=.47, ns [interaction groups x sessions $F_{(3,34)}$=.615, p=.63, ns]; phase 2: $F_{(1,10)}$=1.182, p=.3, ns [interaction groups x sessions $F_{(7,70)}$=2.42, p<.05]; and phase 3: $F_{(1,10)}$=.646, p=.44, ns [interaction groups x sessions $F_{(4,40)}$=1.10, p=.37, ns].

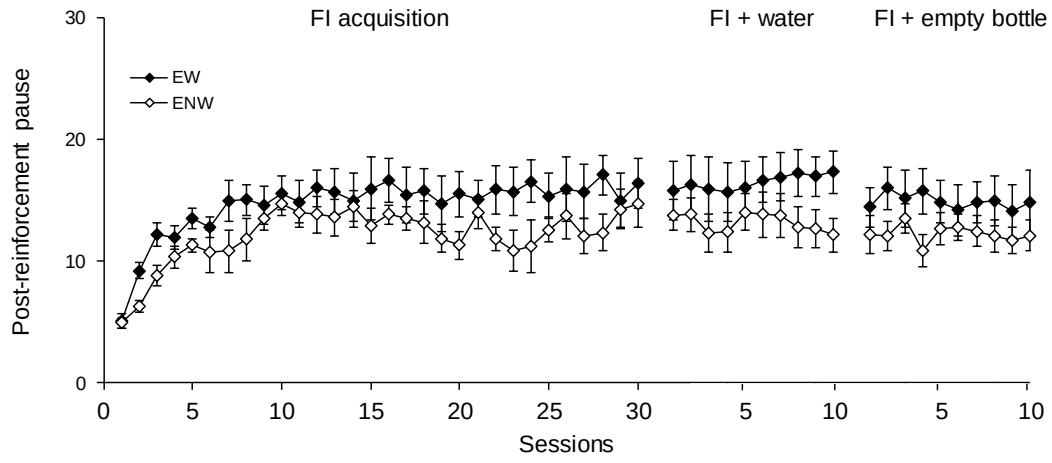

Figure 9. Mean PRP length for each session of the three phases of the experiment: FI acquisition (first 30 sessions); FI + water (middle 10 sessions); and FI + empty bottle (last 10 sessions). Vertical lines show S.E.M.

Distribution of responses during the last 5 sessions of each experimental phase is depicted in Figure 10. During phases 1 and 2, rats of the ENW group started pressing the lever earlier in the interval than rats in the EW group. There were no apparent changes in the distribution of lever presses of the ENW group across the different phases of the experiment, whereas EW rats started pressing the lever earlier during phase 3 (once the water bottle was emptied) than in the previous 2 other phases (graph A). Distribution of licks showed a peak in

the rate of responding at seconds 9-10 of the interval and continued though declining until seconds 18-19 (graph B).

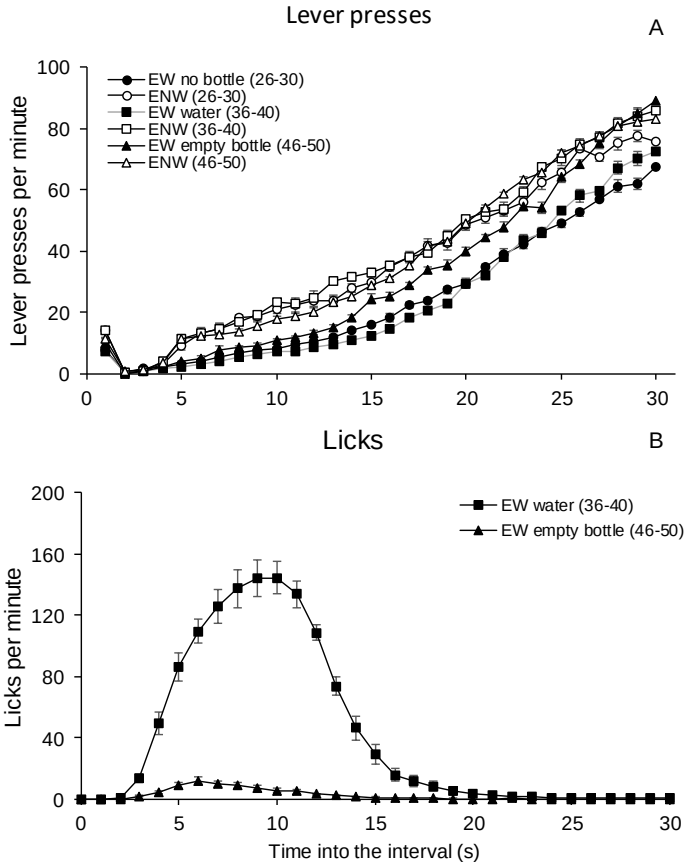

Figure 10. A: Distribution of lever presses during sessions 26 to 30 of phase 1: FI acquisition (circles); the last 5 sessions (36-40) of phase 2: FI + water (squares); and the last 5 sessions of phase 3: FI + empty bottle (triangles). B: Distribution of licks during the last 5 sessions (36-40) of phase 2: FI + water (squares) and the last 5 sessions of phase 3: FI + empty bottle (triangles). White symbols represent the groups of rats with previous experience with water and black symbols represent the groups of rats without experience with water. Vertical bars show S.E.M.

Discussion

The aim of this experiment was to compare the acquisition of the FI scallop when subjects had previously developed SID in a separate and different temporal task. Subjects with previous experience with SID showed lower lever-pressing rates during the FI acquisition phase than subjects without such experience. Other studies have reported that engaging in collateral or schedule-induced behaviours decreases the number of target behaviours (Laties et al., 1969), nevertheless, the lever-pressing rate stayed at similar levels when the bottle with water was introduced for the EW group and slightly increased when the empty bottle was available during phase 3. On the other hand, lever pressing for the ENW group increased throughout the experiment, showing an apparent steady state in the last phase, even though all sessions were identical for this group.

In general, lever-pressing rate was lower for the EW group throughout the experiment, although differences between groups were not statistically significant, is important to note that both groups were exposed to the same schedule in this experiment, but the previous experience with water decreased the number of lever presses in the EW group, as was further confirmed in the PRP. It seems that the effect of having a history of developing SID is strong, because it is not altered by the presence/absence of water in experimental sessions.

When a bottle filled with water was introduced only for the rats in the EW group, subjects showed SID, which rapidly increased, but there were no apparent changes in lever pressing. It is possible that because SID usually occurs mostly during the first 15 s of the interval (Álvarez, et al., 2016; Lawler & Cohen, 1992), rats could drink before they started lever pressing, which is observable in the distribution of both behaviours. Particularly, distribution of SID in this phase was similar to the distribution of SID during FI 30-s in Experiment 1, with rats drinking in the first 15 s of the interval and peaking around second 9-10.

When the bottle was emptied of water, licking decreased dramatically, as previously reported by Clark (1962) and Stein (1964). This decrease could be related to licking being a consummatory response that only occurs when water is consumed, so the feedback that water provides seems to be determined to maintain licking in the SID situation.

Another finding is that when rats were exposed to empty bottles, lever pressing increased as seen in how responses distributed along the inter-reinforcement interval. Distribution of responses showed that rats in the EW group started lever pressing earlier than in previous phases. According to the hypothesis that organisms develop behavioural patterns that go from one state to another and that are repeated in every interval (Killeen & Fetterman, 1988; Ruiz et al., 2016), rats probably started lever pressing right after they finished licking the spout and because they licked at really small rates during the last phase, they would start lever pressing earlier than when the bottle was filled with water (phase 2) or when there was no water bottle to lick (phase 1). Distribution of responses was similar in all phases for the ENW group.

In general, data in this experiment show that experience with certain environmental features, for example, access to water, can influence learning of a new task, even if those characteristics are not present at the moment (Johnson, Bickel, Higgins & Morris, 1991; Williams, Tang & Falk, 1992). But how can non-present stimuli affect behaviour? The hypothesis proposed here could explain it by assuming that rats developed a specific pattern that included drinking and lever pressing, and that once water was removed, lever pressing remained occurring at the same time given that other schedule-induced behaviours that are not being measured can replace schedule-induced drinking, following the logic outlined by Pellón and Killeen (2015) that behaviours compete and shape the distribution of each other.

General Discussion

The main goal of this study was to assess the effect of SID on the performance of rats in FI schedules. Results of Experiment 1 showed that SID affects FI performance in different ways: for shorter FI values rats that developed SID showed a more adjusted performance, whereas rats in the longest FI value performed in a less accurate way. Nevertheless, distribution of responses evidenced that all subjects behaved in a similar way independently of the FI value (after eating the food pellets, rats would drink for a few seconds and then change to lever pressing), thus suggesting that differences between subjects with and without access to water do not portrait differences in timing ability, just differences in the organization of available behaviours.

Moreover, results of Experiment 2 showed that developing SID in a previous timing task can affect the way FI scallop is acquired by delaying the increase of lever pressing compared to subjects without a history of engaging in SID. Also, access to a water bottle did not change the distribution of lever pressing, because licks occurred during the PRP. Interestingly, when an empty bottle was introduced, rats started lever pressing earlier, probably after they finished licking the spout of the empty bottle.

According to the data presented in this study, schedule-induced behaviours seem to influence the behavioural pattern that organisms develop during temporal tasks, but not that much as to affect quantitative timing measures used to assess performance in FI. This type of results leads to the question of what we are really measuring when we talk about temporal learning and/or estimation. As Cleaveland et al. (2003) pointed out, scientist in the field of the experimental analysis of behaviour are usually only concerned with measuring one specific behaviour like a lever press or a key peck, without paying attention to the actual organism behaving.

Killeen and Pellón (Killeen & Pellón, 2013; Pellón & Killeen, 2015) suggested that different classes of behaviours could be reinforced independently of each other, although competing among them, by means of delayed gradients of reinforcement. Furthermore, Ruiz et al. (2016) suggested that it is possible that these different behaviours are not reinforced independently of each other, but as a pattern that fills IRIs and that is repeated trial by trial. Data presented here seem to support these proposals.

SID interact and compete with other behaviours (Pellón & Killeen, 2015), but once a specific pattern develops it remains constant (Cleaveland et al., 2003; Lawler & Cohen, 1992; Segal & Holloway, 1963; Staddon & Ayres, 1975; Staddon & Simmelhag, 1971), and can, therefore, be used as a tool for temporal estimation (Ruiz et al., 2016). This view is consistent with behavioural timing theories proposed by Killeen (Killeen, 1975; Killeen & Fetterman, 1988) and Machado (1997).

Pellón and colleagues were not the first ones to suggest that schedule-induced behaviours are maintained by the delivery of reinforcement, in fact, this hypothesis has been considered since the 60's (Laties, et al., 1969; Segal & Holloway, 1963). Levitsky & Collier (1968) suggested that the reinforcer did not only strengthened the contingent responses, but also increased the probability of all potential responses in the testing situation. Similarly, Dews (1966), Killeen (1969), Catania (1971), and many others, have suggested that the reinforcer does not only affect the reinforced response, why should it be different to other behaviours? As Killeen (2017, pp. 60-61) stated "reinforcers are always reinforcing something, whether we are measuring it or not".

Furthermore, Bruner and Revusky (1961) studied collateral behaviours in humans by exposing them to a task in which they were supposed to press one target key but had three more available keys in the experimental apparatus. Subjects developed systematic response patterns consisting on responding on more than the target key and they reported on post-

experimental interviews that they were convinced they needed to perform the whole pattern to obtain the reinforcer. If this is true for humans, why should we assume that operant conditioning learning occurs in a different way with other organisms?

Baum (2012) stated that all behaviours are induced rather than reinforced, a hypothesis that might be partially true: as many studies have shown, including the present one, behaviours that develop in a specific experimental situation depend both on the environment dispositions and on the organism's species-specific behaviours. Organisms are always behaving, and their specific behaviours are, of course, induced by the environment in which they are, therefore, the role of reinforcement would be that of an organizer (rather than a creator) of those behaviours (Álvarez et al., 2016; Ruiz et al., 2016).

Segal (1969c) proposed a similar idea when she observed that SID during a FI schedule occurred closer to the previous delivery of food until she eliminated the contingency for lever pressing and SID started to show the typical FI scallop. She concluded that schedule-induced behaviours may be an important class of material out of which operants are shaped. Most of an organism's behavioural repertoire is susceptible of operant conditioning if it has a proper environment in which to be displayed. Even Falk (1971) stated that schedule-induced behaviours are not new responses, but responses that previously existed in the situation but increased their rate in the specific experimental situation. This is similar to Killeen's proposition that "interval schedules reinforce any behaviour that precedes a response and takes time" (Killeen, 1969, p. 395).

Killeen and Jacobs (2016) discuss about the importance of the state of the organism to determine which behaviours will be induced by a particular experimental situation, and depending on the schedule of reinforcement, some of those behaviours will be selected (Skinner, 1981) and the distribution of responses will be shaped through several sessions until it reaches a "convenient" state and remains steady as long as the environmental conditions do

not change. This idea resembles the behavioural systems theory proposed by Timberlake, Lucas and their colleagues (Lucas et al., 1988; Timberlake & Lucas, 1985).

In conclusion, for a better understanding of temporal learning, behaviour analysts should take a closer look to the *organism behaving*. Timing seems to consist in the temporal organization of available behaviours that leads to a specific behaviour occurring in a specific time which researchers later interpret as ‘accurate timing’. Organisms are always behaving, the environment provides the opportunities for some behaviours to be induced, and the schedule of reinforcement shapes their distribution.

CHAPTER 3

TEMPORAL ORGANIZATION OF SCHEDULE-INDUCED BEHAVIOUR IN THE PEAK PROCEDURE

Abstract

Periodic delivery of reinforcement serves a triple-task: select from the available behaviours, maintain them as part of behavioural patterns and triggering such patterns. The temporal organization of behaviours in those patterns can have differential effects on timing, depending on the value of the schedule of reinforcement. The aim of this chapter was to analyse the distribution and interaction of SID and lever pressing in the peak procedure. Rats divided in two groups (with and without access to water in the experimental chamber) were exposed to 10 baseline sessions of a FI 15-s or 60-s, and then to 30 sessions of a peak procedure in which FI trials were alternated with peak-interval (PI) trials. The temporal distribution of responses during FI and PI trials was analysed, comparing groups, individual subjects and individual trials. Developing SID had opposite effects for the FI 15-s and the FI60-s groups: the peak occurred later for the W15 compared to the NW15 groups and earlier for the W60 compared the NW60 group. Analysis of individual performance showed that rats that developed SID displayed a more organized pattern, but only in the FI 15-s. Furthermore, analysis of the distribution of responses on individual trials showed that the behavioural pattern only re-started in trials preceded by the delivery of reinforcement, supporting the hypothesis that they are induced by the previous reinforcer, but maintained by the forthcoming one. Data in this chapter supports the idea that timing is the temporal organization of available behaviours, shaped, maintained and induced by periodic delivery of reinforcement.

Temporal Organization of Schedule-induced Behaviour in the Peak Procedure

Schedule-induced behaviours are those that develop without any arranged contingency with the reinforcer. The origin and maintaining mechanism of schedule-induced behaviours have been under debate since they were first described in the 60's (Falk, 1961). Falk (1971) and Staddon (1977) considered schedule-induced behaviours to be different from operant behaviours, induced by the delivery of reinforcement, but not maintained by it. Nevertheless, recent research seems to point towards a different direction by considering schedule-induced behaviours as being maintained by the delivery of reinforcement (Álvarez et al., 2016; Killeen & Pellón, 2013; Ruiz et al., 2016). Moreover, Baum (2012) suggested that all behaviours are induced, and that the role of reinforcers is not to strengthen the response, but that of a discriminative stimulus.

In a more conciliatory approach, the hypothesis that reinforcers first act upon existing behaviours, then select the most appropriate/suitable ones to a specific schedule and organize them into a stable behavioural pattern was proposed in Chapter 2. Reinforcers would therefore serve a triple-task: select from the available behaviours, maintain them as part of a behavioural pattern across time, and triggering such pattern. Similar accounts have been previously proposed by Killeen (1969) and Timberlake, Lucas and their colleagues (Lucas et al., 1988; Timberlake & Lucas, 1985).

Mattel and Portugal (2007) pointed out that tasks designed to evaluate timing behaviour usually elicit not only the 'timing' behaviours, but other *types* of behaviours. Those other types of behaviours usually correspond to what have been categorized as schedule-induced and have been considered the behavioural clock that accounts for performance in temporal tasks (Killeen & Fetterman, 1988; Machado, 1997), or more

recently, as being part of the behavioural pattern shaped, maintained and triggered by intermittent (and usually periodic) delivery of reinforcement, as proposed in Chapter 2 and by Ruiz et al. (2016).

SID is the most studied example of schedule-induced behaviours, as it develops rapidly and consistently under a wide variety of procedures. When rats are exposed to an intermittent schedule of reinforcement (usually food, but see Falk, 1967 and Cantor & Wilson, 1978 for other types of reinforcers) with water available in the conditioning chamber, they will develop an excessive pattern of drinking that after some training will distribute mostly between the first 10 to 20 seconds of each inter-reinforcement interval. The distribution and temporal localization of SID may vary with some experimental manipulations (see Álvarez et al., 2016; Daniel & King, 1975; López-Crespo et al., 2004 for examples), but it occurs consistently for long periods of time if the experimental conditions do not change.

In the previous chapter, differential effects of developing SID were found with short and long fixed interval (FI) schedules. It appears that SID improves performance in short FI but worsen it in longer FI. Nevertheless, both effects appear to be due to the interaction of SID and lever pressing, because when rats stop drinking, they start lever pressing, which is appropriate for shorter intervals, but counterproductive for longer intervals. SID, lever pressing, and other not-measured behaviours seem to be part of a behavioural pattern that organisms repeat during inter-reinforcement intervals.

The peak procedure is a temporal task that has been used to evaluate timing processes in FI schedules (Church, Miller, Meck & Gibbon, 1991). The peak procedure consists on intercalating FI trials with longer non-reinforced trials that are called peak intervals (PI) (Catania, 1970; Roberts, 1981). When plotting mean data of the PI trials, this kind of task produces a gaussian-shaped distribution of responses whose maximum response rate occurs

approximately at the time of the FI and decreases to almost 0 at 2-times the FI value. The first half of the Gaussian-shaped distribution corresponds to the characteristic FI scallop, that consists on a positively accelerated curve that is observable when plotting averaged data (Baron & Leinenweber, 1994).

Distribution of responses during PI changes with training (Balci et al., 2009; Kirkpatrick-Steger, Miller, Betti and Wasserman, 1996) because organisms need to learn to stop responding when the reinforcer is not delivered at the time of the FI (Machado, 1997). Also, some authors have reported a resurgence of responses observed at the last portion of the PI (Church et al., 1991); whereas Kirkpatrick-Steger et al. (1996) reported the development of a second Gaussian peak in the distribution of responses using pigeons as subjects and PIs four times longer than the FI (ratio 1:4).

Sanabria and Killeen (2006) tried to replicate Kirkpatrick-Steger and her colleagues' (1996) results using rats and pigeons as experimental subjects. Rats did not show the double peak distribution but showed some resurgence of responses towards the last part of the interval, even in conditions in which the retraction/insertion of the lever marked the end/beginning of the trial. They also observed that responding started at higher rates in trials following PI trials than in trials following FI. Responding after PI trials seemed to continue the 'resurgence' of responses, even if the inter-trial interval (ITI) occurred between both trials. These results suggest that rats were not following signs such as the retraction/insertion of the lever that marked the end/beginning of a trial. Sanabria and Killeen concluded that resurgence rates are controlled by the forthcoming reinforcers, not the trial termination cues.

There are other findings suggesting that resurgence occurs at least partly in anticipation of the reinforcer in the next trial. Shorter ITIs produce a higher resurgence than longer ones and when the length of the peak trial is random, instead of fixed, organisms do not show resurgence of responses (Church et al., 1991).

Data from PI trials are usually presented as a group mean or as the mean of different sessions for each subject. Nevertheless, the Gaussian distribution is not representative of individual performances, in the same way as the FI scallop is not always representative of individual performances (Baron & Leinenweber, 1994). Instead, organisms tend to do a break-run-break pattern during PI trials, and the apparently smooth decrease in responses is due to individual differences plotted together, rather to what organisms actually do (Church, Meck & Gibbon, 1994). This kind of analyses may be misleading when drawing conclusions about timing strategies (Balci et al., 2009).

The aim of this study was to analyse the distribution and interaction of SID and lever pressing during FI and PI trials in rats. Additionally, a detailed observation of the behavioural pattern developed during PI trials is necessary to further evaluate the role of schedule-induced behaviours in timing.

Method

Subjects

Subjects were 32 male rats with previous experience in a FI schedule (Experiment 1, Chapter 2). Rats were 30 weeks old at the beginning of the experiment. Subjects were housed individually in transparent Plexiglas cages measuring 18 x 32.5 x 20.5 cm in an environmentally-controlled room (22°C temperature and 55% relative humidity) with a 12-hour light-dark cycle (lights on at 8:00 a.m.). Rats' weights were maintained at 85% of their free-feeding weight, by restricting access to food. Their mean weight was 350 g (range: 284-429) at the beginning of the experiment. Water was always available in their home-cages. Animal care procedures were in accordance with the European Union Council Directive

2010/63, the Spanish Royal Decree 53/2013 and with the authorization of the Community of Madrid with reference PROEX 077/18.

Apparatus

Eight Leticia LI-836 conditioning chambers measuring 29 x 24.5 x 35.5 cm were used. The front panel of each conditioning chamber was made of aluminum, the left wall of transparent Plexiglas and the reaming walls of black Plexiglas. The floor consisted on a 16-bar metal grid. In the center of the front wall at a height of 3.7 cm above the floor was located the food tray, at each side of the food tray there was a retractile lever, and above each lever a 3-W round lamp. Only the left lever was active during this procedure. Forty-five mg food pellets were dispensed (Bio-Serv, Frenchtown, NJ, USA) into the food tray by a Leticia Instruments dispenser. In the right wall, there was a 3.2 x 3.9 cm aperture in the wall, situated 20 cm from the front panel and 7 cm from the floor, through which subjects could reach the spout of a water bottle mounted on the exterior of the chamber. The water bottle could be removed if necessary. The spout was placed 2 cm towards the interior of the aperture to allow for licks rather than continuous drinking. Contact between the subject's tongue and the metal spout completed the electric circuit between the floor and the spout that allowed licks registration. Chambers were enclosed in a soundproofed housing equipped with a ventilation system and a small observation window in the left panel. A fan located in the soundproofed housing produced an ambient noise of approximately 60 dB in each chamber to mask any exterior noise. The houselight consisted on an indirect 25-W light mounted in the soundproofed housing. Chambers were controlled using a MED-PC application under a Windows environment.

Procedure

Subjects were divided in groups considering two variables: having/not having water available in the conditioning chamber and the value of the FI schedule. The FI values chosen

for the procedure were FI 15- and FI 60-s because they were the shortest and the longest values evaluated in Chapter 2. These conditions resulted in four groups of 8 subjects each: W15 (FI 15-s, access to water); NW15 (FI 15-s, no access to water); W60 (FI 60-s, access to water); and NW60 (FI 60-s, no access to water).

The experiment had two phases: baseline and peak phase. Baseline lasted 10 sessions during which subjects were exposed to the same FI schedule that they had experienced in Chapter 2, but ITIs were added. At the beginning of each trial the houselight was turned on and the lever inserted into the chamber. The first lever press after 15 or 60 s (depending on the group) delivered one food pellet, turned off the houselight and retracted the levers for the ITI. Each session consisted of 30 trials with ITIs of 3 s.

Peak phase consisted on intercalating FI and PI trails and lasted 30 sessions. Each session consisted of 24 FI trials (as described in the baseline) and six PI trials. At the beginning of each PI trial the houselight went on and the lever was inserted into the chamber, and these conditions were maintained for 45 (for the FI 15-s groups) or 180 s (for the FI 60-s groups) after which the houselight was turned off and the lever retracted. FI and PI trails began in the same way, so that subjects could not predict the type of trial. No food pellets were delivered during PI trials.

Data Analysis

The aim of this study was to observe the interaction between SID and lever pressing and its role in timing, so the focus of data analysis will be on the temporal distribution of responses (lever presses, licks and head entries) during FI and PI. Analysis of the distribution will include comparisons among groups, individual subjects and individual trials.

To provide quantitative analysis of the differences between W and NW groups in timing, a Gaussian function was fitted to the individual data of PIs of the last 5 sessions:

$$A \times \left(f(t, \mu, \sigma) = \frac{1}{\sqrt{2\pi}\sigma} e^{\frac{1}{2}\left(\frac{t-\mu}{\sigma}\right)^2} \right),$$

where, *A* is a free parameter that maps Gaussian probabilities onto response rate, t is time from the beginning of the interval (in seconds), μ is the mean of the distribution (peak time) and σ is the standard deviation (SD, width of the peak). The function was fitted to the data of 2-times the FI value, when the Gaussian shape of the peak is appreciated (for the first 30 s of the PI for the FI 15-s groups and for the first 120 s of the interval for the FI 60-s groups). The best fitting parameters were obtained by the least squares method using Microsoft Excel solver with the constraints that all parameters had to be positive. The Weber fraction was calculated by dividing the SD by the peak time. And the goodness of fitting was calculated using the coefficient of determination (R^2).

The parameters of the function were analysed using a one-way analysis of variance (ANOVA) that compared the means of the two levels (W/NW) of the factor group. The significance level was established at a minimum $p<.05$. DMS adjustment was used in *post hoc* comparisons.

Results

Figures 1 and 2 depict the distribution of responses (lever presses, head entries and licks) during the FI trials in the last five sessions of baseline and the last five sessions of peak phase. Data of FI 15-s groups are displayed in Figure 1. Licking of W15 group peaked at 4 s in both phases and occurred at similar rates; while lever pressing of group W15 showed the characteristic scallop in both phases but increased earlier in the peak phase. Distribution of lever presses of NW15 group was similar in both phases and increased continuously, thus they did not show the FI scallop.

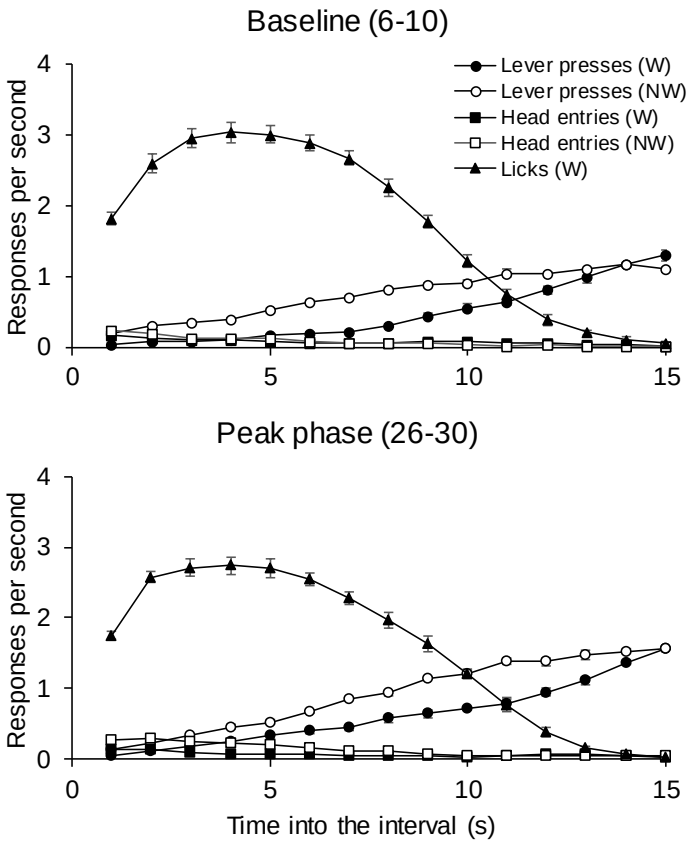

Figure 1. Distribution of responses in the FI trials of the last five sessions of baseline (graph A) and the last five sessions of the peak phase (graph B) for groups exposed to a FI 15-s. Data for the W15 group are represented with black symbols and data for the NW15 group are represented with white symbols. Vertical bars show S.E.M.

Distribution of responses of groups W60 and NW60 is displayed in Figure 2. Distribution of licking of group W60 changed from peaking at second 6 in the baseline to peaking at second 8 on the FI trials of the peak phase and occurred at a lower rate. Distribution of lever pressing of groups W60 and NW60 was similar in both phases, but W60 group had a slightly more pronounced curve than the NW60. Furthermore, head entries occurred at very low levels for all groups in both phases (Figures 1 and 2).

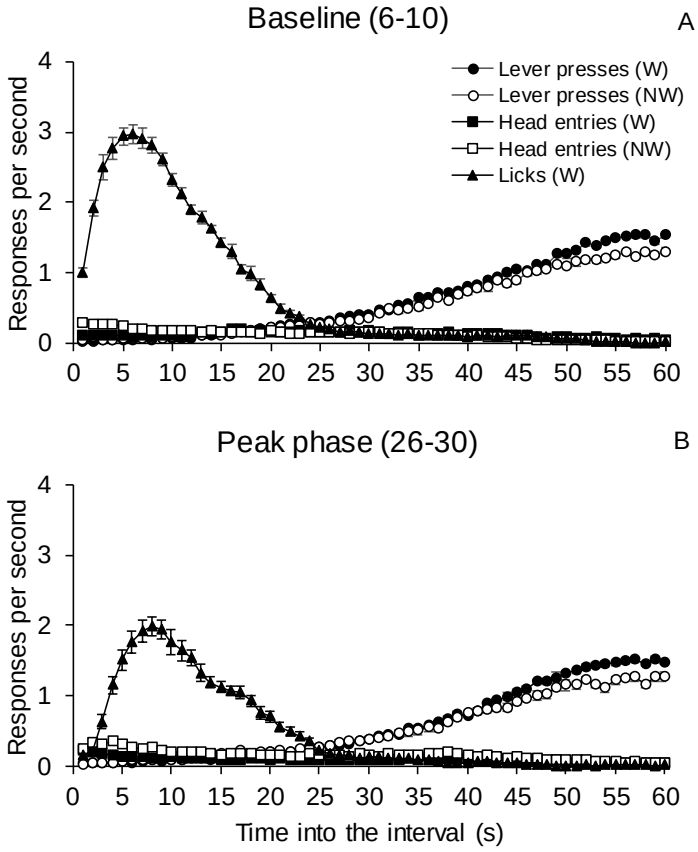

Figure 2. Distribution of responses in the FI trials of the last five sessions of baseline (graph A) and the last five sessions of the peak phase (graph B) for groups exposed to a FI 60-s. Data for the W group are represented with black symbols and data for the NW group are represented with white symbols. Vertical bars show S.E.M.

Figures 3 and 4 show the distribution of behaviours in the PI trials. Data from both the first and last sessions of the peak phase were plotted to appreciate the changes that occurred when the subjects learned to discriminate between a FI trial, that ends with the delivery of reinforcement, and a PI trial, during which subjects should stop pressing the lever once the time of the FI has elapsed.

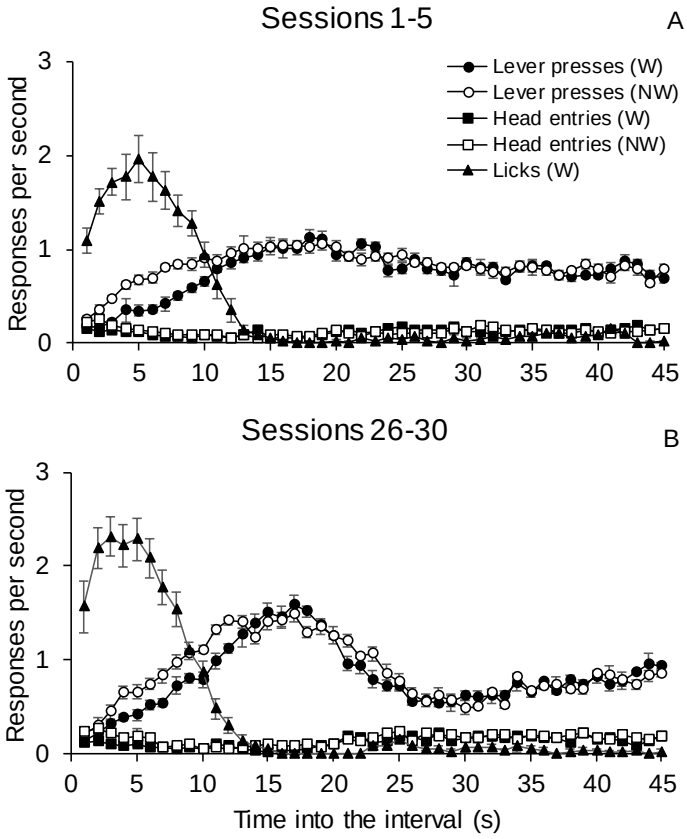

Figure 3. Distribution of responses in the peak trials of the first five (graph A) and last five (graph B) sessions of the peak phase for groups exposed to a FI 15-s. Data for the W group is represented with black symbols and data for the NW group is represented with white symbols. Vertical bars show S.E.M.

Distribution of responses of W15 and NW15 groups is displayed in Figure 3. Licking of the W15 group peaked at second 5 and stopped around second 12. Subjects did some isolated small bursts of licks throughout the rest of the peak trials, but not in a consistent way among subjects, sessions or trials (further details about this are discussed later). Regarding lever pressing, rats in the NW15 group started pressing earlier in the interval than rats in the W15 group in the first and last sessions; furthermore, in the last five sessions the peak of lever pressing occurred later for the W15 group than for the NW15 group. The form of the distribution changed from the beginning to the end of the experiment, the peak being more

accused in the last 5 sessions (graph B). Also, the increase of lever presses was steeper for the W15 groups in the first five sessions, although it decreased similarly for both groups in each phase. Resurgence of lever pressing is visible in the last five sessions (graph B). Some head entries occurred throughout the trial, especially for group NW15 in the last sessions.

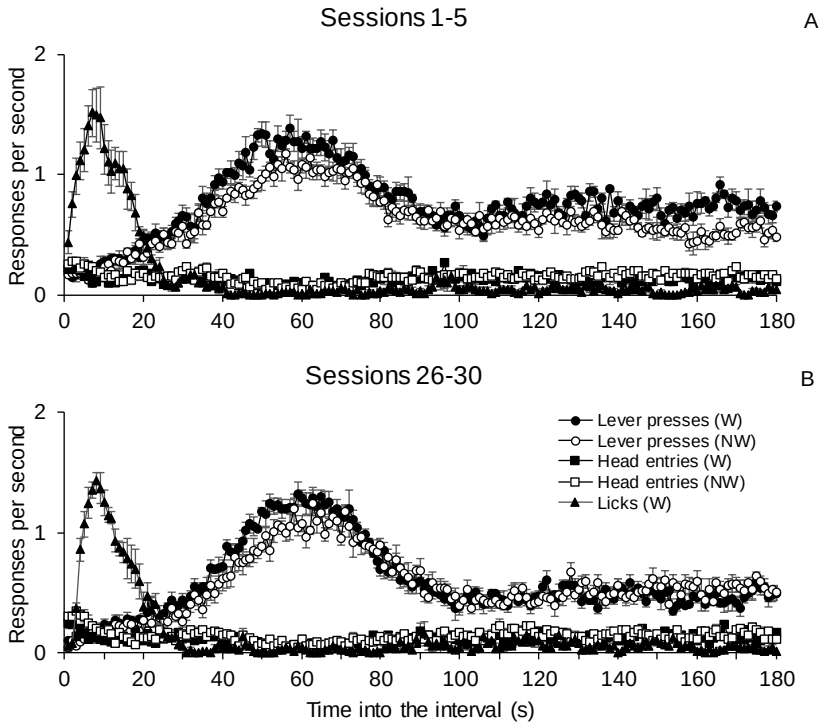

Figure 4. Distribution of responses in the PI trials of the first five (graph A) and last five (graph B) of the peak phase for groups exposed to a FI 60-s. Data for the W group is represented with black symbols and data for the NW group is represented with white symbols. Vertical bars show S.E.M.

Distribution of responses of W60 and NW60 groups is depicted in figure 4. Licking peaked at second 8 and stopped around second 25 during the first and last sessions. Contrary to the FI 15-s groups, lever pressing had similar distributions in both FI 60-s groups, although rats in the W60 groups started pressing the lever slightly earlier and showed a higher rate of lever presses, especially towards the end of the trials in the first five sessions. The

distribution of both groups was narrower, and lever pressing decreased in a steeper way in the last five sessions than in the first sessions. No resurgence is observable, but after the peak, lever-pressing rate did not decrease to 0. Similar to the FI 15-s groups, some head entries occurred throughout the PI trial, at higher rates for the NW60 group.

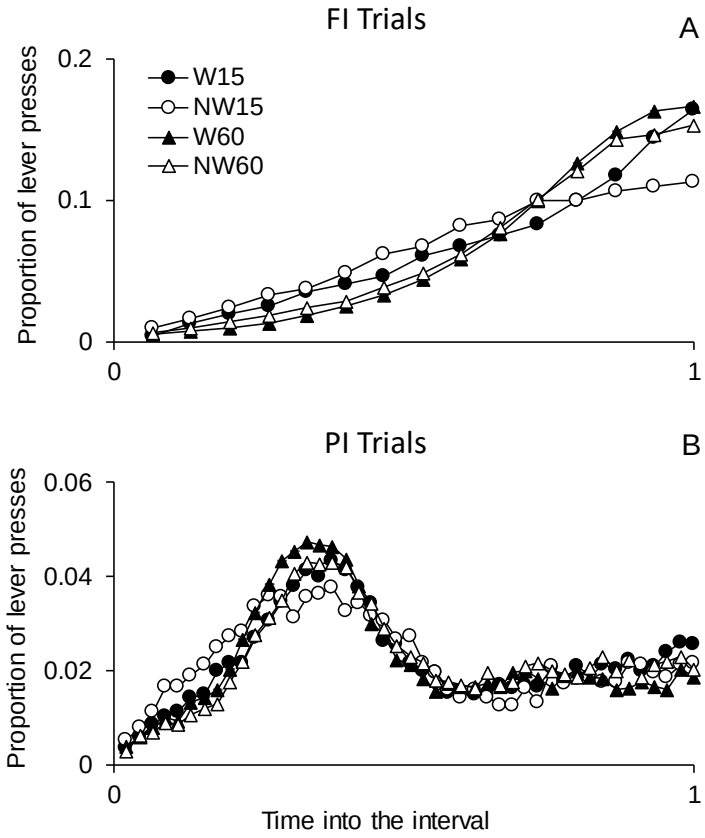

Figure 5. Proportion of lever presses during the relative length of the interval for each group in FI (graph A) and PI trials (graph B).

Proportional data is displayed in Figures 5 and 6 to allow for comparisons of the shapes of the distributions between schedules. Proportional data was calculated by dividing the responses in each unit bin (1 s for FI 15-s and 3 s for FI 60-s) by the total responses in the interval. Figure 5 depicts the distribution of lever presses in the FI trials (graph A) and the PI trials (graph B) of the last five sessions of the peak phase. When displayed proportionally,

lever presses had similar distributions for groups W15, W160 and NW60 groups, whereas distribution for the NW15 group was flatter and did not have the shape of the FI scallop. Similarly, distribution of responses during PI trials was similar for the W15, W60 and NW60 groups, although the W60 group showed a slightly wider peak that started earlier in the interval; again, NW15 had a flatter and wider peak than the other groups. All groups showed a small resurgence of lever presses towards the end of the PI trials.

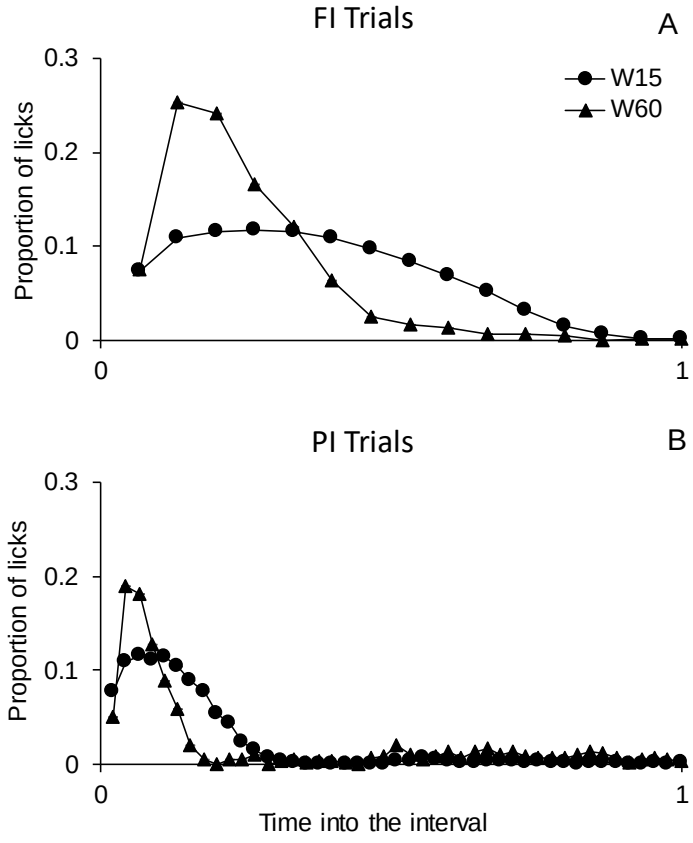

Figure 6. Proportion of licks during the relative length of the interval for groups W15 and W60 in FI (graph A) and PI trials (graph B). Data of the last 5 sessions of peak phase.

On the other hand, distribution of licks (Figure 6) was different for W15 and W60 groups, licks occurred in the first third of the interval for W60 but distributed throughout the

interval for W15 rats (graph A). Something similar happened during PI trials, licking occurred in the first part of the peak interval for both groups but stopped sooner in the interval for the W60 group (graph B).

The Gaussian function was fitted to the individual distributions of lever presses during PI trials of the last five sessions. The mean distribution and the average of the fitted curves of all subjects in each group are displayed in Figure 7.

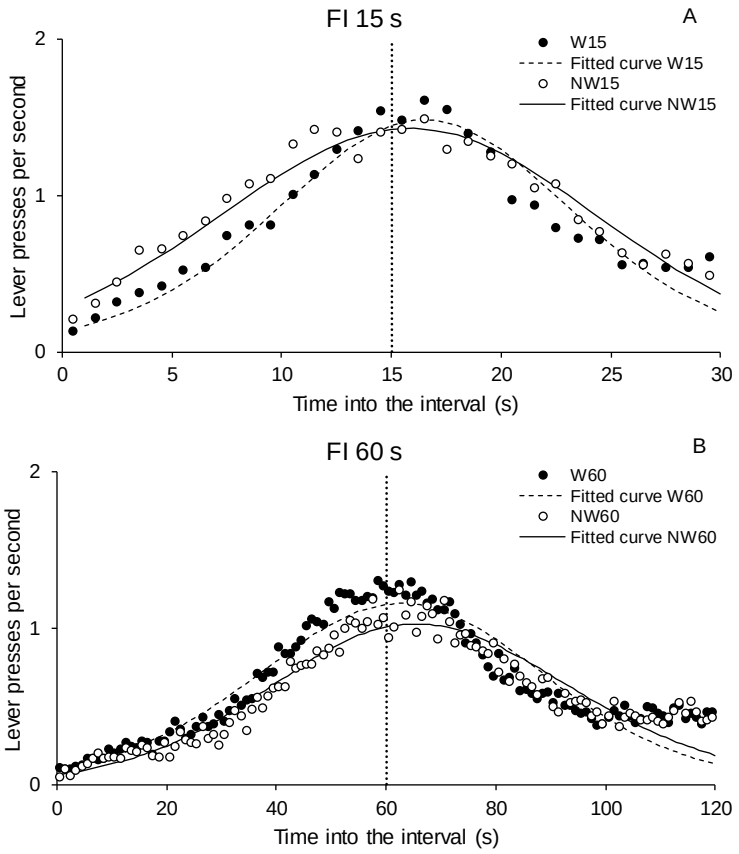

Figure 7. Mean distribution of lever-pressing rate during PI trials and mean individually best-fitted Gaussian curves for FI 15-s (graph A) and FI 60-s (graph B) groups. Dotted vertical line indicates the value of the FI.

Group mean values of the parameters from the Gaussian function fitted to the data, Weber fraction and goodness of fit for each group are displayed in Table 1. The

peak of lever presses occurred later for the W15 group (16.59 s) than for the NW15 group (15.62 s), but differences were not significant $F_{(1,15)}$=2.966, p=.10, ns; whereas for the FI 60-s groups, the opposite effect was observed, the peak for the W60 group occurred earlier (62.74 s) than for the NW60 group (66.41 s), differences were statistically significant $F_{(1,15)}$=4.741, p<.05. Furthermore, the peak was wider for the NW15 group than for the W15 group and differences were close to significance [$F_{(1,15)}$=3.583, p=.07, ns]; whereas NW60 and W60 group had peaks with similar width [$F_{(1,15)}$=0.44, p=.83, ns].

Table 1.

Parameters of the Gaussian function fitted to the data.

Group	Peak* (μ)	Width* (σ)	Weber fraction	Goodness of fit
W15	16.59 ± 1.04	7.19 ± 2.10	0.44 ± 0.14	0.82 ± 0.13
NW15	15.62 ± 1.20	8.80 ± 1.18	0.57 ± 0.10	0.79 ± 0.10
W60	62.74 ± 1.81	27.58 ± 5.24	0.44 ± 0.09	0.73 ± 0.11
NW60	66.41 ± 4.42	27.04 ± 5.00	0.40 ± 0.06	0.76 ± 0.05

Note. Mean ± S.E.M. *Data in seconds.

On the other hand, the Weber fraction was 0.57 for the NW 15 and 0.44, 0.44 and 0.40 for the W15, W60 and NW60 groups, respectively. Differences among groups were significant [$F_{(3,31)}$=4.038, p<.05], a *post hoc* analysis showed that the Weber fraction for NW15 group was different from the other three. The goodness of fitting did not differ among the four groups [$F_{(1,31)}$=1.281, p=.30, ns].

As pointed out in the introduction, the mean distribution of responses does not always represent the individual performance, so individual distributions of responses in the PI trials of the last five sessions of the peak phase are displayed in Figures 8 to 11.

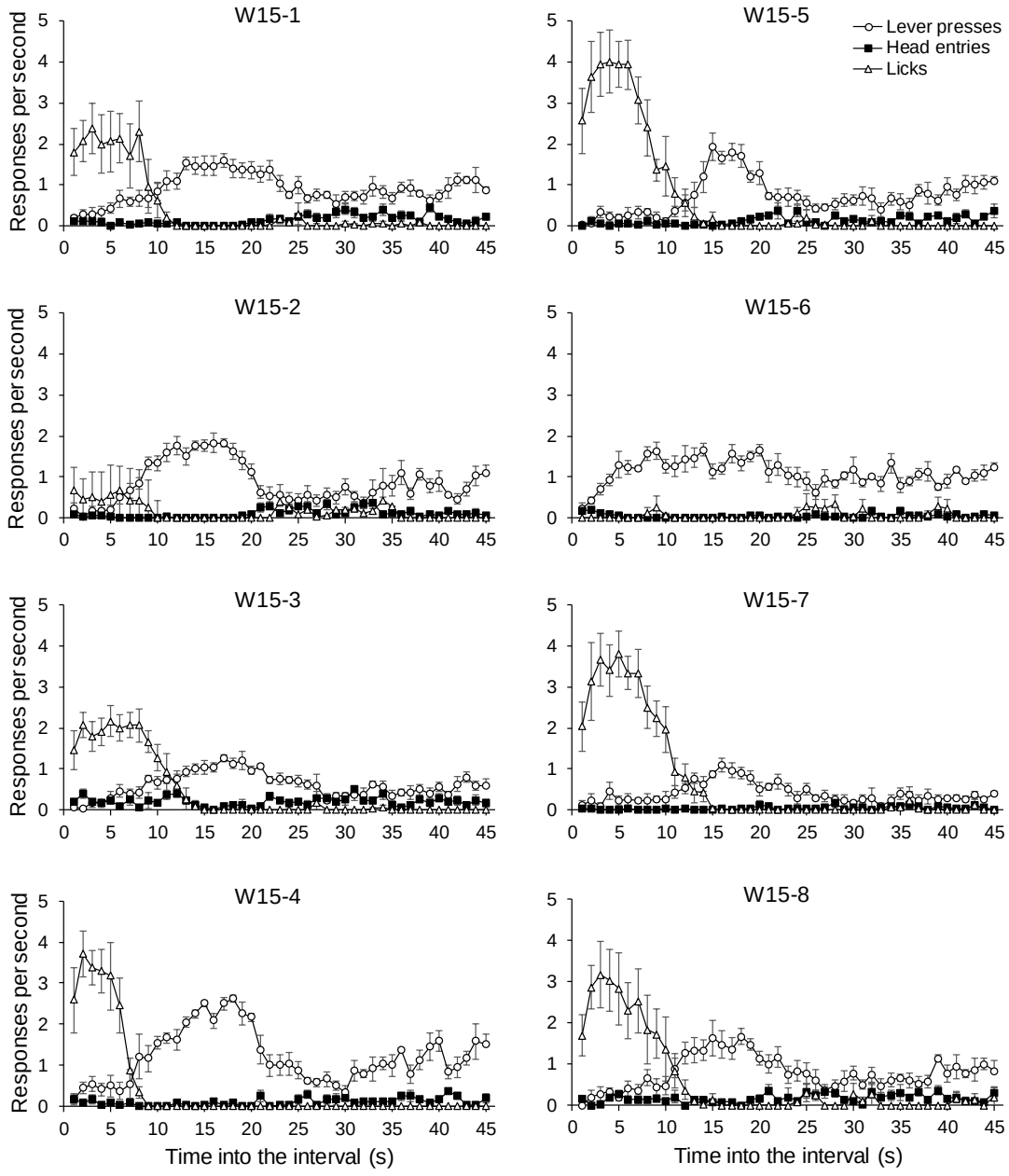

Figure 8. Distribution of responses during PI trials of each subject of the W15 group in the last five sessions of the peak phase. Vertical bars show S.E.M.

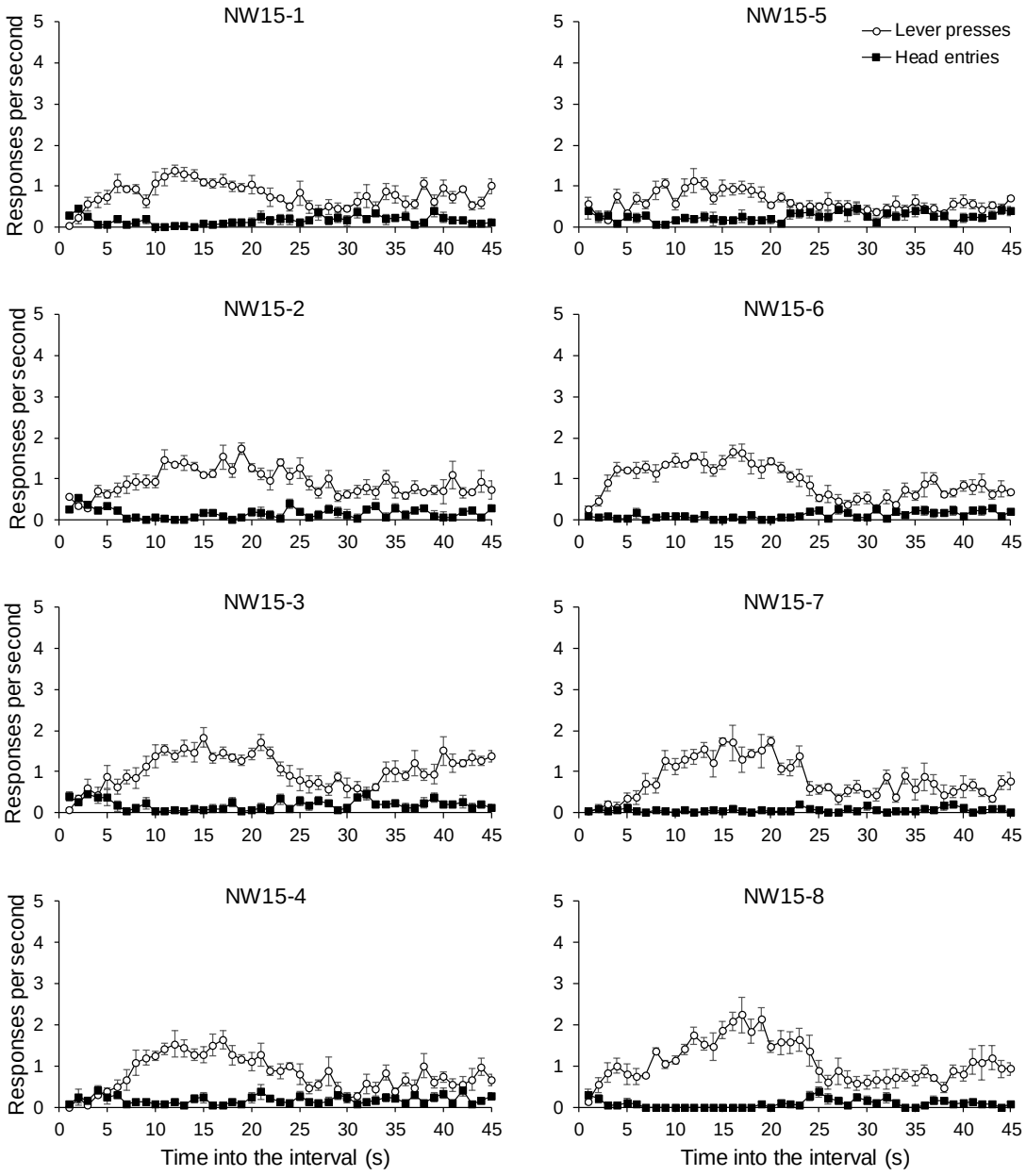

Figure 9. Distribution of responses during PI trials for each subject of the NW15 group in the last five sessions of the peak phase. Vertical bars show S.E.M.

Figure 8 depicts the distribution of responses of each subject in the W15 group. Distribution of lever presses is similar for all subjects, except W15-6 and W15-7. Lever presses started to increase around second 5, peaked at around second 15, decreased to low

rates between seconds 25-30, and started increasing again after second 30 until the end of the trial. W15-6 started lever pressing at a high level in second 3, showed a wide peak from second 5 to 20, slightly decreased at second 25 and stayed at high levels throughout the interval; whereas W15-7 showed a similar peak of lever presses than the other subjects, but display a smaller resurgence. Furthermore, W15-7 was the rat with more difference between the amount of lever pressing and the amount of licking. Interestingly, W15-6 is the subject with less licks in the group, but the one with more licking occurring after the first section of the trial (W15-2 also did some licks after the lever-pressing peak); all other subjects drank during the first 7-10 seconds and then started lever pressing. Head-entering rate is close to zero through most of the interval, although some bursts are observable after the peak of lever presses ends and until the end of the interval.

On the other hand, distribution of responses of subjects in the NW15 group are plotted in Figure 9. The shapes of the distributions seem to be more similar among subjects than for the W15 groups. Lever pressing started around second 5 and usually stayed at a steady level until second 25 (the same as in W15 group), but in a flatter way than the W15 subjects (Figure 8). The Gaussian shape is not as evident as for the W group, lever pressing stayed at a high rate between seconds 10 and 20, except for subjects NW15-1 and NW15-8 that showed a steeper peak. Individual distributions of the NW15 group are similar to the distribution of the W15-6 subject, the one with less licking (Figure 8). Some lever presses occurred after second 30, but only subjects NW15-1, NW15-3, NW15-6 and NW15-8 showed a clear resurgence of responses. The other subjects continued pressing the lever but did not show an increase towards the end of the interval. NW15 subjects did more bursts of head entries than the W15 group, especially subjects NW15-1, NW15-4 and NW15-5; for the latter, lever presses and head entries occurred at similar rates during the last 20 s of the PI trial.

Figure 10 depicts data of subjects in the W60 group. Five subjects showed a clear licking peak in the first 15-25 seconds (W60-1; W60-3; W60-4; W60-5; W60-6); W60-2 showed a small licking peak around second 20 and then bursts of licking after second 80 and throughout the rest of the interval that were intercalated with lever pressing; W60-7 displayed a few licks around second 20, but not enough to produce a clear peak; and W60-8 did some licks in the first 10 s of the interval, but with a lower rate than the other subjects. Lever-pressing peaks occurred between second 30 through 100 with a wider distribution than peaks of W15 subjects (Figure 8). Most subjects (except W60-1 and W60-5) continued lever pressing throughout the interval, but resurgence was not evident for any subject.

Distribution of behaviours of each subject of the NW60 group is displayed in Figure 11. Same as with the W60 group, peaks of lever pressing were flatter and wider than peaks of subjects in the NW15 group (Figure 9). Contrary to the W60 subjects, NW60-1 and NW60-2 showed a clear resurgence of lever presses towards the end of the interval and NW60-3 displayed a second peak between seconds 125 and 160. All other subjects continued to press the lever after second 100 but did not show a clear increase towards the end of the interval. On the last half of the interval subjects NW60-1, NW60-2, NW60-4 and NW60-7 showed bursts of head entries that were intercalated with bursts of lever presses.

Differences in individual data regarding resurgence of lever presses, amount of liking and the form of the peak are interesting because normally mean distributions are compared, but they do not necessarily represent all subjects. For example, the distribution of responses for group W15 (Figure 3, graph B) is only representative of subject W15-4 (Figure 8). On the other hand, distribution of responses of group NW15 (Figure 3, graph B) represents adequately data of NW15-4 and NW15-8, but NW15-3 and NW15-1 showed greater resurgence in lever pressing (Figure 9). Individual differences might be a more reliable source of analysis of the behavioural patterns that account for timing.

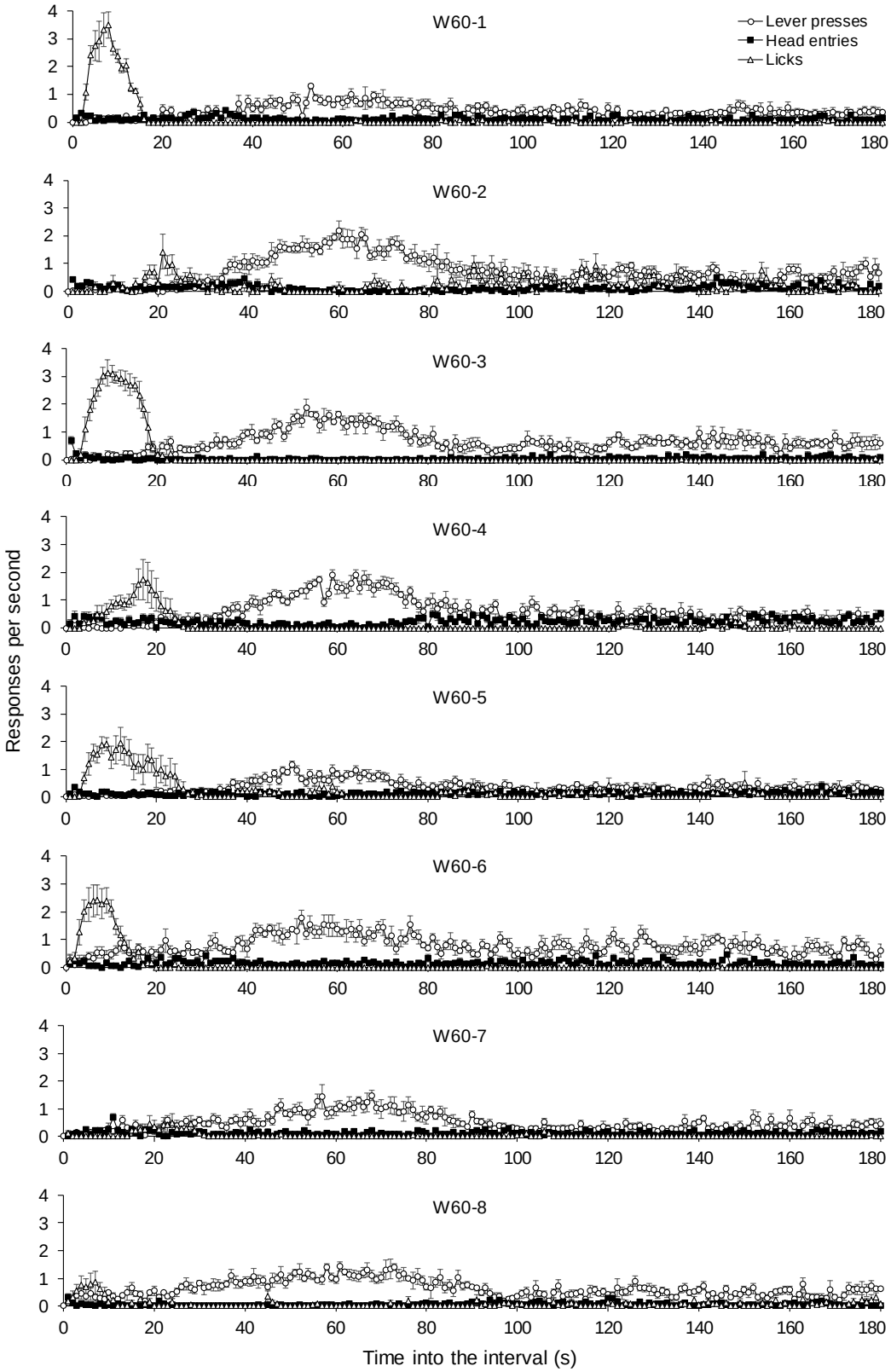

Figure 10. Distribution of responses during PI trials for each subject of the W60 group in the last five sessions of the peak phase. Vertical bars show S.E.M.

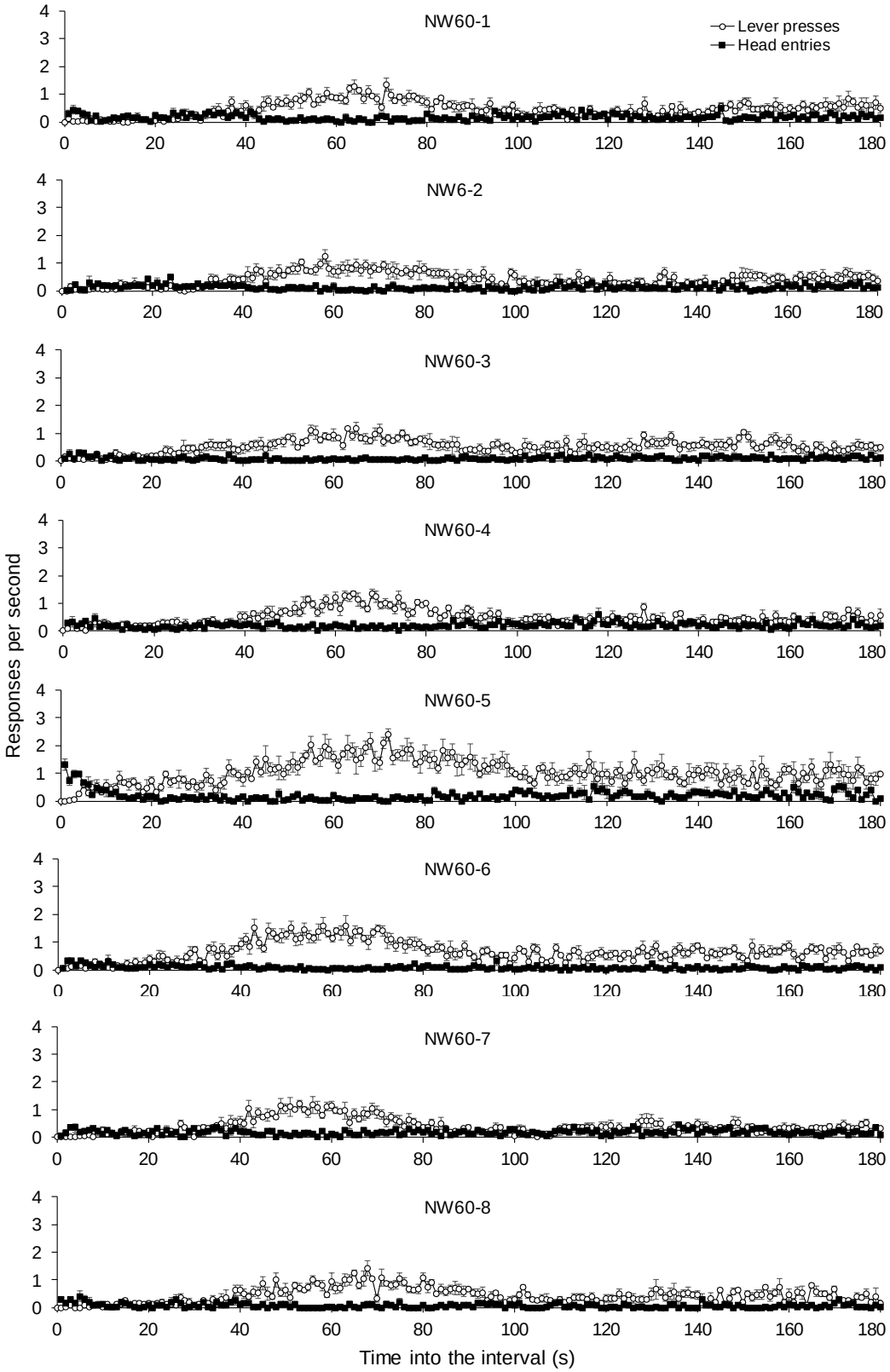

Figure 11. Distribution of responses during PI trials for each subject of the NW60 group in the last five sessions of the peak phase. Vertical bars show S.E.M.

To make a more detailed analysis of the distribution of behaviours, Figures 12 and 13 show the distribution in the six PI trials of the last session of the peak phase of one subject each. Figure 12 shows data of subjects W15-4 (upper panel) and NW15-3(lower panel). These subjects were chosen because they showed resurgence of lever pressing as seen in Figures 8 (W15-4) and 9 (NW15-3).

Distribution of responses of subject W15-4 (Figure 12, upper panel) was not identical in all 6 trials. Licking occurred at a high rate in the first five seconds of PI trials 1, 3, 4 and 5; there was a small amount of licking in PI 6; and no licking in PI 2. Analysis of the distribution of trials during this session revealed that PI trial 2 started immediately after PI trial 1, which could account for the lack of licking. All 6 PI trials have in common that lever pressing started at the same time, although it ended in three different ways: 1) the subject started lever pressing around second 6, stopped around second 19 and started pressing again after second 35 (PI trials 1, 4 and 6); 2) the subject started lever pressing around second 6 and continued throughout the trial (PI trials 2 and 5); 3) The subject started lever pressing at second 6, stopped around second 20, did one lever press at second 27 and did not press the lever again during the rest of the interval (PI trial 3). Head entries occurred in very isolated moments, mostly towards the end of the trial, most of them after second 35 (except for one in PI trial 5).

The lower panel of Figure 12 depicts the distribution of responses in each PI trial for subject NW15-3. Contrary to the subject in the group W15, distribution of responses for this subject are quite similar among trials: lever pressing occurred throughout each PI trial, the subject did between 2 to 4 lever presses per 1-s bin. Contrary to W15-4, NW15-3 alternated between doing head entries and lever presses during most of the PI trial.

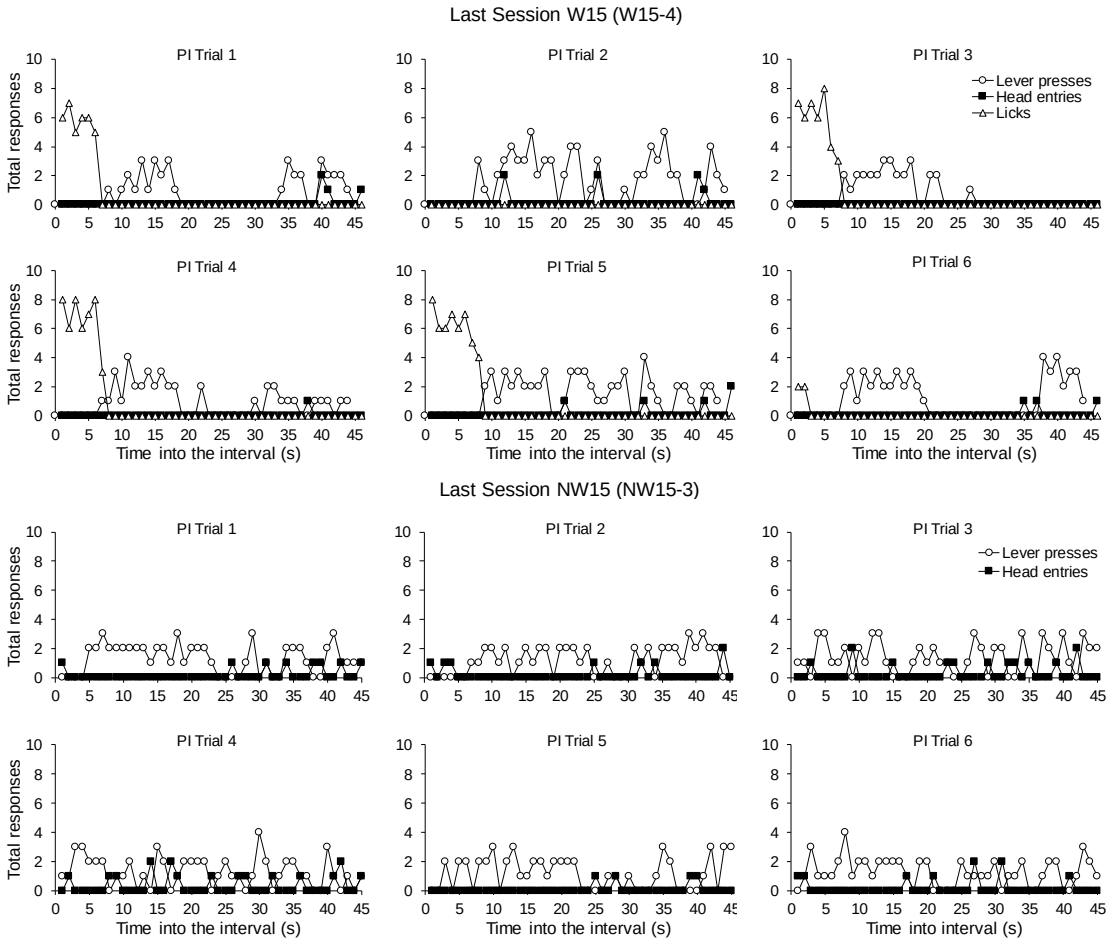

Figure 12. Distribution of behaviours in each peak trial of the last session of the experiment for W15-4 (upper panel) and NW15-3 (lower panel).

Distributions of responses of each PI trial of the last session of subjects W60-6 and NW60-3 are displayed in Figure 13. These subjects were chosen because they showed something closer to resurgence in lever pressing than other subjects in their groups. Data of W60-6 is plotted in the upper panel. Distributions of behaviours were different in each trial. Licking occurred only in PI trials 1 and 2, analysis of the session showed that PI trial 3 immediately followed PI trial 2; and that PI trial 5 immediately followed PI trial 4, that could account for the lack of licks in PI trials 3 and 5, but not for PI trials 4 and 6. Lever-pressing

rate distributed in two different patterns: 1) lever presses started after second 20, occurred mostly between seconds 40 and 80, and continued to appear in isolated bursts towards the end of the trial (peak trials 1, 2 and 5); 2) lever presses occurred in isolated bursts throughout the PI trial (PI trials 3, 4 and 6). Bursts of head entries occurred throughout the trials.

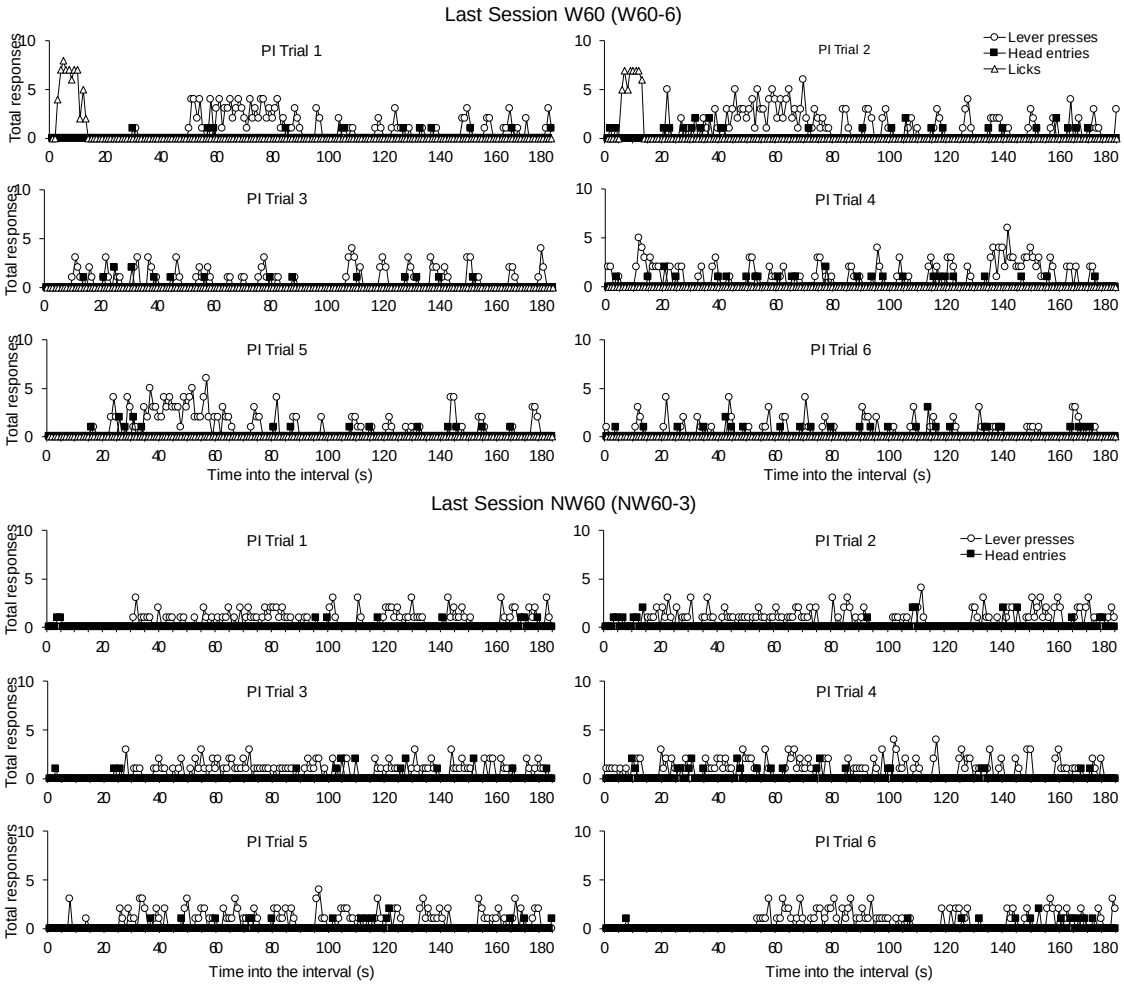

Figure 13. Distribution of behaviours in each PI trial of the last session of the experiment for W60-6 (upper panel) and NW60-3 (lower panel).

Distribution of behaviours of NW60-3 is depicted in the lower panel of Figure 13. Lever presses seem to fall into two patterns: 1) little or no lever presses at the beginning of the interval (PI trial 1, 3 and 6); or 2) lever presses occurred throughout the trial. Similar to

subject NW15-3 (Figure 12, lower panel) and W60-6, lever presses and head entries were intercalated throughout the trials.

Discussion

Results in Chapter 2 suggested that some behaviours are induced by the features present in a specific environment and that their temporal distribution is shaped by the delivery of reinforcement. If reinforcers are delivered periodically, a behavioural pattern will tend to occur in the inter-reinforcement interval in a semi-invariant way. Sometimes the development of those behavioural patterns leads to a better performance in timing tasks, so they have been regarded as the behavioural mechanisms that organisms use to estimate time (Killeen & Fetterman, 1988; Machado, 1997; Ruiz et al, 2016; Segal & Holloway, 1963). Nevertheless, what researchers interpret as "accurate timing", may not be timing *per se*, but the organization of available behaviours that may or may not lead to a better performance in temporal tasks.

The goal of this experiment was to further evaluate this hypothesis by observing the interaction of SID and lever pressing as part of a behavioural pattern developed under a FI schedule and evaluated during PI trials. The induction and reinforcement of behaviours and their subsequent organization into patterns depend on the features of the environment and the state of the organism (Killeen & Jacobs, 2016; Lucas et al., 1988). Therefore, individual differences are not only to be expected, but they need to be considered when drawing conclusions about processes like timing, which are said to be mediated by schedule-induced behaviours.

Distribution of responses in the FI trials was similar to what has been previously reported: licks occurred during the first few seconds of the trial and lever presses increased

after licking ended and were scallop-shaped (Killeen & Pellón, 2013). Also, these results replicated the distribution observed in Chapter 2.

Proportional distribution in this experiment also replicated what have been previously reported. Lever presses showed the scalar property and SID did not. Same as in Experiment 1 of Chapter 2, the development of SID had differential effects with rats exposed to a short or a long FI. Distribution of lever presses of the W15 group was more 'adequate' than performance of the NW15 group; whereas no differences were observable between the FI 60-s groups.

Furthermore, effects of developing SID were different for the FI 15-s groups and the FI 60-s groups in the PI trials. Some changes in the shape of the peak of lever presses were visible from the first to the last sessions, as in other studies (Kirkpatrick-Steger et al., 1996), the shape of the peak became steeper and resurgence appeared with training for groups exposed to the FI 15-s, whereas resurgence disappeared with training in the FI 60-s groups.

Quantitative analysis revealed that the peak occurred later for the NW15 compared to the W15 groups and earlier for the W60 compared the NW60 group, which is consistent with the hypothesis that rats start lever pressing after they finish drinking, which results in differential effects on timing measures depending on the value of the FI, as proposed in Chapter 2. The Weber fraction was higher for the NW15 group than for the other three groups, this suggests that timing accuracy during FI 15-s was equated to performance during FI 60-s when SID was available.

Individual graphs illustrated the differences in the distribution of responses among subjects. These differences support the argument that analysing the mean is not always enough because, although mean data showed differences among groups, it does not provide behavioural information about why these differences occurred, therefore, does not allow to draw truthful conclusions about timing processes (Balci et al., 2009; Cleaveland et al., 2003).

If plotting mean data disguise the real performance of organisms, it might be also disguising the mechanisms that are accounting for their performance.

Analysis of individual performance allowed to observe that rats with access to water displayed a more "organized" (separated in types of behaviour) pattern than those that did not developed SID, but only in the W15 group. There were no apparent relevant differences between W60 and NW60 groups. As mentioned before, reinforcers affect not only the target or last behaviour, but all the previous ones (Catania, 1971; Killeen, 1969; Killeen & Pellón, 2013). So, when water is available rats can engage in different behaviour and a more complex/longer pattern is developed (as occurred in the W15 group); but without access to water rats are only able to alternate between pressing the lever and entering the feeder, in such a way that the alternation pattern would be, most likely, reinforced. During longer intervals, like the FI 60-s and consequently the PI interval of 180 s, alternation is more likely to occur and therefore be reinforced. The decrease of resurgence with training in the FI 60-s groups may be evidence of this process.

Furthermore, distribution of responses during individual trials showed that resurgence can sometimes correspond to an increase in lever pressing after a pause, like Church et al. (1994) reported in the only individual trial that they displayed (see Figure 5 in their study), but that in most cases it is probably the result of averaging the alternation between lever pressing and head entering of many trials, sessions or subjects.

Individual data from each trial showed that distribution of responses during PIs was different when the trial was preceded by a FI than by a PI trial. Sanabria and Killeen (2006) reported that lever pressing following a PI trial started at a higher rate than following a FI, suggesting that those responses were the continuation of resurgence in the PI. Roberts (1981) also reported that the peak of responding decreased in trials preceded by the omission of food. It seems that rats will continue to engage in certain behaviours until they receive the

reinforcer, independently of some environmental changes, like the retraction of the lever. This supports the hypothesis that behavioural patterns (including schedule-induced and target behaviours) are induced by the delivery of the previous reinforcer, but maintained by the forthcoming one (Álvarez et al., 2016).

Similar performances can be observed in other temporal tasks such as bisection task and bi-peak procedure (Ruiz et al., 2016; Yin, Lusk & Meck, 2016): during those tasks rats are supposed to choose between two levers that give a reinforcer after a short or a long time. When exposed to those conditions, rats do not choose, but they start responding to the lever with the short time to reinforcement and if they do not receive the reinforcer then change to the lever that have given them reinforcement after longer periods. Those patterns occur even during test/probe non-reinforced trials. It is possible that during PI trials when rats do not receive the reinforcer, instead of "changing to another lever", they will continue to do the response that have been followed by a reinforcer in the past.

On the other hand, as mentioned above, there is evidence that supports the hypothesis that resurgence occurs in anticipation to the next reinforcer. Resurgence occur at higher rates with short ITI and with fixed rather than random lengths of PI (Church et al., 1991). Nevertheless, when a PI trial was preceded by another PI trial in this study, no licks occurred, and a less orderly behavioural pattern was observed. If resurgence occurred in anticipation of the next reinforcer, rats that had access to water would have shown a resurgence or second peak of licking before lever pressing again. These findings are consistent with the hypothesis that resurgence does not occur in *anticipation* of the next reinforcer, but as a result of *perseverance* to receive the "lost" reinforcer. Moreover, these results also support the hypothesis outlined in Chapter 2 that reinforcers not only mark the end of a trial, but with a short ITI like the one used in this study, they induce/trigger the beginning of the behavioural pattern.

An ‘ideal’ timing performance in a FI (and consequently in a PI) would consist in a single response just after the FI elapsed, but organisms do not usually do that. Mattel & Portugal (2007) regarded those ‘extra’ responses as the result of other ‘non-timing’ processes, such as impulsivity. They reported that rats that could engage in another behaviour while responding on a peak procedure improved their performance as much as rats whose ‘extra’ responses were punished also improved their performance. If the target (explicitly reinforced) behaviour competes with other available behaviours, they will tend to occur in lower rates (Pellón & Killeen, 2015); something similar happened with the FI 15-s groups. Since a 15-s interval is short, licks and lever presses competed (Pellón & Killeen, 2015), and the ‘timing’ performance was more accurate in the W15 group, or in other words, rats were *less impulsive* (Mattel & Portugal, 2007). Moreover, rats in the W60 group did not show a better ‘timing’ performance than the NW 60 rats, because a 60-s interval is a long enough interval for licks and lever presses to develop without overlapping in time; but this result could not be explained by impulsivity.

A more parsimonious explanation than ‘impulsivity’, and even than ‘timing’, that may account for the results in this study is that reinforcers affect all other behaviours that occur in proximity to their delivery (Killeen, 1969; Killeen & Pellón, 2013) and organize them into patterns by competition among them (Pellón & Killeen, 2015; Ruiz et al., 2016). Data presented in this chapter seem to be at least partially explained by the hypothesis that timing is not a different ‘process’ or ‘ability’, but it is the temporal organization of available behaviours, shaped, maintained and induced by periodic delivery of reinforcement.

CHAPTER 4

SCHEDULE-INDUCED BEHAVIOUR AND TEMPORAL DISCRIMINATION: ARE RATS TIMING OR JUST BEHAVING?

Abstract

The behavioural view of timing proposes that organisms develop sequential patterns of behaviours that serve as discriminative stimuli for temporal events. It was suggested in previous chapters that timing consists on the development of patterns of behaviours that are induced, shaped and triggered by the delivery of reinforcement. The aim of this chapter was to evaluate the role of schedule-induced behaviours in a temporal bisection task to assess their role in temporal estimation. In Experiment 1 rats divided in two groups (with and without access to water) were exposed to a discrimination task using 10 and 40-s stimuli, and then tested with stimuli of intermediate durations. Rats with access to water reached the criterion earlier, but there were no differences in timing parameters between groups. Subjects developed SID, but most of it occurred in the ITI. In Experiment 2 rats were exposed to the same procedure, using a shorter ITI. The results of Experiment 1 were replicated, except that SID occurred during the stimuli. Analysis of the temporal distribution of responses showed that rats would drink for 20 s (geometric mean), regardless of the duration of the stimulus. The distribution of head entries was different for both groups, rats with access to water started head entering after they finished drinking, whereas the distribution of rats without access to water resembled the distribution of SID. Lack of difference between groups suggest that rats developed behavioural patterns, whether those behaviours were measured or not, and that behaviours occurring during the inter-reinforcement intervals are the clock that allows organisms to behave in temporal tasks.

Schedule-Induced Behaviour and Temporal Discrimination: Are Rats Timing or Just Behaving?

Throughout their life, organisms have to adapt to temporal regularities of relevant events, so timing becomes an important aspect of their behaviour. The ability to predict a periodic unsignalled event and to discriminate between stimuli of different durations can represent an advantage compared to other individuals that lack those skills (Killeen et al., 1997).

Mechanisms that enable timing have been widely discussed, but two main views predominate: Scalar Expectancy Theory (SET; Church et al., 1994), on one side, offers a cognitive account of timing; whereas Behavioural Theory of Timing (BeT; Killeen & Fetterman, 1988) and Learning to Time (LeT; Machado, 1997), on the other side, provide a behavioural explanation for this process.

SET is a cognitive theory that hypothesises the existence of an internal clock that consists on a pacemaker and an accumulator of pulses; the memory stores values of pulses associated with different stimuli, and if a new stimulus is similar to one of the stored durations, the organism emits a behaviour, and if that behaviour is reinforced, the value in the accumulator is saved in the reference memory (Church, et al., 1994).

On the other hand, BeT proposes that organisms do sequential patterns of classes of schedule-induced behaviours during the inter-reinforcement intervals, and each class of behaviour serve as discriminative stimuli for the temporal moment in which it occurs (Killeen & Fetterman, 1988). Similarly, LeT proposes that timing implies the development of patterns of behavioural states that are activated in a sequential way, each state is coupled with the target response, and the degree of coupling increases with reinforcement and decreases with

extinction. The target response will follow the behavioural state that it has been stronger coupled to during a specific event (Machado, 1997; Machado & Keen, 1999).

The behavioural view of timing (BeT and LeT) is based on the findings that periodic delivery of reinforcement results in the development of behavioural patterns that are repeated during IRIs in a semi-invariant way (Staddon & Simmelhag, 1971). The development of patterns of schedule-induced behaviours depends on the environmental features, the history and state of the organism, the rate and type of reinforcement and the natural behavioural repertoire of the species (Killeen et al., 1997; Killeen & Jacobs, 2016; Staddon & Ayres, 1975; Staddon & Simmelhag, 1971). It was suggested in previous chapters that all behaviours (schedule-induced and target) are induced by the schedule of reinforcement, shaped into a steady behavioural pattern and triggered by the delivery of reinforcement; that process, observed under temporally-defined schedules, is what we call *timing* (Killeen, 1975; Timberlake & Lucas, 1985).

Although it is not assumed that the purpose of schedule-induced behaviours is to aid timing (Killeen et al., 1997), the sequential dependency in the behavioural patterns may turn into a discriminative property that determines the performance of organisms on temporal tasks (Laties et al., 1969).

The role of schedule-induced behaviours is often inferred (Machado, 1997) and not directly measured or evaluated (Lejeune et al., 1998), but the observational evidence for a behavioural mediation of timing is stronger than the assumption of cognitive mediation because the internal clock and its components, “have never been observed” (Fetterman, Killeen & Hall, 1998, p. 219).

There are many types of tasks that involve timing. López (2012) proposed that temporal learning (timing) can be divided in two kinds: temporal learning *per se*, which includes estimation and discrimination of temporal events, and a behavioural adaptation of

the organism to temporal regularities in the environment. Moreover, Richelle and Lejeune (1980) distinguished between procedures that assess temporal estimation and procedures that assess temporal regulation.

A greater part of the direct evaluation of the role of schedule-induced behaviours in timing has focused on the behavioural adaptation to temporal regularities. For example, Segal and Holloway (1963) reported that the development of schedule-induced drinking (SID), which is an excessive pattern of drinking that occurs during inter-reinforcement times (Falk, 1971; Killeen & Pellón, 2013), improves the performance of rats on a differential reinforcement of low rates (DRL) schedule. Also, Laties et al. (1969) observed that the amount of schedule-induced wood chewing correlated with the number of reinforcers rats obtained in a DRL schedule of food reinforcement. Furthermore, Bruner and Revusky (1961) reported that humans exposed to a DRL schedule developed behavioural patterns and that they repeated them because they thought the patterns were necessary to obtain reinforcers.

Lejeune et al. (1998) measured directly the development of behavioural patterns of mongolian gerbils in a procedure in which they had to stay in a platform for a specific time. They observed that subjects developed some consistent sequences, but that each behaviour in the sequence did not occur in the same number in each interval. However, the variability in the organization of behavioural patterns should not be taken as evidence against them acting as discriminative stimuli, in the same way as the different patterns of target responses are taken as evidence of learning in a FI (Baron & Leinenweber, 1994) and other procedures. Moreover, that variability could account for the error present in the performance on temporal tasks (Harper & Bizo, 2000).

Additionally, Mattel and Portugal (2007) compared the effect of having a penalty for responding early in a peak procedure with the possibility of engaging in a behaviour different

than the target one and found that both manipulations had the effect of sharpening the mean peak function.

In Chapter 2, the role of SID on the performance of rats in FI schedules was evaluated and results indicated that the development of SID improved performance in short intervals (FI 15-s and FI 30-s) but worsened it in longer intervals (FI 60-s). Similar effects were observed in the peak procedure in Chapter 3, the peak occurred later for rats that developed SID in a short FI schedule and earlier in a long FI schedule, compared to rats that did not develop SID. These effects seem to have a common mechanism: lever pressing (the target response) started when SID stopped, which was beneficial in short intervals, but counterproductive in long intervals.

Furthermore, the observation of individual performance in Chapter 2 showed that the complete behavioural pattern (licks, lever presses, head entries) only re-started in the trials that followed the delivery of reinforcement. Those findings support the hypothesis that behavioural patterns follow a sequential order that is induced by the delivery of reinforcement.

Given that the effect of schedule-induced behaviours in timing depends on the temporal task and the durations to be timed, their effect should also be evaluated in procedures that assess temporal estimation (Richelle & Lejeune, 1980) or temporal learning *per se* (López, 2012) to have a full understanding of their role.

The temporal bisection task allows to evaluate temporal learning *beyond* an adaptation of temporal regularities, as organisms have to discriminate between the duration of two stimuli, so they do not only have to *adapt their behaviour* to a temporal regularity, but they have *to act upon the environment* in a temporally specified way.

The temporal bisection task consists on a phase of temporal discrimination in which organisms are exposed to two durations of the same stimulus and have to respond to a lever

or key associated to each of them. A “long” response will be understood as a press/peck on the operandum associated to the long duration; and a “short” response as a press/peck on the operandum associated to the short duration. Once subjects learn to discriminate between the two durations they are exposed to intermediate durations of the stimulus that they have to classify as short or long by pressing one of the levers/keys (Church & Deluty, 1977). When the proportion of “long” responses in each duration is plotted, the result is an ogive-like function that starts close to 0 in the short duration and ends close to 1 in the long duration (Machado & Keen, 2003). The bisection point is the duration in which the proportion of “long” responses is exactly 0.5, and it usually corresponds to the geometric mean of the sample durations (Church & Deluty, 1977).

Following the behavioural perspective of timing, organisms would associate behavioural states with the two choice responses during the temporal discrimination phase, so that states occurring at the beginning of the behavioural pattern would be coupled with the short response, and states occurring towards the end of the pattern would be associated with the long response (Machado & Keen, 1999).

Machado and Keen (1999) observed the development and use of schedule-induced behaviours in the bisection task. They trained pigeons to respond to two pairs of discriminations in which the long stimulus of the first pair had the same duration as the short stimulus of the second pair. They observed that pigeons developed a pattern of responses that went as follow: subjects started pecking the stimulus key, and if the stimulus ended, pecked the shortest key; if it did not end, pigeons continued pecking towards the stimulus key until the stimulus that had the same duration in both pairs ended and press the corresponding key (they had different colours for each pair); if the stimulus did not end after that time, pigeons stopped pecking and did some idiosyncratic pattern of responses until the stimulus ended and then pecked the longest key.

In a similar way, Machado and Keen (2003) exposed pigeons to a temporal discrimination task in a long chamber (3-times the length of a regular conditioning chamber) in which the two response keys were on opposite sides. Pigeons developed the pattern of staying in the short side first and changing to the long side at the geometric mean of both durations. As the proportion of correct responses increased, the motion patterns became more differentiated and stereotyped.

Oliveira and Machado (2009) made both choice keys available during the sample stimuli of a procedure in which pigeons where trained to discriminate two pairs of durations. They found that pigeons would start pecking the short key until they received the reinforcer or the time for the shortest stimuli elapsed and then changed to the long key and started pressing it until the end of the long stimuli or the trial. Orduña, Hong and Bouzas (2007) exposed rats to a temporal bisection task with the levers being available during the stimuli and reported that rats pressed them, but they did not analyse the distribution of responses.

The topography of schedule-induced behaviours can be hard to predict and difficult to measure (Machado & Keen, 2003), but that does not mean they do not occur. Yin et al. (2017) stated that when rats are exposed to the temporal bisection task they usually paw or bite in the openings of the levers, starting in the short lever and changing to the long one at approximately the geometric mean of the stimuli. If rats are exposed to a procedure that would allow them to develop a well-studied schedule-induced behaviour, like SID (Falk, 1971; Killeen & Pellón, 2013), the mediation of these behaviours in temporal estimation might be more easily evaluated.

The temporal bisection task typically involves the discrimination of short durations ranging from 1 to 16 s (Church & Deluty, 1977; Galtress & Kirkpatrick, 2010; Machado & Keen, 1999; Orduña et al., 2007), but the occurrence of schedule-induced behaviours during short stimuli is limited, so longer stimuli should be used to properly evaluate them. There is

some evidence of temporal discrimination with long stimulus durations ranging from 10 to 100 s (Russel & Kirkpatrick, 2007), but they did not report the observation or measurement of schedule-induced behaviours.

The aim of this study was to evaluate the role of schedule-induced behaviours in a temporal bisection task to assess their role in temporal estimation. A procedure using 10- and 40-s stimuli will be used to allow for a more exhaustive observation that includes the development of schedule-induced drinking.

Experiment 1

Method

Subjects. Subjects were 12 experimentally naïve male Wistar rats that were 16 weeks old at the beginning of the experiment. Rats were maintained at 85% of their free-feeding weight by feeding them a controlled amount of food every day. They were housed in individual transparent Plexiglas cages measuring 18 x 32.5 x 20.5 cm. Home-cages were maintained in a room with environmentally-controlled conditions (22°C and 55% relative humidity) and with a 12-hour light-dark cycle (lights on at 8:00 a.m.). Rats had water always available in their home-cages. Animal care procedures were in accordance with the European Union Council Directive 2010/63, the Spanish Royal Decree 53/2013 and with the authorization of the Community of Madrid with reference PROEX 077/18.

Apparatus. Eight Letica LI-836 conditioning chambers measuring 29 x 24.5 x 35.5 cm were used. The front panel of each conditioning chamber was made of aluminum, the left wall of transparent Plexiglas and the reaming walls of black Plexiglas. The floor consisted on a 16-bar metal grid. The food tray was in the center of the front wall at a height of 3.7 cm above the floor, at each side of the food tray there was a retractile lever, and above each lever

a 3-W round lamp. Forty-five-mg food pellets were dispensed (Bio-Serv, Frenchtown, NJ, USA) into the food tray by a Letica Instruments dispenser. In the right wall, there was a 3.2 x 3.9 cm aperture in the wall, situated 20 cm from the front panel and 7 cm from the floor, through which subjects could reach the spout of a water bottle mounted on the exterior of the chamber. The water bottle could be removed if necessary. The spout was placed 2 cm towards the interior of the aperture and contact between the subject's tongue and the metal spout completed the electric circuit between the floor and the spout that allowed licks registration. Chambers were enclosed in a soundproofed housing and equipped with a ventilation system and a small observation window in the left panel. A fan located in the soundproofed housing produced an ambient noise of approximately 60 dB in each chamber to mask any exterior noise. The houselight consisted on an indirect 25-W light mounted in the soundproofed housing. Chambers were controlled using a MED-PC application under a Windows environment.

Procedure. Rats were divided into two groups: W rats, that had access to water in the experimental chamber and NW rats, that did not have access to water in the experimental chamber. This experiment had three phases: pre-training, training and test. Pretraining included two conditions: autoshaping and lever-alternating.

Pretraining.

Autoshaping. At the start of the session the houselight went on and both levers were inserted into the chamber. Rats were exposed to an autoshaping-like procedure that consisted on a concurrent variable time (VT) 30-s and fixed-ratio (FR) 1 schedule. On average, every 30 s a food pellet was delivered independently of the rat's behaviour. Also, rats received one food pellet after pressing either lever. Each session lasted 40 trials or 30 minutes. Subjects remained in this condition until they pressed either lever 40 times (earned 40 pellets) in less than 30 minutes for four consecutive sessions.

Lever-alternating. At the beginning of each session the houselight went on and the two levers were inserted into the chambers. During this condition rats had to alternate between levers to earn food pellets, they earned a pellet every time they changed from one lever to the other. The same as in the previous condition, sessions lasted 40 trials or 30 minutes and rats stayed in this condition until they earned 40 pellets in less than 30 minutes for four consecutive sessions.

***Training*.** After pre-training rats were exposed to a training phase, during which they had to discriminate between a 10 and a 40 s stimulus. At the beginning of each trial the houselight went on and after 10 (short stimulus) or 40 seconds (long stimulus) the houselight went off, the levers were inserted into the chamber, and the lights above them went on. Each lever was associated with one stimulus duration, if the rat pressed the correct lever, a food pellet was delivered, both levers were retracted and the inter-trial interval (ITI) began. If the rats pressed the wrong lever both levers were retracted and the ITI began. ITI lasted 25 s. Each session consisted on 40 trials, 20 with each stimulus duration. Trials were randomly alternated. Rats remained in this phase until they made 80% of correct responses in three consecutive sessions. Correction trials were implemented from session 30 onwards for rats that had not made 80% of correct responses in at least one session. Correction trials consisted on repeating the same trial until the rat pressed the correct lever. Assignment of the lever to each stimulus duration was counterbalanced among subjects but remained the same throughout the experiment for each subject.

Test. During test phase rats had to discriminate between training stimuli (10 and 40 s) and probe stimuli were also presented. Trials occurred in the same way as during training phase. Each session consisted on 30 training trials (10 or 40 s) and 10 probe trials that were randomly alternated. Probe stimuli were 15, 20, 25, 30 or 35 s (2 trials of every duration per session). During probe trails one probe stimulus was presented, after the stimuli went off the

rat had to press one lever and the ITI started. There was no reinforcement during probe trials. Rats stayed in this phase until they achieved 10 sessions with at least 80% of correct responses in training trials; if they had less than 80%, then they went back to training phase until they reached the three sessions criterion (re-training), and then back to test. ITI was 25 s. Subjects that received correction trials during training also received them during re-training, but not during test sessions.

Data analysis. Licks and lever presses were recorded and analysed. Data of acquisition was analysed by calculating the number of sessions required to complete training and test phases. Training phase included all the sessions until each subject reached the criterion for the first time, while test phase included all the test and re-training sessions.

Data of the bisection task during test phase was analysed using the proportion of responses to the lever associated with the long stimulus during training ('Long responses'). The proportion of Long responses was calculated by dividing the number of presses to the lever associated with the long stimulus during training by the total number of presses to both levers in each stimulus.

The logistic function proposed by Orduña et al. (2007) was fitted to the data of each subject:

$$\frac{1}{1+\left(\frac{t}{T_{50}}\right)^{\varepsilon}},$$

where T_{50} is the bisection point and ε is the slope of the function. The best fitting parameters were obtained by the least squares method using Microsoft Excel solver. The limen is the difference of the stimulus duration when the proportion of Long responses was .25 and .75. The Weber fraction was calculated using the parameters of this function, dividing the limen by the bisection point. The goodness of fit was calculated using the coefficient of determination (R^2). The parameters of the function were analysed using a one-way analysis of

variance (ANOVA) that compared the means of the two levels (W/NW) of the factor group. The significance level was established at a minimum $p<.05$.

Results

The aim of this experiment was to evaluate the role of SID in a temporal bisection task in which rats had to discriminate between a 10- and a 40-s stimulus during training, and then responded to stimuli of different durations during probe trials.

Table 1 shows the number of sessions that each subject needed to complete the training and test phases and the mean (± S.E.M) for each group. W rats required 27.2 sessions to complete training and NW rats required 33.8 sessions, besides, three subjects from the NW group received correction trials (marked with * in Table 1), whereas only one subject from the W group received correction trials. W rats also required less sessions to complete test phase than NW rats, but differences were not significant in any phase [training: $F_{(1,11)}=1.313$, $p=.27$, ns; test: $F_{(1,11)}=2.932$, $p=.12$,ns].

Table 1.

Number of sessions required to complete training and test phases.

W			NW		
Subject	Training	Test	Subject	Training	Test
1	21	10	1	32	21
2	29	15	2	19	10
3	19	10	3	24	18
4	26	14	4	53*	10
5	41*	18	5	38*	24
6	27	10	6	37*	29
Mean	27.2 ± 3.2	12.8 ± 1.4	Mean	33.8 ± 4.9	18.7 ± 3.1

Note. * Indicates that subject received correction trials. Mean ± S.E.M

The logistic function was fitted to the data of each subject individually. Figure 1 shows the mean proportion of Long responses as a function of stimulus duration and the

mean of individually fitted curves for both groups. There were no differences between groups, as both functions overlap. The goodness of fit (R^2, in Table 2) did not differ between groups [$F_{(1,11)}$=.236, p=.64, ns].

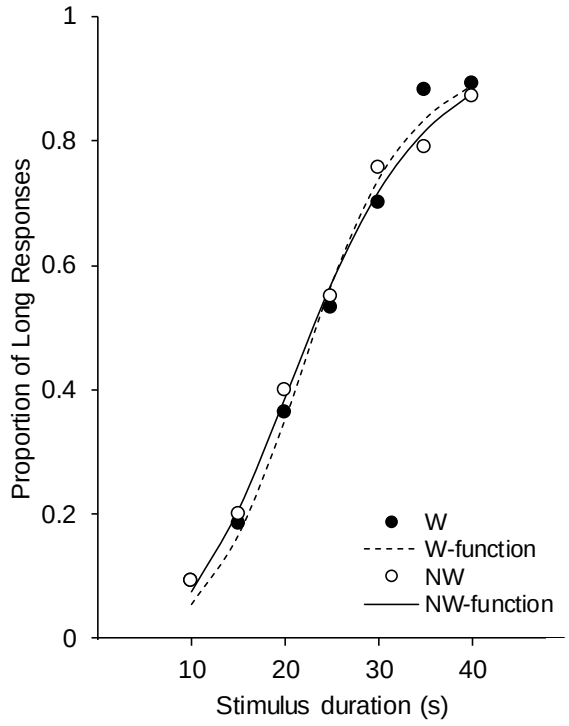

Figure 1. Mean proportion of Long responses in each stimulus duration and mean individual fitted curves of the logistic function.

The individual parameters of the logistic function are depicted in Table 2. The bisection point was 23.17 s for the W group and 22.55 s for the NW group, but differences were not significant [$F_{(1,11)}$=.166, p=.69, ns]; both values are closer to the arithmetic mean of training stimuli (25) than to the geometric mean (20). Limen was 7.11s and 7.4 s for groups W and NW respectively, differences were also not significant [$F_{(1,11)}$=0.21, p=.89, ns]. The Weber fraction was 0.31 for W group and 0.34 for the NW group [$F_{(1,11)}$=.139, p=.72, ns]. Nevertheless, it should be noted that the subject with higher drinking rate (W2) had the

smaller limen and Weber fraction. Statistical analysis confirmed there were no differences between groups during test phase.

Table 2.

Parameters of the logistic function fitted to individual data.

	Bisection point	Limen	Weber fraction	R^2
W				
1	19.21	6.64	0.35	0.96
2	24.67	3.84	0.16	0.98
3	21.74	5.09	0.23	0.97
4	25.83	5.65	0.22	0.96
5	22.78	7.28	0.32	0.95
6	24.80	14.19	0.57	0.72
Mean	23.17 ± 0.99	7.11 ± 1.50	0.31 ± 0.06	0.92 ± 0.04
NW				
1	20.41	8.56	0.42	0.93
2	25.73	6.51	0.25	0.92
3	21.81	6.09	0.28	0.96
4	20.28	7.86	0.39	0.83
5	26.52	5.89	0.22	0.99
6	20.55	9.18	0.45	0.75
Mean	22.55 ± 1.16	7.4 ± 0.56	0.34 ± 0.03	0.90 ± 0.03

Note. Mean ± S.E.M. R^2 is the coefficient of determination.

All subjects developed SID, but there was a lot of variability in the rate of drinking among subjects, ranging from 59.96 licks/min (W2) to 1.25 licks/min (W3). The mean licking rate was 16.18 licks/min in the last 3 sessions of training (criterion sessions) of each rat. Nevertheless, more than 90% of drinking occurred during the ITI, as presented in Table 3.

Due to an error in the programming of the task, the number of licks during tests phase was only recorded for 2 subjects: W2 and W5. Licking rate of W2 was 38.39 licks/min and 99% of the licks occurred during the ITI; whereas W5 drank at a rate of 10.79 licks/min and 75.70% of licks occurred during the ITI. Both subjects decreased their licking rate compared to training phase.

Table 3.

Licking rate and percentage of licks during ITI in training phase.

Subject	Licking rate	% licks during ITI
W1	5.73 ± 1.60	98.31 ± 0.95
W2	59.96 ± 2.47	99.98 ± 0.02
W3	1.25 ± 0.98	100
W4	7.57 ± 1.60	83.55 ± 4.11
W5	17.24 ± 1.65	84.33 ± 3.30
W6	5.33 ± 0.83	86.14 ± 4.72
Mean	16.18 ± 0.24	92.05 ± 0.86

Note. Mean ± S.E.M.

Discussion

The aim of this experiment was to observe the role of schedule-induced behaviour in a task that involves temporal estimation. Rats were exposed to a temporal bisection task with sample stimuli of 10 and 40 s, one group had access to water in the experimental chamber, and therefore could develop SID, and the other group did not have access to water. Nonetheless, the length of the ITI precluded the occurrence of SID during the stimuli.

The temporal bisection task usually involves stimuli ranging between 1 and 16 s and can take more than 20 sessions with correction trials for all subjects to learn it (Galtress & Kirkpatrick, 2010; Orduña et al., 2007). Despite using longer stimuli and the lack of correction trials since the beginning of the experiment, subjects in this experiment learned the

procedure relatively fast. Russel and Kirkpatrick (2007) trained rats in a discrimination task of 20 *vs*. 40 s which took at least 40 sessions of 60 trials (2340 trials), plus correction trials; whereas in this experiment rats required a mean of 27.2 (1080 trials) for W rats and 33.8 (1320 trials) for NW rats to learn the discrimination between 10 and 40 s. Additionally, only 4 of 12 subjects needed correction trials.

Even though SID did not occur during the stimuli, the group that had access to water required less sessions lo learn the discrimination. It is possible that although SID occurred during the ITI, it was part of a behavioural pattern that started after the delivery of the previous reinforcer and continued until the end of the stimuli, at least for some subjects. A similar effect was observed in Chapter 3 during the peak procedure: for rats that developed SID, lever presses peaked at the FI value and then stopped; whereas for rats that did not develop SID, after the peak of lever presses rats continued to alternate between pressing the lever and entering the feeder throughout the trial. A more sequentially-organized pattern could favour the learning of the discrimination in this experiment. Furthermore, there is some evidence that rats do not always follow signals like the retraction of the lever, but their behavioural patterns are induced by the previous reinforcer and continue until the delivery of the following reinforcer (Sanabria & Killeen, 2006).

There were no differences in the logistic functions and the measures derived from it (bisection point and difference limen) between groups, which makes sense because all subjects probably developed similar behavioural patterns that determined their choices, like it has been reported in other studies (Machado & Keen, 1999; Yin et al., 2017). The Weber fraction was higher than has been previously reported with shorter stimuli (Galtress & Kirkpatrick, 2010; Orduña et al., 2007). The bisection point was a bit closer to the arithmetic mean than to the geometric mean, which could be due to a lack of training.

This experiment does not allow to draw conclusions about the development and discriminative use of schedule-induced behaviours in the bisection task, because as in other studies they can only be assumed. In order to evaluate the role of SID, we should have greater amounts of drinking during the stimuli, so a shorter ITI to favour the occurrence of SID will be used in Experiment 2.

Experiment 2

Method

Subjects. The same rats from Experiment 1 served as subjects in this experiment and they were housed and maintained under the same conditions. Animal care procedures were in accordance with the European Union Council Directive 2010/63, the Spanish Royal Decree 53/2013 and with the authorization of the Community of Madrid with reference PROEX 077/18.

Apparatus. The same conditioning chambers as in Experiment 1.

Procedure. During this experiment rats were exposed to two phases: training and test. Sessions occurred in the same way as in Experiment 1, except that the ITI lasted 3 s, instead of 25 and test phase lasted for 20 sessions, instead of 10. Subjects that received correction trials in Experiment 1 also received them during training and re-training sessions in this experiment.

Analysis of data. Licks, head entries and lever presses were recorded and analysed. Analysis of the number of sessions was the same as in Experiment 1.

Only data from the last 10 sessions of test phase were analysed. The proportion of Long responses was calculated in the same way as Experiment 1 and the logistic function by Orduña et al. (2007) was also fitted to individual data. The best fitting parameters were

obtained using Microsoft Excel solver. The goodness of fit of the logistic was calculated using the coefficient of determination (R^2). The parameters of the functions were analysed using a one-way analysis of variance (ANOVA) that compared the means of the two levels (W/NW) of the group factor. The significance level was established at a minimum $p<.05$.

Additionally, distribution of licks and head entries were drawn by calculating the responding rate (licks or head entries per minute) in each 1-s bin of the presentation of the stimuli. The number of bins in each stimulus depended on its duration. Also, the normalized mean distributions were calculated by averaging the response rate in each 1-s bin across stimuli and dividing it by the maximum response rate from that type of behaviour (licks or head entries) for each subject.

Results

The aim of this experiment was to replicate Experiment 1 but providing better conditions for subjects to engage in SID during the presentation of the stimuli. Subjects already had learned to discriminate between stimuli, so the minimum number of sessions during training was 3 (sessions needed to achieve the criterion). As in Experiment 1, W rats needed fewer session to complete training and test phases, but differences were not significant in any phase [training: $F_{(1,11)}=.268$, $p=.62$, ns; test: $F_{(1,11)}=1.179$, $p=.30$,ns]. Table 4 shows the number of sessions each subject needed to complete each phase.

The logistic function was fitted to individual data of the last 10 sessions of test phase. Figure 2 depicts the mean proportion of Long responses and the mean individual best-fitted curves. Same as in Experiment 1, there were no differences between groups. Goodness of fit did not differ between groups [$F_{(1,11)}=.024$, $p=.88$, ns].

Table 4.

Number of sessions required to complete training and test phases.

W			NW		
Subject	Training	Test	Subject	Training	Test
1	3	20	1	3	51
2	8	25	2	10	20
3	8	41	3	4	28
4	4	20	4	20*	36
5	12*	30	5	5*	28
6	8	31	6	10*	40
Mean	7.16 ± 1.33	27.8 ± 3.26	Mean	8.67 ± 2.58	33.8 ± 4.46

Note. * Indicate that subject received correction trials. Mean ± S.E.M.

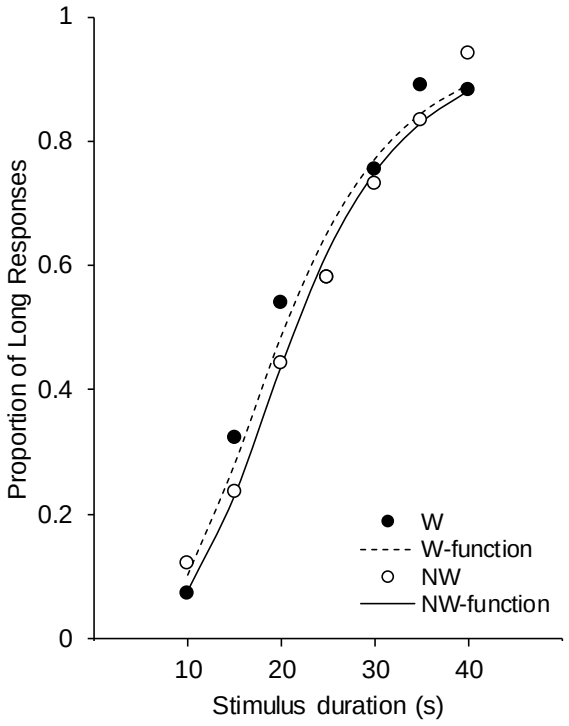

Figure 2. Mean proportion of Long responses in each stimulus duration and mean best-fitted curves of the individual logistic function. Data of the last 10 sessions of test phase.

The parameters of the logistic functions are shown in Table 5. There were no significant differences between groups: bisection point, $F_{(1,11)}$=.615, p=.45, ns; limen $F_{(1,11)}$=.044, p=.84, ns; and Weber fraction $F_{(1,11)}$=.015, p=.91, ns.

Table 5.

Parameters of the logistic function fitted to the data of the last 10 sessions of test phase.

	Bisection point	Limen	Weber fraction	R^2
W				
1	17.84	4.35	0.24	0.99
2	25.71	6.00	0.23	0.89
3	22.63	10.94	0.49	0.85
4	17.80	6.10	0.34	0.97
5	21.11	9.17	0.44	0.94
6	18.13	6.88	0.38	0.93
Mean	20.54 ± 1.31	7.24 ± 0.98	0.35 ± 0.04	0.98 ± 0.02
NW				
1	24.14	8.02	0.33	0.93
2	20.68	4.65	0.23	0.99
3	22.32	10.04	0.45	0.82
4	21.01	8.95	0.43	0.90
5	20.56	6.68	0.33	0.97
6	21.24	6.68	0.31	0.93
Mean	21.66 ± 0.56	7.50 ± 0.78	0.35 ± 0.03	0.99 ± 0.02

Note. Mean ± S.E.M. R^2 is the coefficient of determination.

The ITI was shortened so that SID occurred during the stimuli and not during the ITI. As seen in Table 6, licking rate increased for all subjects compared to Experiment 1 (Table 3), specially during test phase, except for subject W6. Licking rate during training was 32.03

licks/min and 43.35 licks/min during test phase. The percentage of licking during the ITI was 0.73% during training and 2.02% during test phase.

Table 6.

Licking rate and percentage of licks during ITI in training and test phases.

Training phase		
Subject	Licking rate	% licks during ITI
W1	62.60 ± 9.69	0.43 ± 0.05
W2	79.79 ± 3.66	3.85 ± 0.08
W3	3.67 ± 3.40	0
W4	3.05 ± 2.18	0
W5	42.74 ± 0.48	0.12 ± 0.07
W6	0.33 ± 0.09	0
Mean	32.03 ± 1.42	0.73 ± 0.02
Test phase		
Subject	Licking rate	% licks during ITI
W1	54.38 ± 2.96	0.63 ± 0.16
W2	46.37 ± 2.43	5.25 ± 0.50
W3	49.49 ± 7.93	1.29 ± 0.40
W4	35.43 ± 5.52	0.55 ± 0.16
W5	72.82 ± 2.67	0.37 ± 0.06
W6	1.63 ± 0.47	4.03 ± 2.11
Mean	43.35 ± 1.08	2.02 ± 0.32

Note. Mean ± S.E.M.

Figure 3 shows the distribution of licks during training stimuli (graph A) and training and probe stimuli (graph B) of the last 10 sessions of test phase. Licking occurred for the first 20 s, regardless of the duration of the stimulus. Drinking peaked at second 5 and then abruptly stopped after 10 or 15 s during the shorter stimuli but reached to 0 licks/min at second 20 during longer stimuli.

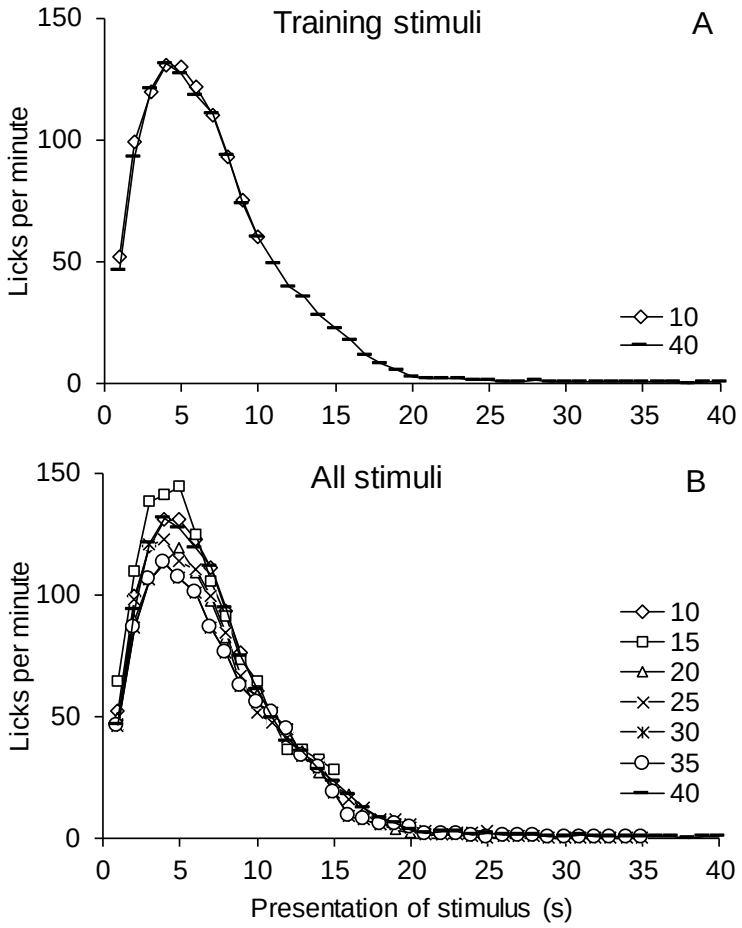

Figure 3. Distribution of licks during the last 10 sessions of test phase. A: distribution of licks during training stimuli. B: distribution of licks during all stimuli. Note that data points represent the licking rate in each 1-s bin, so the number of data points is different for each stimulus duration.

The form of the distribution of head entries was different for W and NW groups (Figure 4). Head entries of W rats increased until second 5, remained at a low rate until second 15 and increased after second 20 for W rats (graph A); whereas the distribution of head entries of NW rats resembled the distribution of licks of W group (Figure 3), they increased during the first few seconds, peaked between seconds 5 and 10 and decreased after second 10 and until the end of the stimulus, but did not stop completely (graph B).

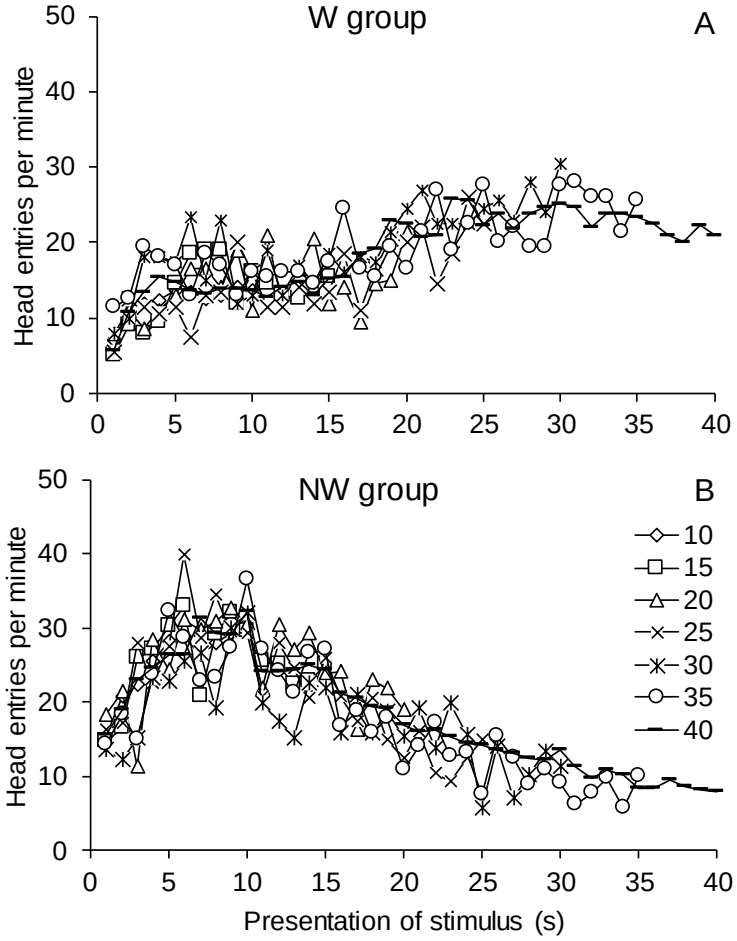

Figure 4. Distribution of head entries during the last 10 sessions of test phase. A: distribution of head entries during training stimuli. B: distribution of licks during all stimuli. Note that data points represent the head-entering rate in each 1-s bin, so the number of data points is different for each stimulus duration.

Licks and head entries occur at very different rates because of the way they are measured in the conditioning chamber, so to observe the interaction between them, the distributions of their normalized rates during all stimuli for W rats are depicted in Figure 5. Licks reached their maximum level at second 5, and then decreased to 0 licks/min at second 20, whereas head entries had a small peak at second 10 (short

training stimulus) and then increased after second 20, the geometric mean of both training stimuli (10 and 40 s).

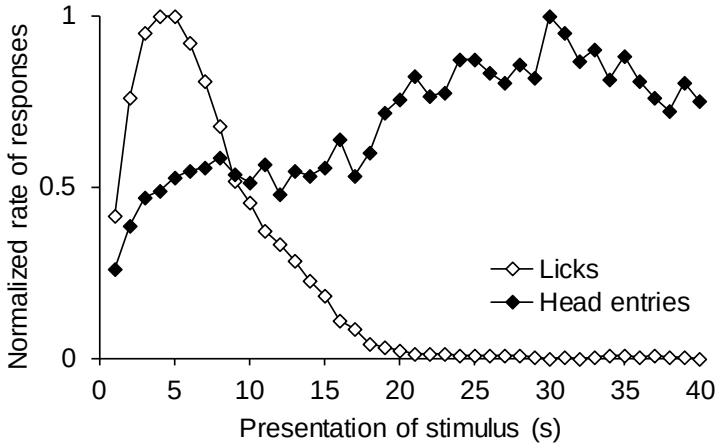

Figure 5. Normalized response rate of licks and head entries during all trials of the last 10 sessions of test phase for W rats.

Discussion

The aim of this experiment was to replicate the procedure of Experiment 1 but favouring the occurrence of SID during the stimuli (not during the ITI) by decreasing the length of the ITI, in order to evaluate its role in temporal estimation. This manipulation was successful because over 90% of licks occurred during the stimuli.

Similar to Experiment 1, the logistic function and its derivates (bisection point, difference limen, Weber fraction) were very similar between groups. Moreover, the bisection point became closer to the geometric mean than in Experiment 1, especially for the W group, probably because of the longer training.

The analysis of the distribution of responses showed that rats developed a sequential behavioural pattern. Rats in the W groups started licking when the trial started and stopped after the time for the short trial elapsed. Licking sopped at 20 s, the geometric mean, which is similar to previous findings with pigeons (Machado & Keen, 1999; Machado & Keen, 2003).

Although some head entries occurred during the first 20 s, they increased after second 20, when rats stopped drinking. It is possible that if two behaviours are associated with a stimulus, subjects alternate between them in different trials (Fetterman et al., 1998), so the increase of head entries in the first 20 s may be due to subjects using the pattern that they learned in Experiment 1, when they did not drink during the stimuli, in some trials.

The occurrence of SID can also account for the bisection point being closer to the geometric mean (20 s) than in Experiment 1, specially for the W group. There is some evidence that the precision in temporal tasks increase with a more sequentially-organized patterns (Oliveira & Machado, 2009), as was also observed in Chapter 3.

On the other hand, rats from the NW group showed a pattern in which head entries peaked between second 5 and 10 and then started decreasing, which is probably the same pattern they developed in Experiment 1. The decrease is probably due to rats engaging in other not-measured behaviours, similar to the experiment by Machado & Keen (1999) in which pigeons pecked the key until the short duration ended or the appropriate time elapsed and afterwards they engaged in idiosyncratic behavioural patterns until the end of the long stimulus.

Furthermore, the increase of head entries when licks decreased replicates the findings of other studies and Chapters 2 and 3, that reported the development of sequential behavioural patterns (Reid et al., 1993; Staddon & Ayres, 1975); although not every trial is the same and the pattern is not exactly the same for all rats (Killeen & Fetterman, 1993).

Taking all of this into account, it makes sense that there are no differences between groups, because all subjects developed behavioural patterns, nevertheless, the development of SID and its combination with head entries allowed to have a more direct measure of how schedule-induced behaviours serve as discriminative stimuli.

General Discussion

From the behavioural point of view, timing is understood as the adaptation of sequential patterns of behaviours that serve as discriminative stimuli of temporally-specified events (Fetterman et al., 1998; Laties et al., 1969). BeT (Killeen & Fetterman, 1988) and LeT (Machado, 1997) theories have provided mathematical support for this hypothesis in a wide variety of procedures, but most of the time they only infer or partially observe the behavioural patterns, rather than directly measure them (Fetterman et al., 1998; Lejeune et al., 1998; Machado, 1997).

Such behavioural patterns are comprised of schedule-induced and target behaviours that are shaped into a particular sequence by the reinforcement schedule and repeated during the inter-reinforcement times in a semi-invariant way (Staddon & Ayres, 1975; Staddon & Simmelhag, 1971; Timberlake & Lucas, 1985).

Some studies have observed the effect of schedule-induced behaviours in timing tasks directly and found that the patterns of behaviour depend on the temporal characteristics of the schedule of reinforcement, but do not necessarily improve the performance on those tasks (Laties et al., 1969; Lejeune et al., 1998; Segal & Holloway, 1963).

Nevertheless, research on this topic has been carried out mostly on tasks involving a temporal adaptation or regulation of behaviour, not on tasks involving time estimation in which organisms have to act upon the environment in a temporally specified way (López, 2012; Richelle & Lejeune, 1980).

The temporal bisection task used in this study allowed to evaluate the role of schedule-induced behaviours in a time estimation task. Even though there were no differences in the timing measures (logistic function and its derivates), the distribution and interaction of licks and head entries in the W group provided evidence of the kind of

sequential behavioural patterns developed during this procedure. This evidence is similar to what has been observed with pigeons (Machado & Keen, 1999; 2003; Oliveira & Machado, 2009).

Furthermore, the lack of differences between groups suggest that the behavioural patterns occur, whether we are measuring them directly or not, and that differences between subjects do not imply differences in timing ability, just differences in the organization of behaviours, as proposed in Chapter 2. Organisms are always behaving, and their behaviours determine their performance in different tasks (Cleaveland et al., 2003; Killeen, 2017).

The behavioural patterns observed in this study were similar to the ones observed under similar conditions in FI and peak procedure in previous chapters. Both FI and the peak procedure are considered tasks that involve temporal adaptation and not time estimation as the bisection task; however, the similarities between them suggest that all timing tasks should be considered of the same kind (Machado & Keen, 2003).

These results go against the idea that schedule-induced behaviours are of a different class of behaviours than operants (as proposed by Killeen & Pellón, 2013), rather they support the hypothesis that behavioural patterns are induced, shaped and reinforced by the delivery of reinforcement.

In conclusion, this study allowed to measure behaviours that are usually only inferred, and thus further support the hypothesis that behaviours occurring during the inter-reinforcement intervals are not a representation of time, but the clock itself (Machado & Keen, 1999). Perhaps talking about organisms ‘using’ their behaviour to estimate time is, to a certain level, comparable to talking about accumulators and internal clocks. Organisms do not *use* their behaviours to time, but the environment shapes their behaviour into a relatively convenient form by reinforcing behaviours that correlate with the reinforcer and

extinguishing non-related or counterproductive behaviours (Killeen & Fetterman, 1993; Machado, 1997; Reid et al., 1993). Timing is, therefore, a side-effect of behaving.

CHAPTER 5

SCHEDULE-INDUCED BEHAVIOUR AND ITS IMPACT ON TIMING IN THE BI-PEAK PROCEDURE

Abstract

The impact of schedule induced behaviour on timing was evaluated in the fixed interval, peak procedure and bisections task in previous chapters. The bi-peak procedure combines elements of those three tasks, so the aim of this experiment was to compare the behavioural pattern developed when rats had the opportunity to engage in SID during this task, in order to replicate and merge the findings presented in previous chapters with different temporal tasks. Two groups of rats (with and without access to water) were exposed to a bi-peak procedure. During training rats learned to discriminate between two levers, one associated with a short FI (20 s) and the other with a long FI (80 s). Trials were randomly alternated and unsignalled. During tests phase rats received short and long training trials and peak trials that were 150 s and ended without delivery of reinforcement. Rats developed a pattern consisting on a peak of licks, a peak of presses to the short lever and a peak of presses to the long lever. The group that had access to water showed a differentiated peak of long responses during peak trials, whereas rats without access to water alternated between short and long lever presses after the peak of short lever presses. The results in this experiment replicate all the other findings reported in previous chapters.

Schedule-Induced Behaviour and its Impact on Timing in the Bi-Peak Procedure

Timing is the ability to predict the occurrence of periodic unsignalled events (Killeen et al., 1997). When organisms are exposed to intermittent and periodic delivery of reinforcement they develop relatively steady patterns of schedule-induced and target behaviours that are repeated during inter-reinforcement intervals. Furthermore, schedule-induced behaviours develop without any arranged contingency between their occurrence and the delivery of reinforcement (Falk, 1971; Killeen & Pellón, 2013); whereas the target responses are contingent with the reinforcer.

The behavioural mechanisms of timing consist on the correlation or coupling of the schedule-induced behaviours in those patterns to the temporal events and the target response; in that sense, those behaviours would serve as discriminative stimuli, as the clock that allows organisms to estimate time (Killeen & Fetterman, 1988; Machado, 1997; Machado & Keen, 1999).

That process has been mathematically modelled (Killeen & Fetterman, 1988; Machado & Keen, 1999), but the occurrence of schedule-induced behaviours is mostly inferred or not directly measured (Lejeune et al., 1998). There is some evidence that engaging in schedule-induced behaviours correlates with a better performance on a differential reinforcement of low rates (DRL) schedule (Bruner & Revusky, 1961; Laties et al., 1969; Segal & Holloway, 1963) and in the peak procedure (Mattel & Portugal, 2007).

Machado & Keen (1999; 2003) described the individual behavioural patterns developed by pigeons in the temporal bisection task, although their goal was no to observe them. On the other hand, Lejeune et al. (1998) directly measured the development of the

behavioural patterns and reported that they occurred in a consistent sequential way, but that each behaviour did not occur at an identical rate in each interval.

In previous chapters, we tested directly the hypothesis that developing schedule-induced drinking (SID), a well-studied schedule-induced behaviour, improves performance in fixed intervals (FI) schedules (Chapter 2), peak-procedure (Chapter 3) and temporal bisection task (Chapter 4). We observed that SID is part of a sequentially-organized pattern that comprises different kinds of behaviours that occur in a successive way during the inter-reinforcement intervals. The instrumental response is the last one in the pattern, and the adequacy of its distribution depends on different parameters of the task, like the length of the IRI, as observed in Chapters 2 and 3.

There were no significant differences in timing accuracy between groups that developed or did not develop SID in previous chapters, suggesting that schedule-induced behaviours are present in every task, whether we are measuring them or not (Cleaveland et al., 2003; Killeen, 2017). Nevertheless, the analysis of the distribution of responses in the peak procedure in Chapter 3 showed that lever pressing, the target response, started after SID decreased, and the pattern only re-started after the delivery of reinforcement. Furthermore, distributions of responses in the groups that developed SID were more organized, meaning that the time for each type of behaviour was more differentiated; whereas for groups that did not develop SID the patterns sometimes implied a constant alternation of two types of behaviours. If rats have a specific/different behaviour to engage in, they will do it and that will result in more organized patterns.

Oliveira & Machado (2009) observed something similar with pigeons exposed to a task in which they had to discriminate between two pairs of durations when both choice keys were available during the sample stimuli. Pigeons usually engage in some idiosyncratic patterns of behaviour (Machado & Keen, 1999; 2003), but when the keys were available

during the stimuli pigeons pecked them. At the beginning of the trial pigeons pecked the key associated with the short duration, and if the time of the short stimulus elapsed they received the reinforcer, if not, they changed to the other key. Subjects learned the task faster when the keys were available since the beginning of the experiment than when they were no.

Leaving both choice keys/levers makes the bisection task similar to the bi-peak procedure. The bi-peak procedure consists on training an organism to respond to two different levers/keys, each associated with a different FI (Heilbronner & Meck, 2014; Yin et al., 2017). Additionally, Yin et al. (2017) stated that during the bisection task, rats usually start pawing or biting the aperture of the short lever and change to the long lever at approximately the geometrical mean of both stimuli; which implies there are no differences between the bi-peak and the bisection task in timing terms, only on how the behaviours are recorded. In that sense, the bi-peak procedure provides an easier environment to measure how behaviours function as the clock.

Furthermore, the bi-peak procedure combines elements of FI, peak procedure and temporal discrimination, providing a complete, yet compacted, view of all timing tasks used in previous chapters. Performance on the bi-peak procedure can be similar to performance on a mixed FI (a short and a long FI presented randomly in the same session, responding to the same lever; see Catania & Reynolds, 1968), in which a peak for the short interval usually develops, and then is followed by a FI scallop for the long FI (Machado, 1997). But the bi-peak procedure has the advantage of having one lever associated to each FI, which allows to analyse both distributions of responses separately in a more reliable way.

Meck and his colleagues analysed the distribution of responses in the bi-peak procedure with rats (Heilbronner & Meck, 2014) and mice (Meck et al., 2012) under the effect of different drugs. Under control conditions they found that the distribution of responses was similar for the short and long FI when plotting the proportion of maximum

response rate of each lever. Similar to other procedures discussed earlier, responses to the long lever increased when responses to the short lever decreased.

The aim of this experiment was to compare the behavioural pattern developed when rats had the opportunity to engage in SID, in order to replicate and merge the findings presented in previous chapters with different temporal tasks.

Method

Subjects

Subjects were 16 experimentally naïve male Wistar rats that were 20 weeks old at the beginning of the experiment. Their weights were progressively reduced before the beginning of the experiment and then they were maintained at about 80-85% of their free-feeding weight with an average at the beginning of the experiment of 351 g (range: 318-379 g). The percentage of weight was calculated considering the theoretical growing curve and the individual subject's baseline weight. They were housed individually in transparent Plexiglas cages measuring 18 x 32.5 x 20.5 cm in an environmentally-controlled room (22°C and 55% relative humidity) with a 12-hour light-dark cycle (lights on at 8:00 a.m.). Water was always available in the home cages. Animal care procedures were in accordance with the European Union Council Directive 2010/63, the Spanish Royal Decree 53/2013 and with the authorization of the Community of Madrid with reference PROEX 077/18.

Apparatus

Eight Leticia LI-836 conditioning chambers measuring 29 x 24.5 x 35.5 cm were used. The front panel of each conditioning chamber was made of aluminum, the left wall of transparent Plexiglas and the reaming walls of black Plexiglas. The floor consisted on a 16-bar metal grid. The food tray was in the center of the front wall at a height of 3.7 cm above

the, at each side of the food tray there was a retractile lever, and above each lever a 3-W round lamp. Forty-five-mg food pellets were dispensed (Bio-Serv, Frenchtown, NJ, USA) into the food tray by a Leticia Instruments dispenser. In the right wall, there was a 3.2 x 3.9 cm aperture in the wall, situated 20 cm from the front panel and 7 cm from the floor, through which subjects could reach the spout of a water bottle mounted on the exterior of the chamber. The water bottle could be removed if necessary. The spout was placed 2 cm towards the interior of the aperture and contact between the subject's tongue and the metal spout completed the electric circuit between the floor and the spout that allowed licks registration. Chambers were enclosed in a soundproofed housing equipped with a ventilation system and a small observation window in the left panel. A fan located in the soundproofed housing produced an ambient noise of approximately 60 dB in each chamber to mask any exterior noise. The houselight consisted on an indirect 25-W light mounted in the soundproofed housing. Chambers were controlled using a MED-PC application under a Windows environment.

Procedure

The experiment was conducted 5 days a week (Mondays to Fridays) at about the same time every day. Subjects were divided into 2 groups: W rats had access to water during the experimental sessions and NW rats did not. The experiment consisted in 3 phases: pre-training, training and test.

Pre-training. Pre-training consisted on three conditions: autoshaping, sequential 10/40 and random 10/40.

Autoshaping. This condition consisted on an autoshaping-like procedure. A food pellet was delivered every 30 s independently of the rat's behaviours and after every time the rat pressed either lever. Rats stayed in this phase until they pressed either lever 40 times in a 30-minutes session for three consecutive sessions.

Sequential 10/40. During this condition food pellets were delivered under a FI 10- or 40-s schedule in a sequentially alternating way (10-40-10-40 and so on). Each lever was associated with one of the schedules. For example, if the right lever was associated with the FI 10-s schedule and the left lever was associated with the FI 40-s schedule, during a FI 10-s trial, the *correct* lever would be the right one and the first press to this lever after 10 s would result in a food pellet, whereas during the FI 40-s trials, the *correct* lever was the left one, so the first press to this lever after 40 s would result in the delivery of a food pellet. The association between lever and FI value was counterbalanced among subjects. At the beginning of each trial the houselight and the two lights above the levers (signal-lights) went on and both levers were inserted into the chamber. There were no discriminative stimuli to indicate the kind of trial (FI 10-s or FI 40-s) that was in effect. After 10 or 40 s (sequentially alternated), a food pellet was made available, and if the subject pressed the correct lever, both levers were retracted, the food pellet was delivered, houselight and normal lights went off and the inter-trial interval (ITI) began. Presses to the incorrect lever were recorded but had no effect. The ITI was 3 s. Each session consisted on 40 trials, and subjects remained in this condition until they earned 40 food pellets in less than 30 minutes in four consecutive sessions.

Random 10/40. This phase was identical to the previous one, except that trials were randomly alternated. Rats remained in this condition until they earned 40 food pellets in less than 30 minutes in four consecutive sessions.

Training. During this phase food pellets were delivered under a FI 20- or 80-s. Trials were similar to trials in the previous two phases. One of the levers was associated with the FI 20-s schedule (‘short lever’) and the other with the FI 80-s schedule (‘long lever’). Trials during which the FI 20-s schedule was in effect will be referred to as ‘short trials’ and trials during which the FI 80-s schedule was in effect will be referred to as ‘long trials’. During

short trials, a food pellet was available after 20 s, and the first press to the short lever resulted in the delivery of a food pellet and beginning of the ITI; on the other hand, during long trials a food pellet was available after 80 s had elapsed, if the rat pressed the long lever after that time a food pellet was delivered and the ITI began. Presses to either lever before the pellet was available and presses to the incorrect lever after the food pellet was available were recorded but had no effect. At the beginning of each trial the signal and houselight went on and the two levers were inserted into the chamber. During the 3 s ITI both levers were retracted and the houselight and signal-lights were switched off. Each session consisted on 20 short and 20 long trials that were randomly alternated. This phase lasted 30 sessions.

Test. During this phase food pellets were delivered under a FI 20-s or a FI 80-s schedule, and peak non-reinforced trials were intercalated. This phase was identical to training, except that it had 3 types of trials: short (FI 20-s), long (FI 80-s) and peak. During peak trials both levers were inserted into the chamber and the houselight and signal lights went on for 150 s, after that time elapsed, both levers were retracted, the houselight and signal lights went off, and the 3 s ITI began. Presses to either lever during peak trials were recorded but had no effect. Each session consisted on 32 training trials (16 short and 16 long trials) and 8 peak trials. This phase lasted 30 sessions.

Data analysis

Licks and lever presses were recorded. Short LP correspond to presses to the short lever and long LP correspond to presses to the long lever. Distribution of licks, short LP and long LP were drawn by calculating the response rate in each 2-s bin of the trial.

The overall rate at time t, $OR(t)$, was calculated by adding the responses on the short and long levers (short LP + long LP) during the peak trials in 1-s bins. We described the resulting function by a weighted average of two Gaussians (WAG), the first Gaussian was

centred around the short interval and the second one was centred around the long interval. Its equation was

$$OR(t) = p \times A_s \times f(t, \mu_S, \sigma_S) + (1 - p) \times A_l \times f(t, \mu_l, \sigma_l),$$

where p is the weight given to the "short" Gaussian, A_s and A_L map the Gaussian probabilities onto response rate, and $f(t, \mu, \sigma)$ represents the Gaussian density function with mean μ and standard deviation σ evaluated at *t*, that is,

$$f(t, \mu, \sigma) = \frac{1}{\sqrt{2\pi}\sigma} e^{\frac{1}{2}\left(\frac{t-\mu}{\sigma}\right)^2}.$$

In the equation for OR, parameters μ_S and σ_S are the mean and standard deviation of the "short" Gaussian, and μ_L and σ_L are the mean and standard deviation of the "long" Gaussian. The best fitting parameters were obtained by the least squares method using Microsoft Excel solver with the constraints that all parameters had to be positive. The mean and standard deviation corresponded to the peak and width of the peak, respectively.

The goodness of fit of the WAG function was calculated using the coefficient of determination (R^2). The parameters of the functions were analysed using a one-way analysis of variance (ANOVA) that compared the means of the two levels (W/NW) of the factor group. The significance level was established at a minimum $p<.05$.

Results

Rats were exposed to a bi-peak procedure with and without access to water to observe the effect of engaging in SID in the behavioural pattern developed under this procedure. Rats

with access to water developed SID, the licking rate was 32.06 licks/min in the last five sessions of training and 17.19 in the last five sessions of test phase. Individual data is displayed in Table 1.

Table 1.

Licking rate in the last 5 sessions of training and test phases.

Subject	Training	Test
W1	44.79 ± 4.90	20.11 ± 3.43
W2	3.49 ± 0.75	4.65 ± 2.30
W3	21.11 ± 2.74	4.45 ± 2.22
W4	9.26 ± 0.75	6.49 ± 1.25
W5	75.49 ± 5.76	42.68 ± 2.84
W6	63.60 ± 1.28	36.81 ± 1.36
W7	31.28 ± 1.56	17.86 ± 2.05
W8	7.42 ± 3.1	4.48 ± 0.76
Mean	32.06 ± 9.55	17.19 ± 5.41

Note. Mean ± S.E.M.

Distribution of responses during the first five sessions of training was similar between groups (Figure 1), short LP increased for the first 10 s and stayed at high rates until the end of both types of trials and long LP increased slowly and reached high rates around second 46 for W rats (graph A) and around second 38 for NW rats (graph B); both short and long LP remained at similar rates towards the end of the interval in long trials. Licks peaked around second 6 and showed a steep decrease until second 10, then slowly decreased until second 40 and remained at a low rate until the last 10 s, when a small increase is appreciated.

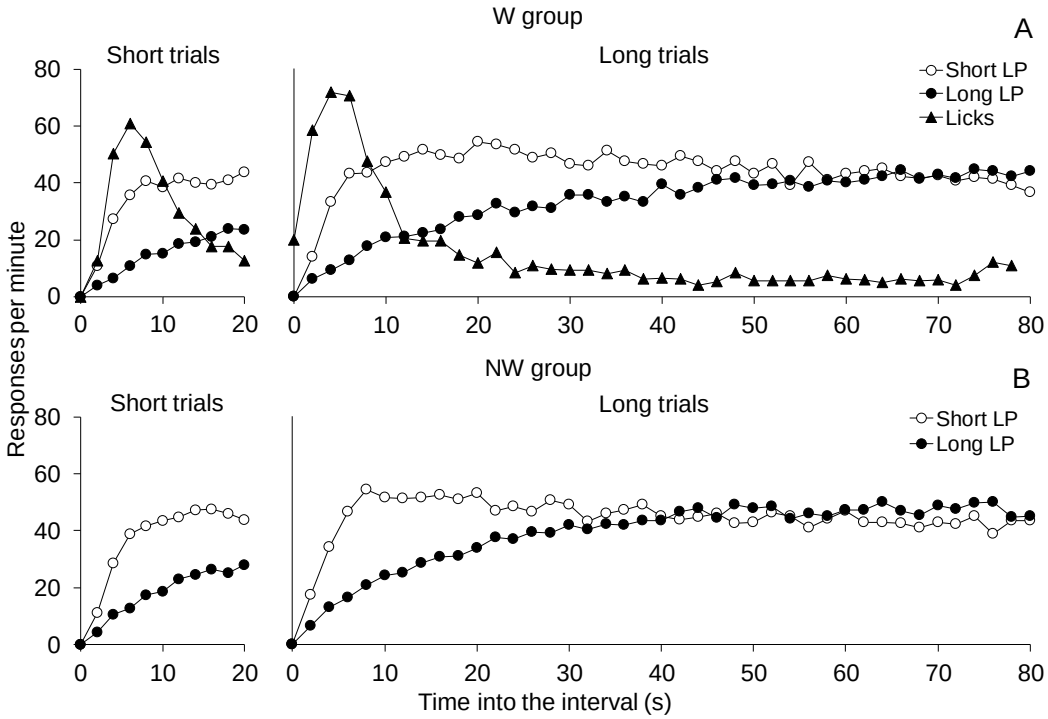

Figure 1. Distribution of responses during the first five sessions of training phase. A: W group. B: NW group. Each data point represents the response rate in a 2-s bin.

Distribution of responses changed with training but remained similar between groups, as can be observed in Figure 2. Short LP increased until second 20 in both types of trials, showing a FI-scallop pattern in short trials and a gaussian-shape in long trials. The scallop was steeper and the peak narrower for W rats (graph A), but both groups of rats showed lower rates of short LP towards second 40 and until the end of the trial. Long LP increased around second 40 and stayed at higher levels than short LP after second 50 for W rats (graph A) and second 60 for NW rats (graph B). Licks peaked at second 6 and decreased to 0 licks/min at second 16.

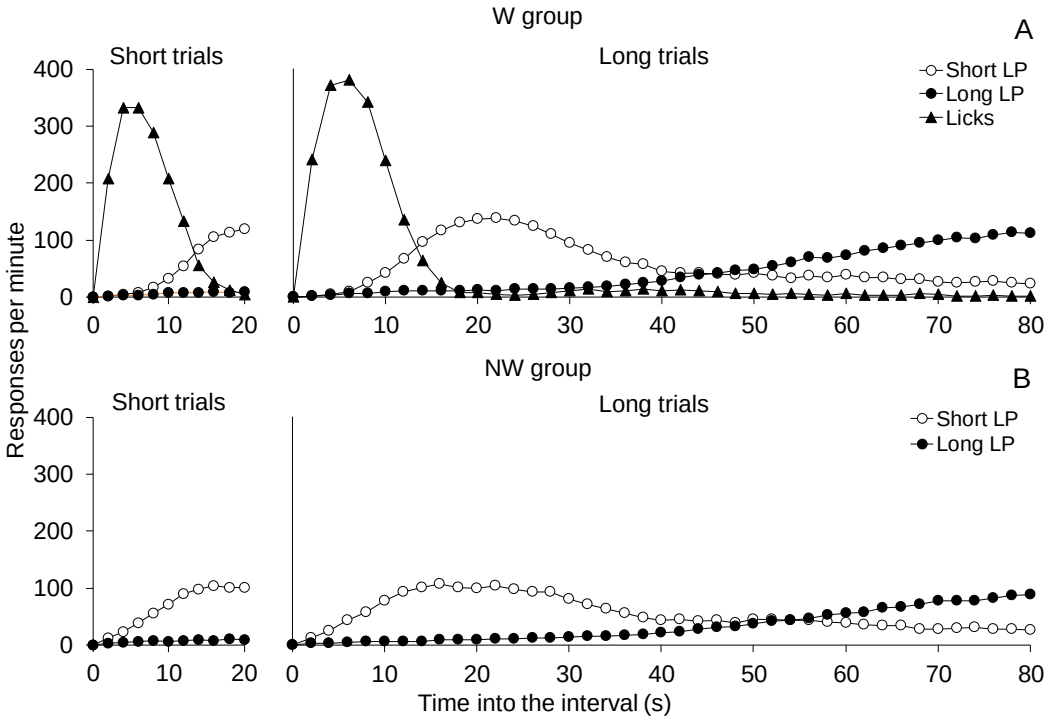

Figure 2. Distribution of responses during the last five sessions of training phase. A: W group. B: NW group. Each data point represents the response rate in a 2-s bin.

Distributions of responses in training trials during the last five sessions of test phase are depicted in Figure 3. Distribution of short LP remained similar to distribution during training phase, they increased until second 20 in both types trials, and decreased (end of the peak) at second 40 in long trials; nevertheless, they stayed at lower rates than long LP towards the end of the interval for W rats (graph A) but stayed at similar levels than long LP for NW rats (graph B). Similar to training, the scallop of short LP was steeper and the peak narrower for W rats (graph A). Distribution of long LP was similar, although it showed a slightly higher rate towards the end of the interval for the W group (graph A). Distribution of licks in the last sessions of test phase was similar to the distribution in the last five sessions of training (Figure 2); licking peaked at second 6 and decreased to 0 licks/min at around second 16.

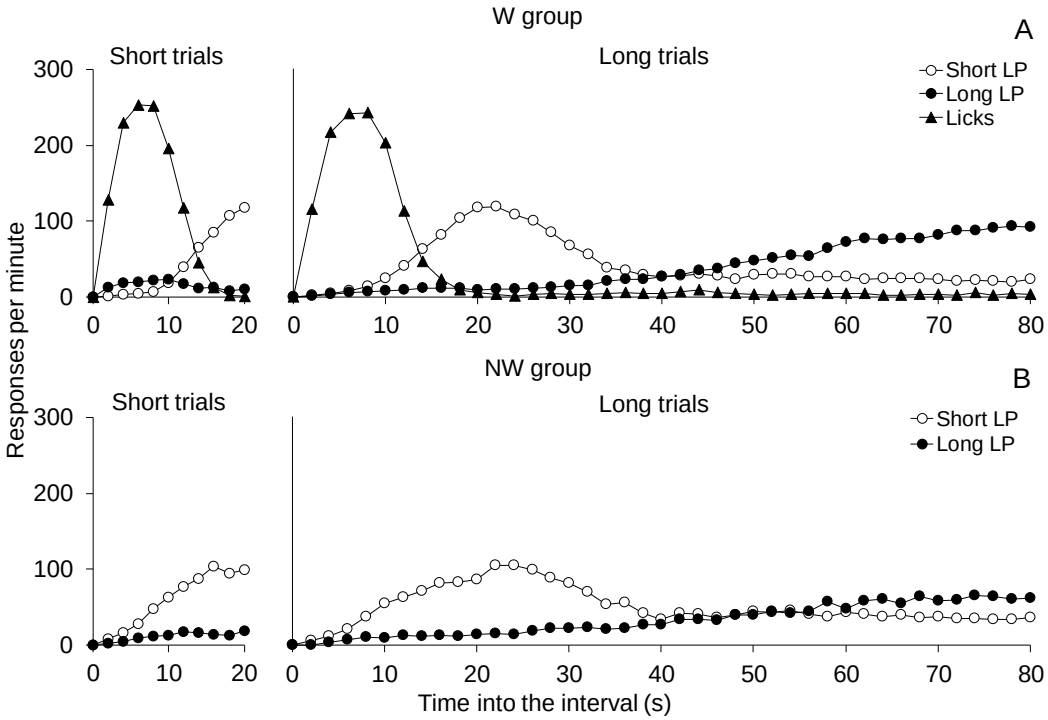

Figure 3. Distribution of responses during training trials in the last five sessions of test phase. A: W group. B: NW group. Each data point represents the response rate in a 2-s bin.

Figure 4 depicts the distribution of responses during peak trials of the last five sessions of test phase. Short LP peaked at second 20 for both groups (although the peak was narrower for W rats), decreased around second 40 and stayed at a low rate throughout the trial. The rate of short LP slightly increased between seconds 40 and 50 for NW rats. On the other hand, the distribution of long LP was different for both groups: for W rats it increased and peaked between seconds 80 and 90, occurring at a higher rate than short LP during that part of the interval; for NW rats it increased and peaked around second 80, and although it occurred at a higher rate than short LP between seconds 60 and 120, the difference between short and long LP rate was small.

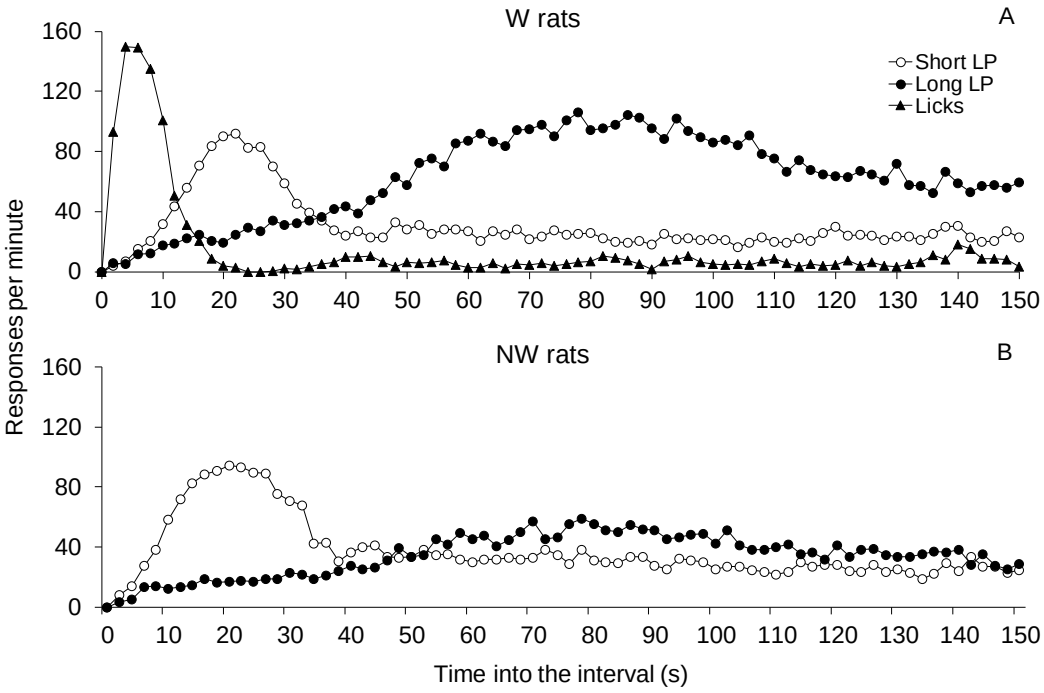

Figure 4. Distribution of responses during the peak trials in the last five sessions of test phase. A: W group. B: NW group. Each data point represents the response rate in a 2-s bin.

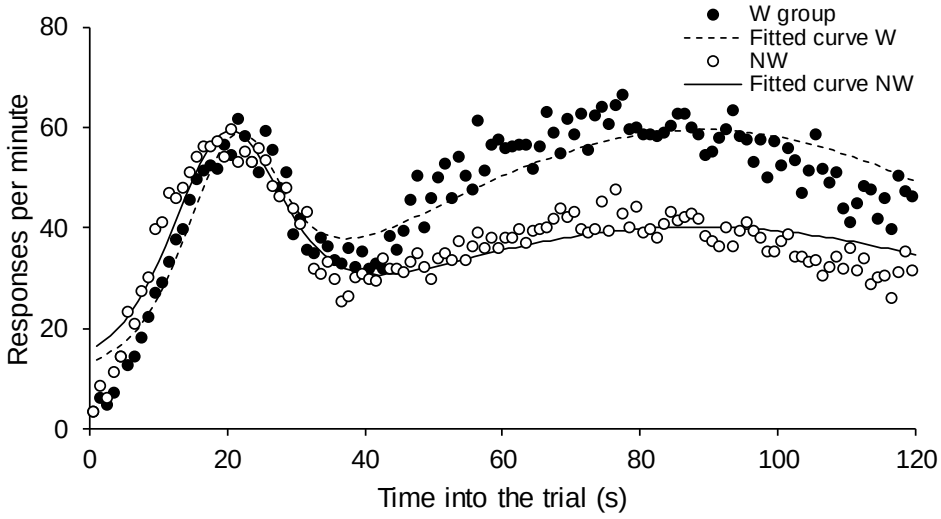

Figure 5. Mean overall response rate and mean of individual WAG fitted functions.

The WAG function described earlier was fitted to individual data of the absolute response rate. Mean absolute response rate and mean of the individual best fitted curves is shown in Figure 5. Both distributions are similar, except that the response rate for W group was higher than for NW group. The goodness of fit was not very good, the mean was 0.7 for W group and 0.6 for NW group, differences between groups were not significant $F_{(1,15)}$=3.240, p=.093, ns.

Table 2.

Parameters of the weighted average of two Gaussians function fitted to the data.

Subject	PeakS μ_S	WidhtS σ_S	PeakL μ_L	WidthL σ_L	p	R^2
W						
1	16.15	4.89	90.19	50.85	0.28	0.79
2	19.56	5.24	86.82	54.52	0.34	0.72
3	21.06	6.83	87.39	38.39	0.44	0.70
4	19.60	7.38	83.52	48-09	0.39	0.75
5	21.17	4.03	93.79	56.49	0.31	0.72
6	23.71	3.61	86.30	47.96	0.25	0.75
7	25.55	8.58	89.24	62.39	0.29	0.55
8	22.95	7.80	101.78	61.71	0.33	0.56
Mean	21.2 ± 1.0	6.1 ± 0.7	89.9 ± 2.0	52.6 ± 2.8	0.3 ± 0.02	0.7 ± 0.03
NW						
1	21.76	9.21	86.04	67.66	0.28	0.39
2	21.10	8.95	99.12	84.10	0.28	0.31
3	18.87	8.83	87.35	38.25	0.48	0.76
4	17.15	5.57	85.24	55.75	0.22	0.52
5	19.64	7.62	76.15	71.06	0.25	0.59
6	19.35	5.49	77.98	55.18	0.31	0.75
7	18.94	7.23	103.38	62.88	0.33	0.70
8	24.41	10.01	101.94	65.63	0.38	0.57
Mean	20.2 ± 0.8	7.9 ± 0.6	89.7 ± 3.8	62.6 ± 4.8	0.3 ± 0.03	0.6 ± 0.06

Note. Mean ± S.E.M.

The individual parameters of the best-fitted curves are displayed in Table 2. The peak for the "short" Gaussian curve was 21.2 s for W group and 20.2 s for NW rats [$F_{(1,15)}$=.680, p=.42, ns] and the width of the "short" peak was 6.1 s for W rats and 7.9 s for NW rats [close to significance, $F_{(1,15)}$=4.234, p=.059, ns]. Similarly, the peak for the "long" Gaussian distribution was 89.9 s and 89.7 s for W and NW rats, respectively [$F_{(1,15)}$=.003, p=.95, ns]; the peak was narrower for the W rats (52.6 s) than for NW rats (62.6 s), but differences were not significant [$F_{(1,15)}$=3.287, p=.09, ns]. The weight of the "short" curve was .03 for both groups [$F_{(1,15)}$=.61, p=.809, ns].

Discussion

In previous chapters we evaluated the effect of developing SID in FI schedule, the peak procedure and the bisection task, and found that, although there were no significant differences in timing ability, rats that developed SID had a more organized pattern in which types of behaviours developed under the procedure were more differentiated and occurred sequentially during the inter-reinforcement intervals. This study aimed to replicate and merge those results using a bi-peak procedure that comprises elements of the other temporal tasks.

Rats developed SID, although drinking rate decreased in the test phase. It is possible that it decreased because rats did not drink after peak trials, since there is evidence that the pattern only re-starts in trials that follow the delivery of the reinforcer (Segal & Holloway, 1963).

The distribution of responses changed from the first to the last sessions of training. Long trials are equivalent to peak trials for responses to the short lever, so, as expected, the peak of the short FI was shaped during training sessions (Kirkpatrick-Steger et al., 1996; Machado, 1997). The end of the peak of short LP was followed by an increase in long LP,

around the geometric mean of both FI values (40 s). This distribution of LP to both levers is similar to the one observed in Chapter 4 in the temporal bisection task with licks and head entries, although in this chapter SID occurred earlier in the interval.

Furthermore, it is important to note that the response patterns to both levers were differentiated, even though there was no punishment for responding to the wrong lever, suggesting that behaviours that aid timing and correlate with the reinforcer will be strengthened by the reinforcer, even if there is no explicit contingency requiring a specific pattern (Killeen & Fetterman, 1993; Skinner, 1948). In this case, short LP correlated to the delivery of reinforcement in the first part of the interval and long LP correlated to the delivery of reinforcement in the last part of the interval.

The behavioural pattern for rats with access to water consisted on drinking, pressing the sort lever and pressing the long lever. During short trials the pattern ended with short LP and re-started after the delivery of the reinforcer; whereas during long trials, the pattern was completed; which is in accordance with previous findings that different types of behaviours peak at different times and are repeated in a regular sequential way (Killeen & Pellón, 2013; Reid et al., 1993; Staddon & Ayres, 1975).

Even though no specific pattern was required, W rats seemed to learn a pattern consisting on three states of behaviours: licking, pressing the short lever and pressing the long lever; whereas the NW group learned to press the short lever, and then to alternate between short and long levers. The patterns observed in this study were similar to the ones observed in Chapter 3 during the peak procedure, in which NW rats learned to intercalate between short and long LP after the time for the reinforcer elapsed.

Analysis of the distribution of responses of the W group showed that they had a more accurate performance than the NW group: the scallop of short LP was steeper in short trials, the peak of short LP was narrower during long trials, and both peaks were narrower during

peak trials. Actually, the peak of long LP was clearly differentiated only for the W group, as observed in the distribution of responses and the fitting of the WAG function. Meck and colleagues (Heilbronner & Meck, 2014; Meck et al., 2012) did not report absolute rates of responding, so it is not possible to compare that aspect of the results.

The results in this experiment replicate all the other findings reported in previous chapters. When rats developed SID, licks occurred in a fixed part of the interval; the FI scallops were steeper and peaks were narrower; behavioural patterns in which one behaviour increases when the previous one decreases were developed; adding SID provides a more organized (behaviour-type differentiated) pattern; and choosing between two options does not seem to be *one* specific response, but *two* parts of the same pattern.

In conclusion, SID do not aid timing *per se*, rather, different schedule-induced behaviours are developed in every temporal task, but developing SID provides a more efficient and sequentially-organized pattern, which may result in a more efficient performance on certain temporal tasks. The more available behaviours an organism have, the more state-differentiated the patterns it develops.

CHAPTER 6

GENERAL CONCLUSION

General Conclusion

When exposed to intermittent reinforcement schedules, organisms usually develop sequential patterns including schedule-induced and target behaviours. The semi-invariance of those patterns has led them to be the basis of the behavioural account of timing, in which behaviours on those patterns are regarded as discriminative stimuli of temporal events (Killeen & Fetterman, 1988).

There is some evidence that schedule-induced behaviour improves performance on temporal tasks, but the hypothesis has not been thoroughly tested. The aim of this thesis was to observe the development of schedule-induced behaviour in different behavioural tasks in order to evaluate its impact on timing. A series of experiments using four different temporal tasks was carried out to achieve that.

In Chapter 2 the effect of developing SID on the performance in FI schedules was tested using three values of FI and comparing rats that had or did not have access to water in the experimental chamber (Experiment 1); and comparing performance on FI when rats had previous experience developing SID (Experiment 2). In Chapter 3 the temporal organization of behaviours was observed in the peak procedure, comparing rats with and without access to water. The effect of developing SID in the bisection task was tested in Chapter 4 using a long ITI (Experiment 1) and a short ITI (Experiment 2). Finally, in Chapter 5 rats were exposed to a bi-peak procedure, which combines elements of the three previous tasks, in order to try to replicate and merge the findings of previous chapters.

Subjects in all experiments developed sequential behavioural patterns. The distribution of SID and lever presses changed with training, suggesting that behaviours induced by intermittent reinforcement are shaped into a sequentially organized pattern that is

repeated during IRIs and strengthened by the delivery of reinforcement (Álvarez et al., 2016; Killeen, 1975; Killeen & Pellón, 2013; Ruiz et al., 2016).

Developing SID improved performance of W rats in short intervals but worsened it in long intervals during FI and peak procedure. Both effects were due to organisms developing a pattern of behaviour in which drinking occurred in the first part of the interval, and lever pressing started immediately afterwards (Fetterman et al., 1998; Killeen & Fetterman, 1988; Lejeune et al., 1998).

On the other hand, there were no differences in timing measures in the bisection task in Chapter 4 between groups with and without access to water, but analysis of the distribution of responses indicated that W rats developed a pattern consisting on drinking and then head entering; whereas NW rats developed a pattern that consistent on head entering and then probably engaging in some idiosyncratic not-measured behaviours, as has been previously reported by Machado & Keen (1999; 2003). These results also indicate that behavioural patterns occur in all procedures, whether we are measuring them or not (Cleaveland, 2003; Killeen, 2017; Yin et al., 2016).

Nevertheless, engaging in SID had an effect in the organization of the behavioural patterns. Rats that developed SID showed a more behaviour-differentiated pattern in the peak and bi peak procedures. Analysis of individual trials in Chapter 3 suggest that the reinforcer do not only determine the shape of the pattern, but it is necessary to re-start it (Sanabria & Killeen, 2006; Roberts 1981). Patterns of behaviours seem to be induced by the delivery of the previous reinforcer (Baum, 2012), but maintained by the forthcoming one (Álvarez et al., 2016). Also, results on the Bi-peak procedure replicated the observations reported with the other temporal tasks.

Findings in this thesis support the hypothesis that schedule-induced and target behaviours are induced and maintained by the delivery of reinforcement (Killeen & Pellón,

2013; Ruiz et al., 2016), thus eliminating the necessity to distinguish between types of behaviours (operant *vs*. schedule-induced). Reinforcers, then, serve a triple task: select from the available behaviours, maintain them as part of a behavioural pattern, and triggering such pattern.

In conclusion, timing seem to be a product of the development of sequential patterns of behaviour, shaped by the environment and delimited by temporal parameters. These results contribute to the understanding of schedule-induced behaviour, in particular; and to the field of the Experimental Analysis of Behaviour, in general. Researchers should aim to understand the relation between organisms and their environment beyond the terminology employed to describe it. Timing is a term used to refer to behaviour occurring on a particular set of procedures defined by temporal parameters, and one should not forget about the organisms behaving in order to explain processes that cannot be directly observed, for behaviour is, after all, the object of study of the field of Experimental Analysis of Behaviour.

References

Álvarez, B., Íbias, J. & Pellón, R. (2016). Reinforcement of schedule-induced drinking in rats by lick-contingent shortening of food delivery. *Learning & Behavior, 44* (4), 329-339.

Balci, F., Gallister, C. R., Allen, B. D., Frank, K. M., Gibson, J. M. & Brunner, D. (2009). Acquisition of peak responding: What is learned? *Behavioural Processes, 80*, 67-75.

Baron, A. & Leinenweber, A. (1994). Molecular and molar analyses of fixed-interval performance. *Journal of the Experimental Analysis of Behavior, 61*, 11-18.

Baum, W. M. (2012). Rethinking reinforcement: Allocation, induction and contingency. *Journal of the Experimental Analysis of Behavior, 97*, 101-124.

Bruner, A. & Revusky, S. H. (1961). Collateral behavior in humans. *Journal of the Experimental Analysis of Behavior, 4*(4), 345-350.

Buriticá, J. & dos Santos, C. V. (2017). Reinforcement value and fixed-interval performance. *Journal of the Experimental Analysis of Behavior, 108*, 151-170.

Camacho Candia, J. A. & Cabrera González, F. (2014). Allocation of behavior in a simple discrimination task. *Conductual, International Journal of Interbehaviorism and Behavior Analysis, 2*(3), 4-16.

Cantor, M. B. & Wilson, J. F. (1978). Polydipsia induced by a schedule of brain stimulation reinforcement. *Learning and motivation, 9*, 428-445.

Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behaviour. In W. N. Shoenfeld (Ed.), *The theory of reinforcement schedules*. New York: Appleton-Century-Crofts.

Catania, A. C. (1971). Reinforcement schedules: the role of responses preceding the one that produces the reinforcer. *Journal of the Experimental Analysis of behavior, 15*, 271-287.

Catania, A. C. & Reynolds, G. S. (1968). A quantitative analysis of the responding maintained by interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior, 11,* 327-383.

Church, R. M. (2002). Temporal learning. In C. R. Gallistel (Ed.), *Stevens' Handbook of Experimental Psychology: Learning, Motivation, and Emotion* (Vol. 3). New York: John Wiley & Sons.

Church, R. M. & Deluty, M. Z. (1977). Bisection of Temporal Intervals. *Journal of Experimental Psychology: Animal Behavior Processes, 3*(3), 216-228.

Church, R. M., Meck, W. H. & Gibbon, J. (1994). Application of scalar timing theory to individual trials. *Journal of Experimental Psychology: Animal Behavior Processes, 20*(2), 135-155.

Church, R. M., Miller, K. D., Meck, W. H. & Gibbon, J. (1991). Symmetrical and asymmetrical sources of variance in temporal generalization. *Animal Learning & Behavior, 19*(3), 207-214.

Clark, F. C. (1962). Some observations on the adventitious reinforcement of drinking under food reinforcement. *Journal of the Experimental Analysis of Behavior, 5*(1), 61-63.

Cleaveland, J. M., Jäger, E. Röβner & Delius, J. D. (2003). Ontogeny has a phylogeny: background to adjunctive behaviors in pigeons and budgerigars. *Behavioural Processes, 61,* 143-158.

Daniel, W. & King, G. D. (1975). The consequences of restricted water accessibility on schedule-induced polydipsia. *Bulletin of the Psychonomic Society, 5*(4), 297-299.

Dews, P. B. (1962). The effect of multiple S^{Δ} periods on responding on a fixed-interval schedule. *Journal of the Experimental Analysis of Behavior, 5*, 369-374.

Falk, J. L. (1961). Production of polydipsia in normal rats by an intermittent food schedule. *Science, 133*(3447), 195-196.

Falk, J. L. (1966). Schedule-induced polydipsia as a function of fixed interval length. *Journal of the Experimental Analysis of Behavior, 9*, 37-39.

Falk, J. L. (1967). Control of schedule-induced polydipsia: type, size, and spacing of meals. *Journal of the Experimental Analysis of Behavior, 10,* 199-206.

Falk, J. L. (1969). Conditions producing psychogenic polydipsia in animals. *Annals of the New York Academy of Sciences, 157*(2), 569-589.

Falk, J. L. (1971). The nature and determinants of adjunctive behavior. *Physiology and Behavior, 6,* 577-588.

Fetterman, J. G., Killeen, P. R. & Hall, S. (1998). Watching the clock. *Behavioural Processes, 44*(2), 211-224.

Ferster, C. B. & Skinner, B. F. (1957). *Schedules of Reinforcement.* Massachusets: Copley Publishing Group.

Flory, R. K. & O'Boyle, M. K. (1972). The effect of limited water availability on schedule-induced polydipsia. *Physiology & Behavior, 8*(1), 147-149.

Freed, E. X. & Hymowitz, N. (1969). A fortuitous observation regarding "psychogenic" polydipsia. *Psychological Reports, 24,* 224-226.

Galtress, T. & Kirkpatrick, K. (2010). Reward magnitude effects on temporal discrimination. *Learning and Motivation, 41,*108-124.

Gilbert, R. M. (1974). Ubiquity of Schedule-induced polydipsia. *Journal of the Experimental Analysis of Behavior, 21,* 227-284.

Harper, D. N. & Bizo, L. A. (2000). Mediation of timing accuracy by operant behavior. *Behavioural Processes, 50,* 143-154.

Heilbronner, S. R. & Meck, W. H. (2014). Dissociation between interval timing and intertemporal choice following administration of fluoxetine, cocaine, or methamphetamine. *Behavioural Processes, 101,* 123-143.

Johnson, L. M., Bickel, W. K., Higgins, S. T., & Morris, E. K. (1991). The effect of schedule history and the opportunity for adjunctive responding on behavior during a fixed-interval schedule of reinforcement. *Journal of the Experimental Analysis of Behavior, 55*, 313-322.

Killeen, P. (1969). Reinforcement frequency and contingency as factors in fixed-ratio behavior. *Journal of the Experimental Analysis of Behavior, 12*, 391-395.

Killeen, P. R. (1975). On the temporal control of behavior. *Psychological Review, 82*(2), 89-115.

Killeen, P. R. (2014). A theory of behavioral contrast. *Journal of the Experimental Analysis of Behavior, 102*, 363-390.

Killeen, P. R. (2017). The trajectory of my life, so far, in Camacho Candia, J. A., Cabrera González, F., Zamora Arévalo, O., Martínez Sánchez, F. H., Irigoyen Morales, J. J. (eds). *Aproximaciones al estudio del comportamiento y sus aplicaciones. Volumen 1*. Tlaxcala: Universidad Autónoma de Tlaxcala.

Killeen, P. R. & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological Review, 95* (2), 274-293.

Killeen, P. R. & Fetterman, J. G. (1993). The behavioral theory of timing: Transition analyses. *Journal of the Experimental Analysis of Behavior, 59,* 411-422.

Killeen, P. R., Fetterman, J. G. & Bizo, L. A. (1997). Time's causes, in Bradshaw, C. M., Szabadi, E. (Eds.), *Time and behaviour: Psychological and neurobehavioural analyses*. Amsterdam: Elsevier.

Killeen, P. R. & Jacobs, K. W. (2016). Coal is not black, snow is not white, food is not a reinforcer: the roles of affordances and dispositions in the analysis of behaviour. *The Behavior Analyst, 40*(1), 17-38.

Killeen, P. R. & Pellón, R. (2013). Adjunctive behaviors are operants. *Learning and Behavior, 41*, 1-24.

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*(4), 447-460.

Knutson, J. F. & Schrader, S. P. (1975). A concurrent assessment of schedule-induced aggression and schedule-induced polydipsia in the rat. *Animal Learning & Behavior, 3*(1), 16-20.

Lawler, C. P. & Cohen, P. S. (1992). Temporal patterns of schedule-induced drinking and paw grooming in rats exposed to periodic food. *Animal Learning & Behavior, 20*(3), 266-280.

Laties, V. G., Weiss, B. & Weiss, A. B. (1969). Further observations on overt "mediating" behavior and the discrimination of time. *Journal of the Experimental Analysis of behavior, 12*, 43-57.

Lejeune, H., Cornet, S., Ferreira, M. A. & Wearden, J. H. (1998). How do Mongolian gerbils (*Meriones unguiculatus*) pass the time? Adjunctive behavior during temporal differentiation in gerbils. *Journal of Experimental Psychology: Animal Behavior Processes, 24*(3), 352-368.

Lejeune, H. & Wearden, J. H. (1991). The comparative psychology of fixed-interval responding: some quantitative analyses. *Learning and Motivation, 22,* 84-111.

Levitsky, D. & Collier, G. (1968). Schedule-induced wheel running. *Physiology and behavior, 3,* 571-573.

López-Crespo, G., Rodríguez, M., Pellón, R. & Flores, P. (2004). Acquisition of schedule-induced polydipsia by rats in proximity to upcoming food delivery. *Learning & Behavior, 32*(4), 491-499.

López-Tolsa, G. E., Ardoy, J. & Pellón, R. (*in preparation*). Behavioral history effects on the maintenance of schedule-induced drinking in rats.

López, F. (2012). Aprendizaje y control temporal: Adquisición y transferencia. En P, Guilhardi, M. Menez y F. López (Eds.), *Tendencias en el estudio contemporáneo de la estimación temporal*. México: Universidad Nacional Autónoma de México.

López, F. & Menez, M. (2005). Effects of reinforcement history on response rate and response pattern in periodic reinforcement. *Journal of the Experimental Analysis of Behavior, 83,* 221-241.

López, F. & Menez, M. (2012). Transference effect of prior non-contingent reinforcement on the acquisition of temporal control on fixed-interval schedules. *Behavioural Processes, 90,* 402-407.

Lucas, G. A., Timberlake, W. & Gawley, D. J. (1988). Adjunctive behavior of the rat under periodic food delivery in a 24-hor environment. *Animal Learning & Behavior, 16*(1), 19-30.

Machado, A. (1997). Learning the temporal dynamics of behavior. *Psychological Review, 104*(2), 241-265.

Machado, A. & Keen, R. (1999). Learning to time (LeT) or Scalar Expectancy Theory (SET)? A Critical test of two models of timing. *Psychological Sciences, 10*(3), 285-290.

Machado, A. & Keen, R. (2003). Temporal discrimination in a long operant chamber. *Behavioural Processes, 62*, 157-182.

Mattel, M. S. & Portugal, G. S. (2007). Impulsive responding on the peak-interval procedure. *Behavioural Processes, 74*, 198-208.

Meck, W. H., Cheng, R., MacDonald, C. J., Gainetdinov, R. R., Caron, M. G. & Çevik, M. O. (2012). Gene-dose dependent effects of methamphetamine in interval timing in dopamine-transporter knockout mice. *Neuropharmacology, 62*, 1221-1229.

Millenson, J. R., Allen, R. B. & Pinker, S. (1977). Adjunctive drinking during variable and random-interval food reinforcement schedules. *Animal Learning & Behavior, 5*, 285-290.

Miller, J. S. & Gollub, L. R. (1974). Adjunctive and operant bolt pecking in the pigeon. *The Psychological Record, 24*(2), 203-208.

Oliveira, L. & Machado, A. (2009). Context effect in a temporal bisection task with the choice keys available during the sample. *Behavioural Processes, 81*, 286-292.

Orduña, V. Hong, E. & Bouzas, A. (2007). Interval bisection in spontaneously hypertensive rats. *Behavioural Processes, 74*, 107-111.

Pellón, R. & Killeen, P. R. (2015). Responses compete and collaborate, shaping each others' distributions: Commentary on Boakes, Patterson, Kendig and Harris. *Journal of Experimental Psychology: Animal Learning and Cognition, 41*(4), 444-451.

Reid, A. K., Bacha, G. Morán, C. (1993). The temporal organization of behavior in periodic food schedules. *Journal of the Experimental Analysis of Behavior, 59*, 1-27.

Richelle, M. & Lejeune, H. (1980). *Time in animal behaviour.* New York: Pergamon Press.

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

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

Roper, T. J. (1978b). The effect of food deprivation on drinking and running in mongolian gerbils. *Animal Behavior, 26,* 1264-1272.

Roper, T. J. (1981). What is meant by the term "schedule-induced," and how general is schedule induction? *Animal Learning & Behavior, 9*(4), 433-440.

Rosellini, R. A. & Burdette, D. R. (1980). Meal size and intermeal interval both regulate schedule-induced water intake in rats. *Animal Learning & Behavior, 8*(4), 647-652.

Ruiz, J. A., López-Tolsa, G. E., & Pellón, R. (2016). Reinforcing and timing properties of water in the schedule-induced drinking situation. *Behavioural Processes, 127,* 86-96.

Russel, R. & Kirkpatrick, K. (2007). The role of temporal generalization in a temporal discrimination task. *Behavioural Processes, 74,* 115-125.

Sanabria, F. & Killeen, P. R. (2006). Temporal generalization accounts for response resurgence in the peak procedure. *Behavioural Processes, 74,* 126-141.

Segal, E. F. (1969a). The interaction of psychogenic polydipsia with wheel running in rats. *Psychonomic Science, 14*(3), 142-144.

Segal, E. F. (1969b). Schedule-induced polydipsia: Effects of providing an alternate reinforced response and of introducing a lick contingent delay in food delivery. *Psychonomic Science, 15*(3), 153-154.

Segal, E. F. (1969c). Transformation of polydipsic drinking into operant drinking: A paradigm? *Psychonomic Science, 16*(3), 133-135.

Segal, E. F. & Holloway, S. M. (1963). Timing behavior in rats with water drinking as a mediator. *Science, 140*(3569), 888-889.

Segal, E. F., Oden, D. L. & Deadwyler, S. A. (1965). Determinants of polydipsia: IV. Free-reinforcement schedules. *Psychonomic Science, 3*, 11-12.

Shaeffer, R. W. & Slazberg, C. L. (1967). Schedule-induced polydipsia: An atypical case. *Psychological Reports, 20*(3), 1071-1076.

Silva, K. M. & Timberlake, W. (1998). The organization and temporal properties of appetitive behavior in rats. *Animal Learning & Behavior, 26*(2), 182-195.

Skinner, B. F. (1948). Superstition in the Pigeon. *Journal of Experimental Psychology, 38,* 168-172.

Skinner, B. F. (1981). Selection by consequences. *Science, 213,* 501-504.

Skuban, W. E. & Richardson, W. K. (1975). The effect of the size of the test environment on behavior under the two temporally defined schedules. *Journal of the Experimental Analysis of Behavior, 23*, 271-275.

Staddon, J. E. R. (1977). Schedule-induced behavior. In W. K. Honing & Staddon (eds.), *Handbook of operant behavior* (pp. 125-152). Englewood Cliffs, NJ: Prentice-Hall.

Staddon, J. E. R. & Ayres, S. L. (1975). Sequential and temporal properties of behavior induced by a schedule of periodic food delivery. *Behaviour, 54*, 26-49.

Staddon, J. E. R. & Simmelhag, V. L. (1971). The "superstition" experiment: a re-examination of its implication for the principles of adaptive behavior. *Psychological Review, 78*(1), 3-43.

Stein, L. (1964). Excessive drinking in the rat: superstition or thirst? *Journal of Comparative and Physiological Psychology, 58*(2), 237-242.

Tang, M., Williams, S. L., & Falk, J. L. (1988). Prior schedule exposure reduces the acquisition of schedule-induced polydipsia. *Physiology & Behavior, 44*, 817-820.

Timberlake, W. & Lucas, G. A. (1985). The basis of superstitious behavior: chance contingency, stimulus substitution, or appetitive behavior? *Journal of the Experimental Analysis of Behavior, 44*, 279-299.

White, N. R. & Wong, P. T. P. (1982). A behavioral field analysis of adjunctive activities. *Bulletin of the Psychonomic Society, 20*(5), 266-268.

Williams, S. L., Tang, M. & Falk, J. L. (1992). Prior exposure to a running wheel and scheduled food attenuates polydipsia acquisition. *Physiology & Behavior, 52*(3), 481-483.

Yin, B., Lusk, N. A. & Meck, W. H., (2017). Interval-timing protocols and their relevancy to the study of temporal cognition and neurobehavioral genetics, in Tucci, V. (Ed.). *Neuro-phenome: Cutting edge approaches and technologies in neurobehavioral genetics.* Ney Jersey: Wiley-Blackwell.