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Timing in Possums:
Accounting for Resurgence in the Peak Procedure

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Abstract

This study attempted to account for resurgence on the Peak Procedure using 6 possums (*Trichosurus vulpecula*) as subjects. The Peak Procedure is made up of randomly mixed fixed intervals (FI) and peak intervals (PI), with the ratio of FI trials to PI trials being 4:1 respectively. Conditions 1-4 were used to replicate Church et al.'s (1991) procedure from their second experiment. The authors found that when the PI trial length was variable, data from PI trials showed that responding did not resurge, as it did when the PI duration was fixed. Condition 1 used a FI 20 s and a variable PI with a mean of 80 s. Responding did not resurge, but rather decreased to a low level throughout the PI trial. Condition 2 used a FI 20 and a fixed PI of 100 s. Responding resurged for this condition. Condition 3 and 4 repeated Condition 1 and 2 respectively to give an ABAB design. Responding again decreased and increased as the PI changed to being variable and fixed respectively. These results are similar to that found by Church et al. (1991), and show support for what Sanabria and Killeen (2007) call the anticipation theory (where escape from a non-reinforced PI trial is negatively reinforcing). The PI duration was shortened to twice the FI length in Condition 5 and lengthened to 300 s, or 15 times the FI in Condition 6. This was in order to investigate whether responding would resurge at very short and very long PI durations. Responding did not resurge at the shorter PI length, and this may be due to there not being enough time to do so. At the extreme length of 300 s, responding was seen to resurge; a result that is not consistent with other studies that used a similar procedure (Sanabria & Killeen, 2007). When the procedure returned to using a FI 20 s and a variable PI with a mean of 80 s in Condition 7, resurgence decreased to a minimum and remained stable till the end of the trial.

Results from the present study support Church et al.'s (1991) anticipation theory, and that as long as the animals can track the end of the PI trial, responding will resurge; if it is variable, animals cannot predict the end of the trial and so response resurgence does not occur.

Acknowledgements

My Aunty Marg once remarked that people think they achieve great things solely on their own. They forget that without the help of all of the people around them, they couldn't have come close. So on that note, I would like to acknowledge the following people, who are just a few of the many who helped me to complete this thesis. Thank you to my supervisors, Dr Lewis A. Bizo and Dr James S. McEwan, for your insight and guidance throughout this process. Thank you to the staff and students of No. 3 Dairy for helping the data collection process to go smoothly. Thanks to Mike O'Connor and Dave Swney for feeding and housing me over the last couple of years. To my Uncle Dave and Aunty Pam; thank you for playing a huge part in my academic career and for providing immeasurable support every step of the way. Thanks to my family for taking a genuine interest in the foreign world of the Peak Procedure, and for providing so much valuable support. Thanks especially to my mum and my brother Nick for encouraging me to further my education. Lastly I want to acknowledge my fiancée Rebecca Grace; the girl for whom I do all this. Thank you for nodding your head when I explain the ins and outs of my research, for your patience over the last 3 years, and for showing me how to work hard and encouraging me to go beyond what I thought I could do.

Table of Contents

List of Tables

List of Figures

List of Appendices

Introduction

To quote John Gibbon, 'Timing is everything; in making shots, in making love, in making dinner. Indeed it is difficult to conceive of an action that doesn't require temporal control' (Malapani & Fairhurst, 2002, pg 157). Humans have developed clocks in order to help them time necessary intervals. Without clocks, animals must rely on their own ability to time. For many animals the ability to time is essential to survival; for example, a foraging animal that can only spend a certain amount of time in one area before moving on in order to evade predators, or before a food reinforcer is exhausted (Roberts, 1998). Cats howling by their bowls at feeding time, dogs waiting at the door for the mailman to arrive and wild birds hunting in the same area each day are all observations which suggest that animals are indeed all able to time (Roberts, 1998).

Knowing how animals time is an important area of research because of the similarity of the way humans and other animals (rats and pigeons) perform in interval timing tasks (Church, 1993). Church conducted an analysis of three previously published studies, where experiments by various authors used similar experimental procedures to test time estimation in rats (Church & Deluty, 1977), pigeons (Stubbs, 1968) and humans (Allan & Gibbon, 1991). These studies showed that when plotted as a function of time, results from different estimated durations would superimpose on one another. Based on a timing theory (called scalar timing theory/ scalar expectancy theory (SET Gibbon, 1977, discussed later), Church proposed that the analogous results from these studies gives credible support for the similar use of cognitive processes to time, by the three species.

Wearden and McShane used data from their 1988 timing experiment with humans, and compared it to similar data from Roberts (1981) study with rats. They designed their experiment to control for chronometric counting (e.g. "One-thousand and one, one-thousand and two, etc.), which can aid humans in timing. They too found a similar pattern of results between the two species, which are interpreted in terms of SET.

Timing is important for all animals in everyday life. Animals and humans have shown similarities in the way each times. The peak procedure has become a popular method to test an animal's temporal accuracy.

Peak Procedure

In 1970, Catania described a study examining temporal discrimination in pigeons. Fixed interval (FI) trials lasting 10 s were used, and the pigeon's key pecking was reinforced with food after this time. One in every ten trials lasted the initial 10 s plus an additional 38 s, and the birds were not given reinforcement. The procedure was then changed so that trials resulting in reinforcement occurred once in every ten trials. The results showed that on trials without reinforcement, responding increased to the time at which reinforcement usually occurs and then decreased at about the same rate, and were well described as a unimodal curve when graphed. Additionally, when the probability of reinforced trials was high, rate of responding was much greater; when the probability of reinforced trials was low, rate of responding was much lower.

Roberts (1981) reports results from a series of five experiments with rats, using what he termed the "Peak Procedure"; a slight modification of the procedure used in Catania's study. It is so named because of the peak of the bell shaped curve that occurs around the time of reinforcement. Since Roberts's 1981 publication, the peak procedure has become a popular way in which to measure different animals' ability to time (e.g. Church, Miller, Meck, & Gibbon 1991; Sanabria & Killeen, 2007; Taylor, Haskell, Appleby, & Waran, 2002; Wearden & Doherty, 1995).

The peak procedure is made up of two different trials mixed together. The first, as previously mentioned in Catania's study (1970) is a FI trial where responding is reinforced. The second is a longer FI trial where no reinforcement is given. This longer trial is called the peak interval (PI). Typically the ratio of FI trials to PI trials is around 4:1 respectively (Leak & Gibbon, 1995; Roberts, 1981) and PI trials are at least 1.5 times longer than FI trials (Taylor et al., 2002). Kirkpatrick-Steger, Miller, Betti, & Wasserman (1996) found that the normally distributed curve that develops, does so following prolonged exposure to the peak procedure. They found that the peak that usually occurs at the time of reinforcement developed over a number of sessions, and was not evident during the initial stages of testing.

There are two hypothesised sources of learning during the peak procedure. The first is that the animal learns to respond at a high rate at the time that reinforcement is delivered on FI trials. The second is that the animal learns to

withhold responding after that time has passed on PI trials (Kirkpatrick-Steger et al., 1996). Roberts (1981) found he could manipulate two aspects of performance on the peak procedure. They were peak time (the time of maximum responding), and peak rate (maximum response rate). The aim of his first experiment was to determine whether or not peak time and peak rate were dependent variables, and whether one could be changed while the other remained constant. In part one of the experiment, 10 rats were trained on either a 20 s, or 40 s fixed interval (FI). The PI lasted 80 s plus a variable interval (VI) with a mean of 80 s, and made up 20% of total trials. In part two, light signalled a FI:PI ratio of 4:1, and sound signalled a FI:PI ratio of 1:4. Roberts termed these 'High Food', and 'Low Food', respectively. Results showed that Peak rate occurred close to the time of reinforcement on FI trials. Peak rate was greater when there was a higher ratio of FI trials to PI trials than it was when the ratio of FI trials to PI trials was smaller. His results proved that Peak Rate and Peak Time were indeed two independent measures, and gave support to his theory of an internal clock, which is used to time intervals. In the same paper he included a theory and diagram of how an animal might time (*Figure 1*). His results support his hypothesis that 'a manipulation that does not change the clock should not change peak time'.

Balci, Gallistel, Allen, Frank, Gibson, and Brunner (2008) looked at how long it took to acquire peak responding. They used an algorithm to measure the start and stop times of responding by mice on the peak procedure. They found that temporal precision was mediated by the stop times (decrease in responding following peak time) shifting closer to the peak, rather than the start times (increase in responding preceding peak time) shifting closer to the peak on peak trials. Stop times appeared, or rather were *acquired* after only three to five sessions for individual animals.

The peak procedure has been developed by various authors since its conception by Catania in 1970, and later Roberts in 1981. It is made up of randomly mixed reinforced FI and nonreinforced PI trials. It has proved popular when measuring the timing ability of various animals, and testing the effect of drugs on animals' temporal accuracy.

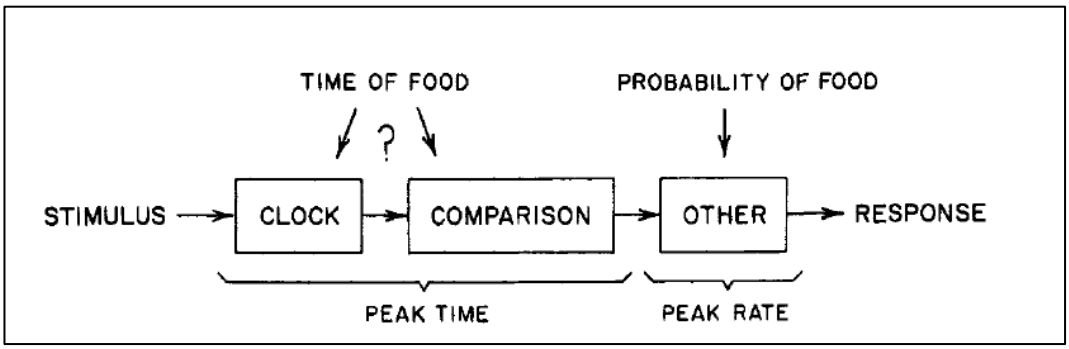

Figure 1. The first stage of Robert's working of an internal clock is the animal's timing of the current trial. The second, comparison stage is the time of the current trial in comparison to a past trial's durations. Peak time accounts for the first two stages. The third stage merely accounts for the rate of responding, and is determined by peak rate. From Roberts. S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes, 7,* 242-268, pp. 247 (with permission).

Popularity of the Peak Procedure in other Research

The peak procedure has proven a popular method of measuring the timing abilities of a number of species, commonly rats (Church, Lacourse, & Crystal, 1998; Meck, Komeily-Zadeh, & Church, R. M, 1984) and pigeons (Cheng & Westwood, 1993; Leak & Gibbon, 1995), but it also includes humans (Wearden, & McShane, 1988); black-capped chickadees (Brodbeck, Hampton, & Cheng, 1998); domestic hens (Taylor et al., 2002); possums (Lockhart, 2011); and goldfish (Drew, Couvillon, Zupan, Cooke, & Balsam, 2005). All of these studies report a similar pattern of results.

Saulsgiver, McClure, and Wynne (2006) administered four differing amounts of D-amphetamine (0.75 to 3.0 mg/kg) were administered to four groups of pigeons exposed to the peak procedure with either an FI 30 s or FI 45 s, and a PI three times that of the FI. Their results found that, at the highest dose (3.0 mg/kg) of D-amphetamine, using a FI duration of 45 s, there was a significant reduction in peak time. This result shows support for the notion of an internal pace maker, as D-amphetamine would have, in theory (Meck, 1983), sped it up, causing the shift in peak time.

Meck and Church (1987) aimed to manipulate the brain cholinergic systems, said to effect memory processes, of rats using two types of cholinergic drugs, anticholinesterases and cholinergic receptors. Using a peak procedure with a FI duration of 20 s and a PI duration of 130 s, data from peak trials show that anticholinesterases reduce peak time, while cholinergic receptor blockers increase peak time. Their results give support to the suggestion that brain cholinergic systems play a part in memory processes, and therefore, based on timing theories such as SET and BeT (discussed in detail later), animals' ability to time.

Cholinergic systems in the brain are thought to change as an animal ages; thus changing the way an animal times. Lejeune, Ferrara, Soffié, Bronchart, and Wearden (1998) exposed two groups of rats, aged 4 months and 24 months, to the peak procedure. Their results found that in the older rats, peak time displaced to the right. The authors state that this is due to 'misremembering' (see page 214). Decreases in acetylcholine levels as the animals age may affect memory and attention.

Drugs affect an animal's timing accuracy and have been hypothesised to also affect their internal pacemaker. The pace maker lies at the heart of timing theories such as SET and BeT. At the core of SET is the scalar property of timing.

Scalar Property of Timing/ Weber's Law

The scalar property of timing states that the coefficient of variation should remain constant for different timed intervals, as the mean and standard deviation are in proportion to the particular interval being timed (Gibbon, 1977). The scalar property of timing is comprised of two parts. The first is *mean accuracy*. On the peak procedure this equates to peak rate occurring near the time of reinforcement. The second part is called *scalar variance*. This is where the "…standard deviation of measures of behaviour varies linearly with the mean" (Legeune & Wearden, 2006). Weber fractions are calculated by dividing the standard deviation (s) by the mean (m). This is equivalent to the coefficient of variation (CV); (Eq. (1)) below.

$$CV=s/m. \quad (1)$$

If Weber's law holds for time, the CV should remain constant across a range of durations (Legeune & Wearden, 2006). This is similar to Weber's law. In the case of the peak procedure, Weber's law states that when estimating greater magnitudes of time, the variability of an animal's estimates increases proportionally to the magnitude itself (Taylor et al., 2002). On the peak procedure this equates to a steeper function when FI trials are short and broader functions as the duration of FI trials increase. In support of this notion are Sanabria and Killeen's (2002) results showing normalised response rates for FI and PI trials of varying lengths, superimposed on one another (*Figure 2*). Taylor et al. (2002) provided additional support for the use of Weber's Law in relation to timing, when they used a peak procedure with a FI duration of 6 minutes and a PI duration of 9 minutes. Their results, using greater intervals than previous studies, produced a much broader peak. Weber's Law has been shown to fail on certain timing tasks (Bizo, Chu, Sanabria, & Killeen, 2006; Getty, 1975). Bizo et al. exposed pigeons to two procedures to measure time perception. The first was a production task, where the subjects responded on one of two keys depending on the temporal window (either short or long). The second was a categorisation task,

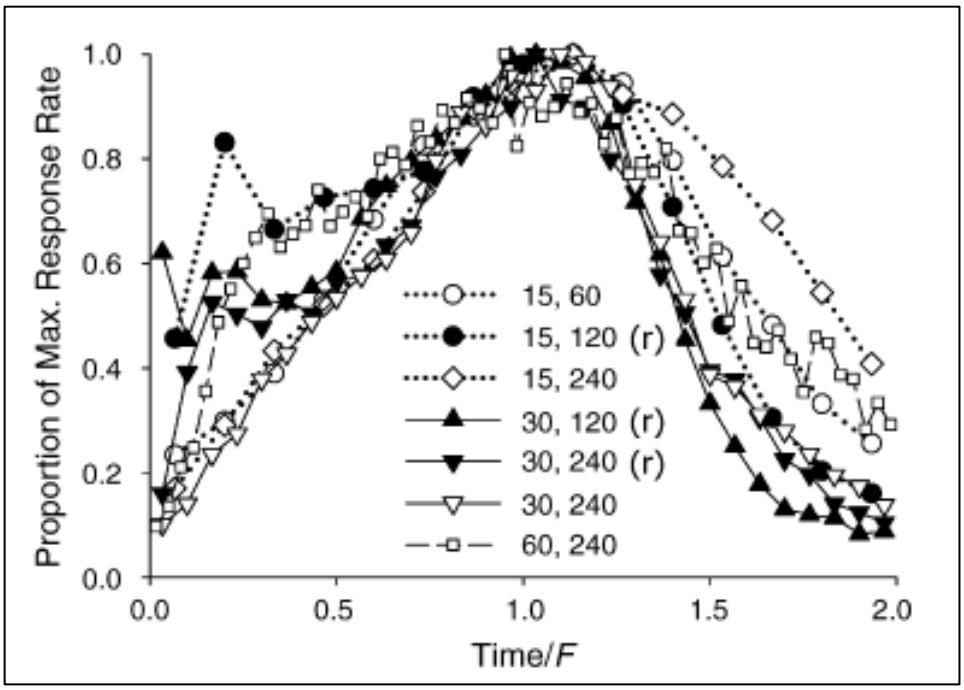

Figure 2. Shows peak interval performance of rats with different FI and PI lengths superimposed. Mean response rates are normalised and displayed in 2 second bins. From Sanabria. F., & Killeen. P. R. (2007). Temporal generalization accounts for response resurgence in the peak procedure. *Behavioural Processes, 74*, 126-141, pp. 131 (with permission).

where they responded on one of two keys depending on whether they classed a stimulus as long or short. Their results found that the Weber fractions taken from these tasks created a U shaped function. This is a violation of Weber's Law as it contradicts the typically found flat function (Weber's Law), or reversed J-shaped function (Generalised Weber's Law, Getty, 1975). Getty (1975) used human subjects to respond to the longest of two stimulus durations on a two-alternative, forced-choice procedure, and found that Weber's law failed to predict a rise in standard deviation that was found for durations longer than 2s. Weber's law has been applied to the timing domain and has been renamed scalar variance. Weber fractions are renamed as coefficients of variation CV. CV are calculated by dividing the standard deviation (s) by the mean (m) of the peak function. Scalar variance lies at the core of timing theories and in particular SET.

Theories of Timing

'Scalar Expectancy Theory (SET; Gibbon, 1977) remains the most prominent of the theoretical accounts of animal and human timing' (Malapani & Fairhurst, 2002). It is a cognitive rather than behavioural theory of timing (Machado, 1997) and is based on the scalar property of timing (previously mentioned). Gibbon first described how his theory of scalar expectancy worked in his 1977 paper. Consequent papers by Gibbon and his colleagues (Church et al., 1991; Gibbon, 1991; Gibbon & Church 1984) have built on those initial ideas. There are three parts that make up the SET model (see Gibbon, 1991, pg 20). The first part is an arbitrary signal of some sort (in an operant chamber this may be the onset of an LED light). The signal starts the first part of the 'clock', which is an internal pacemaker that emits pulses in time. The second part of the clock is an accumulator which counts all the pulses emitted since the signal. Some times may be marked by the animal as important (for example the time of reinforcement, and times that recur), and so are stored in long-term, or reference memory. The third part of the model is the comparator, which takes time from the current trial and compares it with various times from the animal's reference memory. A decision is then made, based on this comparison, whether to respond or not (Gibbon, 1991). Gibbon explains that an animal responding on a fixed interval schedule of reinforcement will respond later into a trial following a period of training (Gibbon, 1977). Therefore, it takes time to store values in reference memory, which can

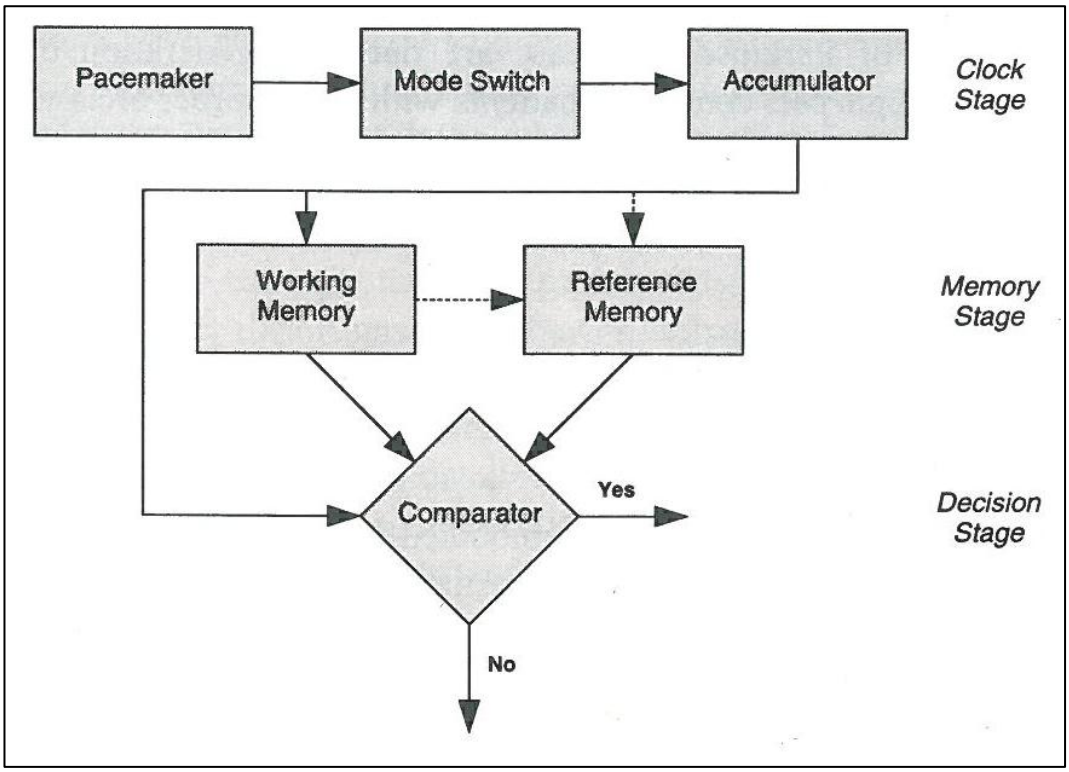

Figure 3. An information-processing model of timing. The pacemaker sends constant pulses to the accumulator, which are first gated by the mode switch in the Clock Stage. Pulses are stored in both the Working Memory (trial-by-trial memory), and Reference Memory (long term memory) in the Memory Stage. Pulses from the current trial are compared with those stored in long term memory in the Decision Stage to determine whether the subject will respond or not. Reprinted from Bradshaw, C. M., & Szabadi, E. (Eds). (1997). *Time and Behaviour: Psychological and Neurobehavioural Analyses*. Amsterdam: Elsevier, pp. 411 (with permission).

then be used to compare the current trial with. *Figure 3* shows a diagram of how the model works.

Zeiler (1991) criticises SET for not being able to account for behaviour outside the laboratory. He used a closed economy feeding procedure for pigeons that resembled natural feeding opportunities, typically found outside the operant chamber; that is, free feeding and subjects determining the size of their meal. He compared this with an open economy procedure, where the birds were maintained at 80% of their target weights, were allowed a maximum of 30 food deliveries a day, and were given supplementary food as required. His results found that the pigeons in an open economy would respond earlier into a trial than those exposed to a closed economy. This may be due to food deprivation and a need to respond for food at every opportunity. Such tight constraints led to greater temporal control, and support for SET. Zeiler argues that while SET may be a theory that works well when dealing with timing behaviour in an open economy (operant chamber), it may not be able to account for the way animals time in the wild, where animals don't always find themselves food deprived and without an abundant food source.

In Killeen and Fetterman's behavioural theory of timing (BeT, Killeen & Fetterman, 1988), animals are in a particular behavioural state, which is determined by a pulse from an internal pacemaker, which has a Poisson distribution. Associated with each behavioural state are *adjunctive* responses or behaviours. States vary in duration, and responses within a state occur at different rates. "Conditioning to the adjunctive behavior that characterizes the state aids counting, in much the same manner as does the use of fingers and feet by civilizations not blessed with numbers" (Killeen & Fetterman, 1988, pg 274). Machado (1997) gives a good example of how BeT works by saying that a hen might be engaged in a particular behavioural class when pecking a key, at the time of reinforcement. That behavioural class has now come to be associated with key pecking. Killeen and Fetterman further explain that behaviour associated with particular behavioural *states* come to act as discriminative stimuli for responding. Furthermore, according to BeT, it is reinforcement rate that drives the rate of the internal pacemaker. Therefore a higher magnitude of reinforcement will increase the rate of the pacemaker (Hinton & Meck, 1997).

Learning to Time (LeT, Machado, 1997) is a similarly behavioural theory of timing. Like BeT, behavioural states are 'linked' with an operant's response. Machado's basic model (see Machado, 1997, pg 242) is explained as a time marker (e.g. food) which activates a number of behavioural states (for a pigeon these might include pacing around the chamber, pecking at the wall, or some other behaviour.). If reinforcement and a corresponding response occur during a particular behavioural state, then that state's association with the response is strengthened. Alternatively, if a particular behavioural state is not active at such time, then its association with the response is weakened. The stronger the association, or 'links' are, the more likely a response is to occur at the time of the current FI. As Whitaker, Lowe, and Wearden. (2003) explain further, no response will occur if either no behavioural states are associated with reinforcement, or no associated behavioural states are currently active. Machado himself admits that his model cannot account for responding on individual trials, but rather focuses on a larger aggregation of trials.

Resurgence

Church et al. (1991) reported that following the initial peak, there was an increase in responding near the end of the PI. They described this as asymmetrical variance in temporal generalisation. This was later referred to as response resurgence by Sanabria and Killeen (2007). Based on their first experiment which showed resurgence, Church et al. (1991) theorised that it was in anticipation of reinforcement on the next FI trial following the PI trial that gave rise to responding. In other words, animals learn to discriminate between the FI trials which provide reinforcement and the longer PI trials which provide no reinforcement. An increase of responding on PI trials may be negatively reinforced by the termination of the PI and beginning of the FI trial. Effectively this can be viewed as two FI trials; where one is reinforced by food on FI trials, and the other negatively reinforced by the ending of the PI and introduction of the FI. Church et al. (1991) tested this, using rats, in their second experiment by randomly altering the PI trial lengths. They hypothesised that by reducing the rats' ability to accurately time PI trials, resurgence should decrease. For half the rats a 40 s PI trial was presented. For the other half, 10 s food trials were matched with a PI trial of 10 s plus an equiprobable random duration with a mean of 110 s; 20 s

food trials were matched with a PI trial of 20 s plus an equiprobable random duration with a mean of 100 s. Therefore total trial duration had a mean of 120 s. The authors found that the random 120 sec PI trials reduced resurgence, and produced a flat asymptotic response rate occurring above zero. During their investigations into the rate of development of the initial peak, Kirkpatrick-Steger et al. (1996) discovered a unique pattern of resurgence of a second distinct peak. Secondary peaks were found when PI lengths were four times greater than that of FI lengths. The authors reinforced half of the subjects at the end of the PI. For these animals, no second peaks were evident. These findings are not accounted for by proposed models of timing such as SET (Gibbon & Church, 1984), and BET (Killeen & Fetterman, 1988). Sanabria and Killeen theorise that secondary peaks may be due to the lack of saliency of interval marking cues (see Sanabria & Killeen, 2007, p 139), and that animals lose track of these markers, causing a second peak to occur.

Resurgence in responding occurs following the initial peak on the peak procedure. Church et al. (1991) found that resurgence occurs when the PI has a fixed duration and does not occur when the PI is variable. The authors theorise that the animals' anticipate the end of the PI and can do so when it is fixed. The end of the longer and unreinforced trial may be negatively reinforcing, which is supported by the similar results from Whitaker et al. (2003) who used multiple reinforced FI schedules.

Multiple Interval Timing

Whitaker et al. (2003) conducted a study using multiple FI schedules. Similar to the peak procedure there was a short FI trial (FI S, between 15-75 s), and a longer FI trial (FI L, between 45-300 s). Trial length duration differed over experiments. Trial length ratios for FI S to FI L ranged from 1:1.3 to 1:20. As evidenced in the graphs below, Whitaker et al.'s results show that when FI S to FI L ratios were less than 1:4 the second peak of responding is higher than the first. When the same ratios are 1:4 or higher, it is the initial peak which has a higher rate of responding. Also of note is the similarity of the results of this study to that achieved using the peak procedure. The bottom two graphs of *Figure 4* below in particular could pass as data from a peak procedure study.

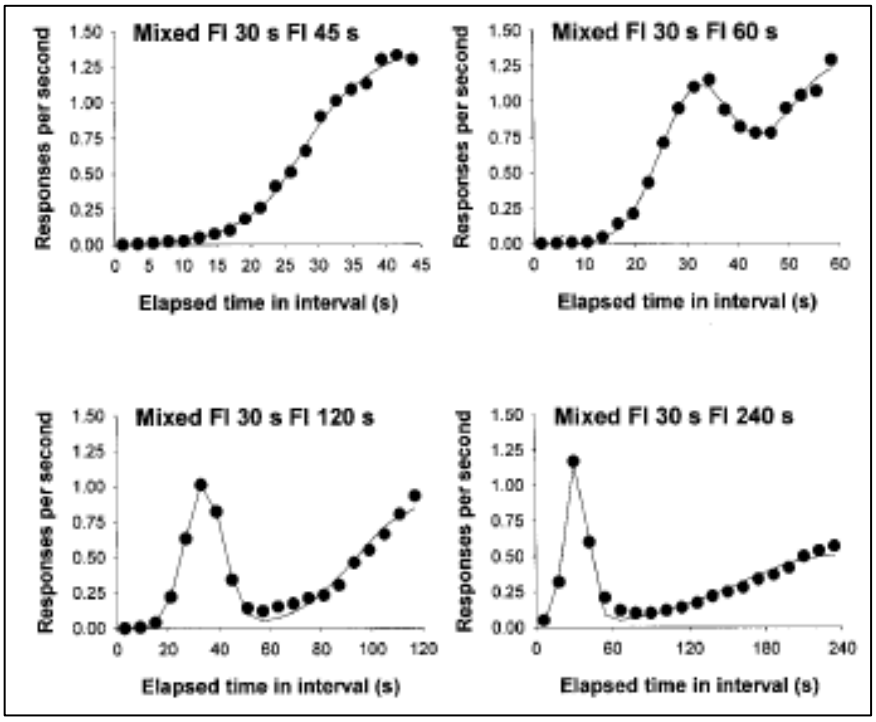

Figure 4. Shows the results of four procedures from Whitaker et al's third experiment which used multiple FI trials of short (FI S) and long (FI L) duration.. Results are similar to that of a peak procedure. From Whitaker, S., Lowe, C. F., & Wearden, J. H. (2003). Multiple-interval timing in rats: Performance on two-valued mixed fixed-interval schedules. *Journal of Experimental Psychology: Animal Behavior Processes, 29,* 277-291, pp. 285 (with permission).

Whitaker et al.'s (2003) results are similar to those found using the peak procedure. These results may show support for Church et al.'s (1991) theory that the peak procedure may provide two sources of reinforcement, where food is the reinforcer at the later FI in Whitaker et al.'s study, and escape from a potentially aversive PI trial is negatively reinforcing in Church et al.'s study.

This study attempted to account for resurgence on the peak procedure. Experiment 1 attempted to replicate Church et al.'s (1991) data from their second experiment using a similar procedure. Based on the results of their first experiment, the authors theorised that the rats anticipated the end of the PI trial and the beginning of the next FI trial. Sanabria and Killeen termed this the *Anticipation Hypothesis* (Sanabria & Killeen, 2007, pp. 127). Escape from the non-reinforced PI acted as negative reinforcement; responding therefore increased towards the end of the PI trial in expectation of reinforcement on the next trial. By varying the length of the longer peak trial, they hypothesised that the resurgence in responding should decrease. For half the rats a 40 s nonfood trial was presented. For the other half, 10 s food trials were matched with a nonfood trial of 10 s, plus an equiprobable random duration of 110 s; 20 s food trials were matched with a nonfood trial of 20 s, plus an equiprobable random duration of 100 s. Therefore total PI trial duration had a mean of 120 s. Results show that shorter (40 s) nonfood trials produced a more positive skew than longer (120 s) nonfood trials. The random 120 s trials produced a flat asymptotic response rate occurring above zero. Nonfood trials signalled by 20 s showed higher albeit flat response rates compared with those with a 10 s signal. Sanabria and Killeen (2007) hypothesised that resurgence may not be due to an animal's anticipation, but rather down to the experimenters' procedure. That is that trial termination cues helped the animals to predict the end of a fixed probe trial. Their results however could not prove this, but rather showed support for Church et al.'s anticipation hypothesis.

In order to test the effect of fixed versus variable PI trials in the peak procedure on possums, this study began by comparing performance on the peak procedure with a variable PI in Condition 1, and a fixed PI in Condition 2. This was repeated in Conditions 3 and 4 respectively to give an ABAB design. Subsequent conditions looked at the length of PI trials on resurgence. These included a much shorter PI (Condition 5, two times that of the FI length), and a

much longer PI duration (Condition 6, 15 times that of the FI length). Sanabria and Killeen (2007) found that when the PI duration was 16 times the FI duration, response rates flattened following the initial peak. Condition 7 returned to a variable PI to further show the reliability, or not, of the effect of changing from a fixed PI to a variable PI.

Experiment 1

1.1 Method

Subjects

The subjects were five female (subjects 1, 2, 4, 6, and 7), and two male (subjects 3 and 5) common brushtail possums (*Trichosurus vulpecula*). Subject 5 died during the first condition of Experiment 1 due to liver failure. All seven subjects were caught in the wild. *Table 1* shows each possum, their age at the beginning of experiment 1, sex, and target weight.

Table 1. *Possums age at the beginning of experiment 1, possums' sex, and possums' target weights (80% of free-feeding weight).*

Subject	Age (years)	Sex	Target Weights (kg)
1	12	F	2.95
2	7	F	3.4
3	6	M	3.3
4	7	F	3.5
5	7-8	M	3.5
6	9	F	4.2
7	2	F	3.3

The possums were weighed weekly, and maintained at their target weight which was 80% of their highest free feeding weight. This was to ensure that they would continue to be motivated to work for the reinforcer. Post experimental food amounts were adjusted for each animal to maintain target body weights. Dock, carrot, apple (depending on availability), and possum pellets were given to possums as a post experiment feed. A mix of barley and cocoa puffs were used as reinforcers during experiments. Possum pellets were given as supplement feed when the possums were not run in an experiment. The possums were exposed to a reverse day/night schedule; where lights came on from 9pm to 9am. Red lights

were used to help experimenters see during feeding and while experiments were running during the possum's night cycle. Experiments began at around 9.30am and occurred 7 days a week. The University of Waikato Animal Ethics Committee gave permission for the subjects to take part in this study (protocol number: 852).

Apparatus

The possums lived and worked in their home cages; Home cages were made of galvanised steel wire, and measured .52 m (w) X 1 m (h) X .56 m (l). Wooden nest boxes were located above the home cages. A sheet of stainless steel acted as a partition between individual cages. Val-Co standard drinkers gave the possums continual access to water in their home cages. The possums worked on a response panel measuring 32.5cm (w) X 35cm (h), which was attached to the front of their home cages. They worked for reinforcement by pressing down on a lever and releasing it. Levers were located at the middle of the response panel. Situated just above the lever was a yellow LED light. Below the lever was an opening allowing the possums access to the food from the magazine during reinforcement. *Figure 5* shows the layout of the response panel.

Procedure

Magazine Training and Lever Shaping

Subject 5 was experimentally naïve and so was shaped to press the lever reliably for food. Following this, the possum was exposed to the peak procedure with very short trial intervals. Reinforced FI trials with a length of 5 s were randomly mixed with nonreinforced trials with a length of 10 s; the ratio of trials was 4:1 respectively. There were 50 trials per session. One session was run each day for four days. At this point, the subject was responding reliably and was getting all possible reinforcers.

Condition 1: FI 20/VI 80 Procedure

Sessions began with the illumination of the light above the levers. Possums were exposed to FI and PI trials, randomly mixed. FI trials lasted 20 s, where food reinforcement was available at the end of the trial (food trials). PI trials were made

Figure 5. Two photographs of the response panel used in the experiments.

up of a fixed interval of 20 s (FI20), and a random interval with a mean of 60 s (VI60). PI trials therefore had a mean time of 80 s. No food reinforcement was available at the end of the trial (empty trials). The ratio of FI trials to PI trials was 4:1 respectively. Trials were separated by a 10 s inter-trial-interval (ITI). On food trials, possums gained 3 s access to reinforcer. Sessions occurred such that no two PI trials could occur back-to-back, and FI trials did not occur four times in a row. Sessions ended after 50 trials or an hour; whichever occurred first. Condition one lasted for at least 50 days for each animal.

Condition 2: FI 20/PI 100 Procedure

The procedure for Condition 2 was the same as for condition 1, except that the PI had a fixed interval of 100 s. Condition 2 lasted for at least 55 days for each animal.

Conditions 3 and 4

Condition 1 and Condition 2 were repeated for at least 15 days (Condition 3 and 4 respectively) for each animal, following the completion of Condition 2. Therefore, Conditions 1-4 acted as an ABAB design.

Condition 5: FI 20/PI 40 Procedure

The procedure for Condition 5 was the same as that for Condition 1-4; except that the PI had a fixed interval of 40 s. Condition 5 lasted for at least 15 days for each animal.

Condition 6: FI 20/PI 300 Procedure

The procedure for Condition 6 was the same as that for Condition 1-4, except that the PI had a fixed interval of 300 s. Condition 5 lasted for at least 15 days for each animal. Sessions ended after 40 trials or 90 minutes, whichever occurred first.

Condition 7: FI 20/VI80 Procedure

The procedure for Condition 7 was the same as Condition 1 and 3. Condition 7 lasted for at least 10 days for each animal.

Table 2 shows the details, and the order of conditions for this experiment.

Table 2 *Order of conditions, the FI length, PI duration, and the number of days spent by each subject in each condition.*

Experiment 1								
			Subject (in bold) and number of days spent in each condition					
Condition	FI	PI	**1**	**2**	**3**	**4**	**5**	**6**
1	20	Variable 80 s	51	58	53	53	0	70
2	20	Fixed 100 s	55	55	56	56	61	61
3	20	Variable 80 s	30	30	30	30	30	30
4	20	Fixed 100 s	15	15	15	15	16	15
5	20	Fixed 40 s	15	15	17	15	15	15
6	20	Fixed 300 s	22	17	20	22	16	22
7	20	Variable 80 s	11	10	10	10	10	11

1.2 Results

Figure 6 displays the data for all six subjects for Conditions 1, 2, 3, and 4. For each animal and condition, the last ten days data were averaged. After Condition 1, Subject 7 died. No data was presented for Condition 1 as this was not collected. Data for Subject 5 was used for remaining conditions. For all graphs, Response Rate per second is shown on the Y axis and Time in seconds is displayed on the X axis. Response rates were calculated using the number of responses made during the peak trials, divided by total time. Data points are average response rates for each 5s. Results for all animals, for all conditions show response rates increased to a peak near the time of reinforcement. When the length of the PI was varied (Conditions 1 and 3), response rates following the initial peak reduced to a rate just above zero. When the length of the PI was fixed (Condition 2 and 4), responding increased. Responding increased to a maximum level of responding in the initial peak for Subjects 1, 2, and 3 during Conditions 2 and 4. Peak rates of responding were higher when the PI was fixed (Condition 2 and 4) than when it was variable, for Subjects 3, and 6.

In *Figure 7* the top axis shows Condition 1 (variable PI) superimposed on top of Condition 2 (fixed PI). Data is averaged over all subjects for the last ten days of each condition. The bottom axis shows Condition 3 (variable PI) superimposed on top of Condition 4 (fixed PI). Data is averaged over all subjects for the last ten days of each condition. The Y axis for both axes shows relative response rate. Time (in seconds) is shown on the X axis. Relative response rates were calculated by dividing each response by the maximum response rate at the peak. Response rates decreased following the initial peak to a minimum near 40 s, or twice the length of expected reinforcement, and then resurged when the duration of the PI was fixed. Response rates at twice the FI (40 s) do not converge for Conditions 1 and 2, as it does for Conditions 3 and 4.

Figure 8 displays the data for all six subjects, for Conditions 5, 6, and 7. For each subject and condition, the last five days data were averaged. For all graphs, Response Rate (in 5 s bins) is shown on the Y axis and Time (in seconds) is displayed on the X axis. Response rates were calculated using the number of responses made during the peak trials, divided by total time.

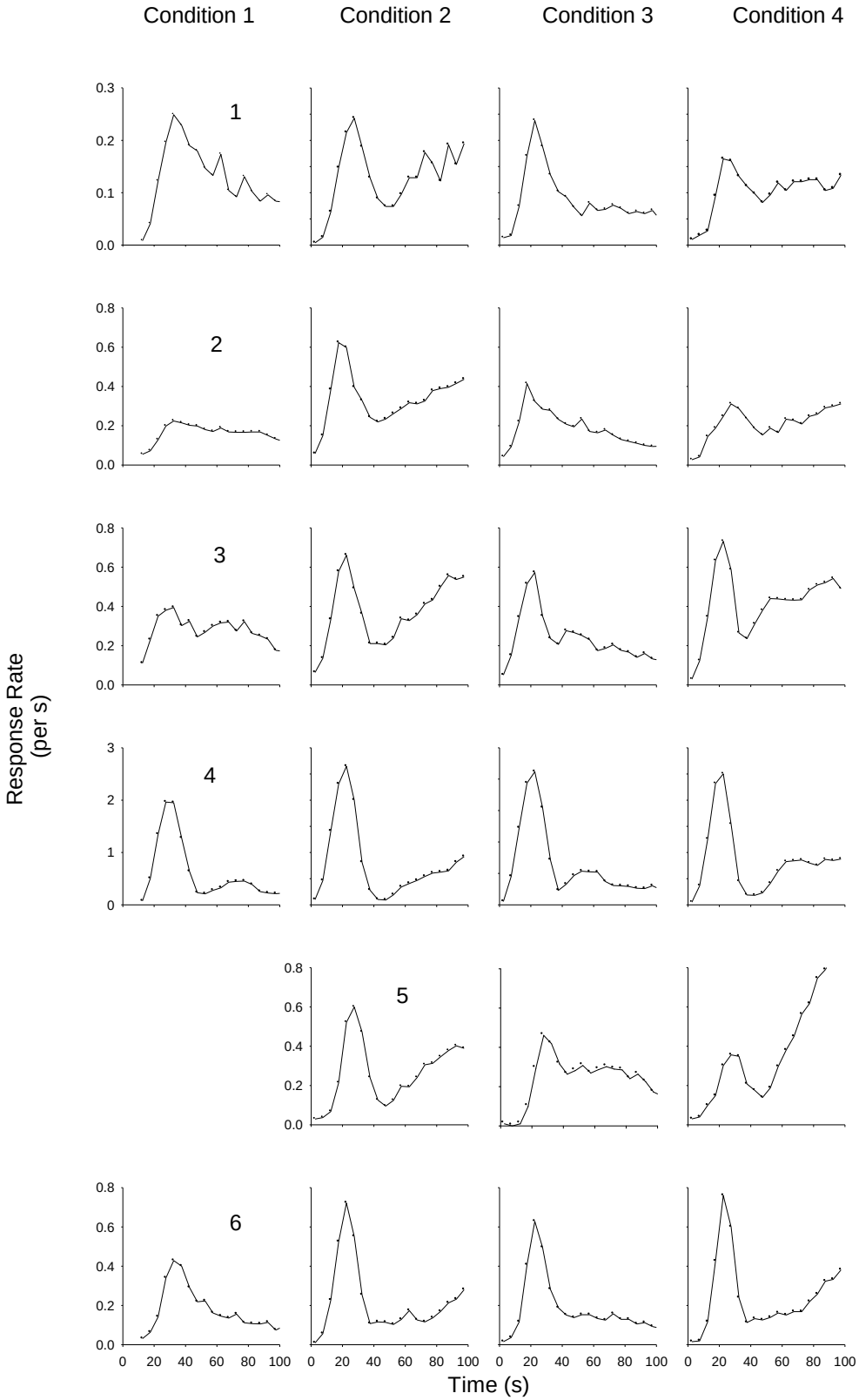

Figure 6. Shows response rate in 5 second bins plotted against time in seconds, for the last 10 days, for each subject, for the first four conditions of this experiment.

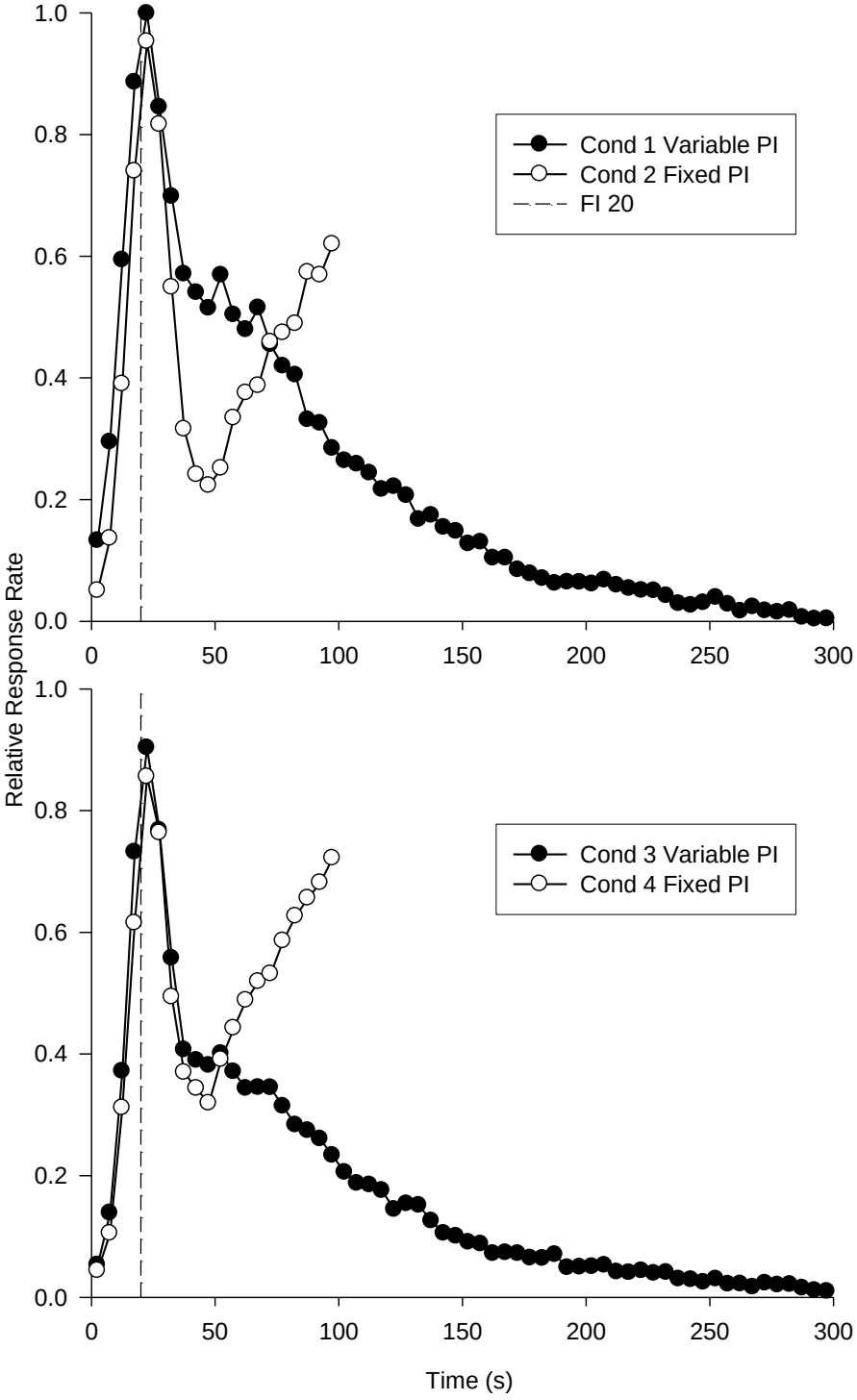

Figure 7. Shows mean relative response rate plotted against time in seconds for all possums, for the last 10 days. Response rates for Condition 1 are superimposed over response rates for Condition 2 in the top axis. Response rates for Condition 3 are superimposed over response rates for Condition 4 in the bottom axis.

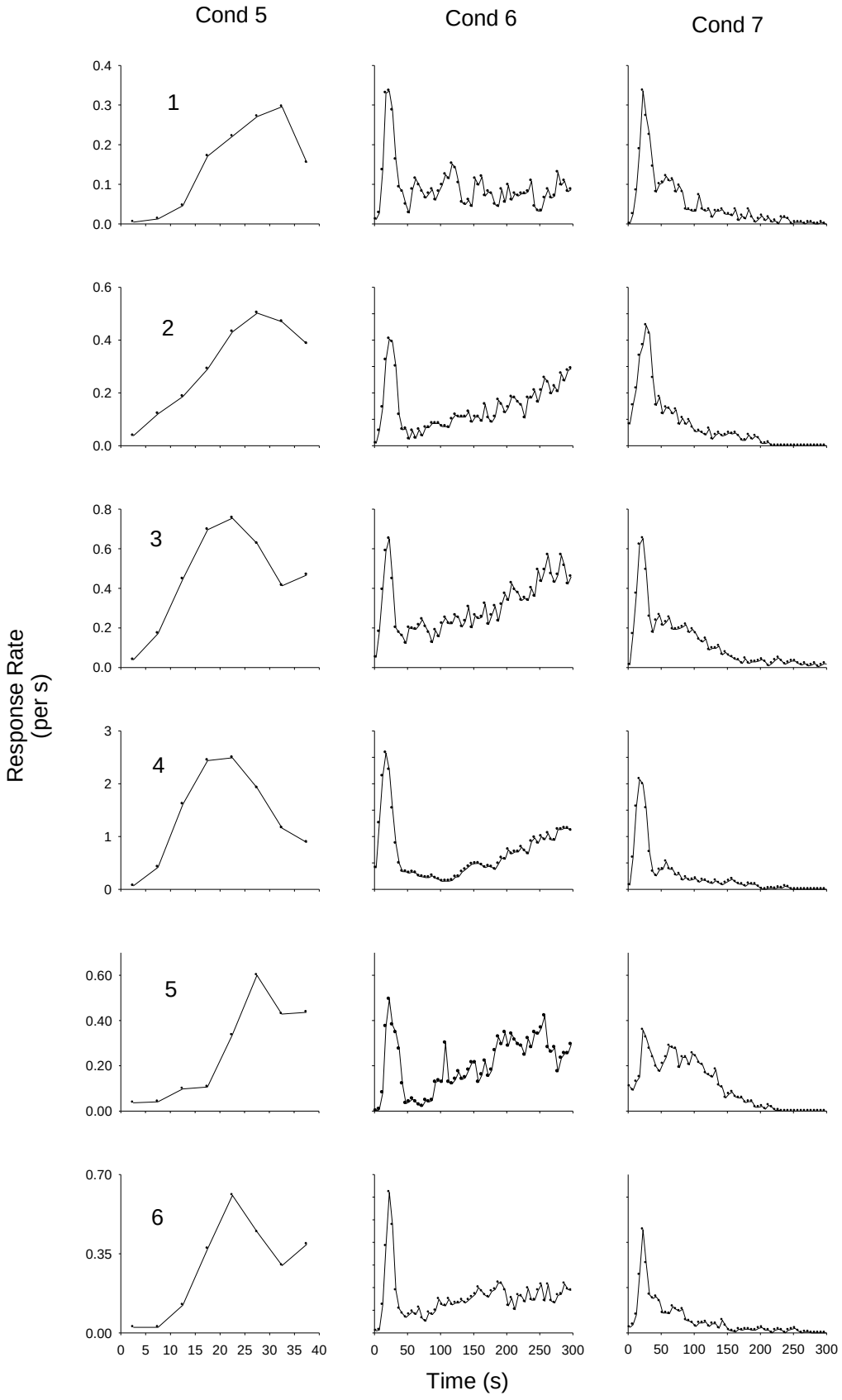

Figure 8. Shows response rate plotted against time in seconds, for the last 5 days, for each subject, for Conditions 5, 6, and 7 of this experiment.

Data points are average response rates for each 5 s. Results for all subjects, for all conditions show response rates increased to a peak near the time of reinforcement. When the length of the PI was fixed (Conditions 5 and 6), response rates following the initial peak increased. When the length of the PI was varied (Condition 7), response rates reduced to a rate just above zero. For Condition 5, for Subjects 3, 5, and 6, some initial resurgence can be evidenced between 30 s and 40 s.

In *Figure 9*, average relative response rates for all animals for the last five days of Conditions 5, 6, and 7, are plotted against the last ten days of Conditions 2 and 4 (averaged together). Relative response rates were calculated by dividing each response by the maximum response rate at the peak. The Y axis shows relative response rate per second. Time is shown on the X axis in seconds. Results show response rates increased to a maximum around the time of reinforcement for all conditions. Responding then dropped away to a minimum around twice the length of the FI. When the PI is fixed, Conditions 2 and 4 averaged together (Fixed PI 100 s), and Condition 6 (Fixed PI 300 s) response rates resurge following the initial peak. When the PI is variable (Condition 7), responding decreased to a rate just above zero.

Figure 10. shows relative response rates, averaged for all animals, for the first trial, first day, first third, second third, and last third of the first four conditions of Experiment 1. Response rates for the last third of Condition 1 are plotted against the first day of the Condition 2, and are indicated by a grey line. Relative response rates for the last third of Condition 2 are plotted against the first day of Condition 3. Relative response rates for the last third of Condition 3 are plotted against the first day of Condition 4. Response rate is plotted on the Y axis. Time in seconds is plotted on the X axis. The graph shows resurgence decreases when the PI is variable (Conditions 1 and 3), and increases when the PI is fixed (Conditions 2 and 4) after one day's exposure to each schedule. Curves for each condition become smoother; both as more days are averaged together over condition thirds, and as the animals' exposure to each condition progresses. *Table 3* shows the mean (this is the equivalent of what Roberts (1981) calls *peak time)* and standard deviation of the function, and Weber fractions (coefficients of variation) for all six animals, for each condition. Weber fractions were calculated

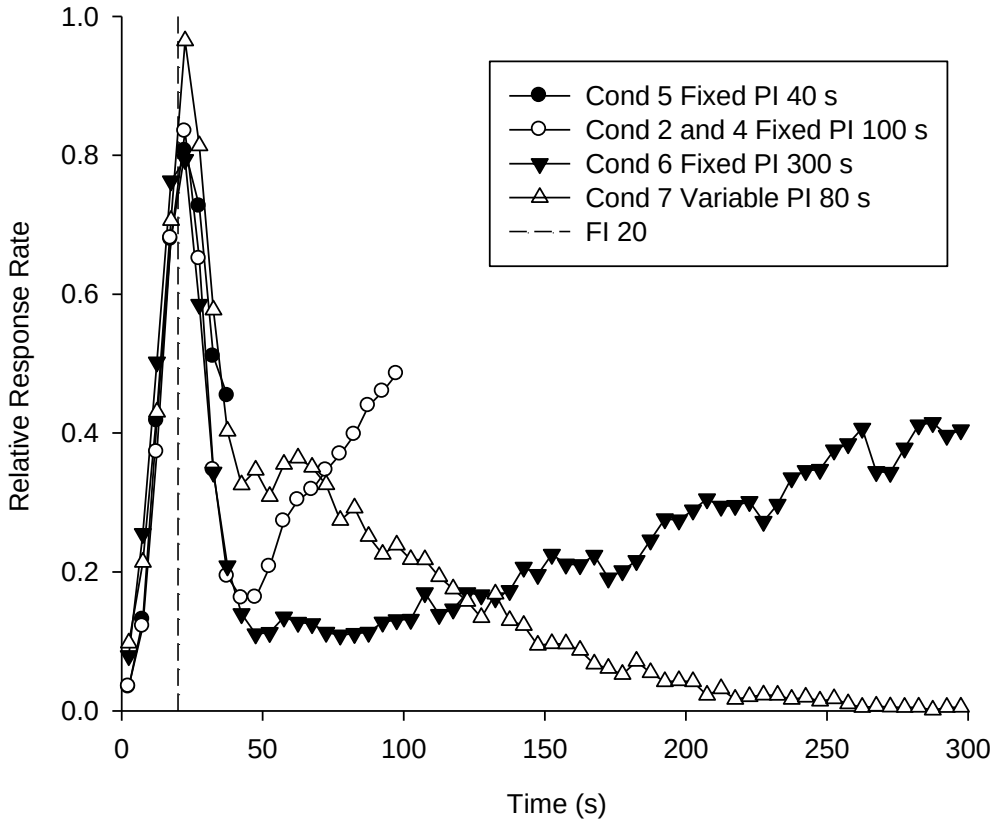

Figure 9. Shows mean relative response rate plotted against time in seconds for all possums, for the last 10 days. Response rates for condition 5 (Fixed PI 40 s), 2 and 4 (Fixed PI 100 s), 6 (Fixed PI 300 s), and condition 7 (Variable PI 80 s) are plotted against each other.

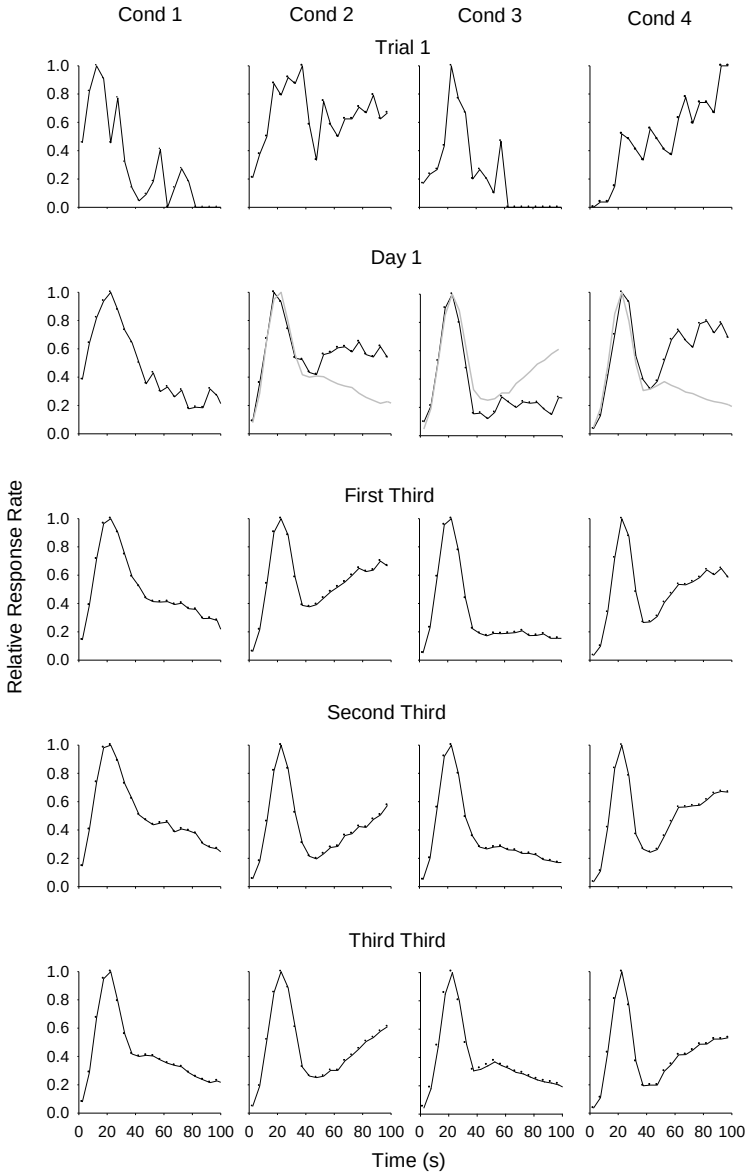

Figure 10. Shows response rates in 5 s bins for all animals, for the first trial, first day, first third, second third, and last third of the first four conditions of Experiment 1. Note the solid grey lines which are the last third of responding for the previous condition plotted against the first day of the current condition

Table 3. *The standard deviation (Sd), mean, and Weber Fractions (WF) for all subjects, for each of the seven conditions. Averages are displayed in the bottom row.*

	Cond 1 (Variable PI 80 s)			Cond 2 (Fixed PI 100 s)			Cond 3 (Variable PI 80 s)			Cond 4 (Fixed PI 100 s)			Cond 5 (Fixed PI 40 s)			Cond 6 (Fixed PI 300 s)			Cond 7 (Variable PI 80 s)		
Subject	Mean	Sd	WF	Mean	Sd	WF	Mean	Sd	WF	Mean	Sd	WF	Mean	Sd	WF	Mean	Sd	WF	Mean	Sd	CV
1	24.55	8.23	0.34	25.80	7.45	0.29	24.93	8.17	0.33	23.97	8.52	0.36	26.88	7.26	0.27	23.03	7.25	0.31	25.47	7.42	0.29
2	24.14	9.60	0.40	20.83	8.25	0.40	23.14	9.50	0.41	24.92	8.67	0.35	25.04	9.02	0.36	24.10	7.55	0.31	23.60	9.45	0.40
3	21.04	9.71	0.46	22.79	8.34	0.37	21.17	8.02	0.38	22.73	7.55	0.33	23.42	8.73	0.37	21.07	8.17	0.39	21.84	7.83	0.36
4	20.23	7.52	0.37	21.15	6.97	0.33	21.87	7.00	0.32	20.41	6.68	0.33	22.43	8.00	0.36	19.24	8.44	0.44	20.61	7.61	0.37
5				26.82	7.29	0.27	29.20	6.53	0.22	24.61	8.59	0.35	27.90	8.07	0.29	26.01	7.15	0.27	23.96	10.06	0.42
6	25.10	8.09	0.32	22.55	6.26	0.28	24.52	7.27	0.30	23.89	6.20	0.26	25.72	7.83	0.30	23.77	6.31	0.27	24.08	7.67	0.32
Ave	23.01	8.63	0.38	23.33	7.42	0.32	24.14	7.75	0.33	23.42	7.70	0.33	24.70	8.17	0.33	22.24	7.54	0.34	23.12	7.99	0.35

for the first 40 s (twice the FI duration) of each trial using the formula given in Equation 1. Weber fractions were calculated for the first 40 s of PI trials because the decrease in responding following the first 40 s on variable PI conditions (Conditions 1, 3, and 7) would make it hard to compare with fixed PI conditions (Conditions 2, 4, 5, and 6) where responding increased.

Results show that as standard deviation varies, so too does the mean. Weber fractions therefore, remain relatively constant throughout conditions. With the exception of a slightly higher Weber fraction for Condition 1, there is little change throughout the rest of the experiment. A one way repeated measures analysis of variance (ANOVA) was conducted and revealed that there was no significant differences between Weber fractions for the seven conditions $F(6, 29) = 1.140$, $p = 0.365$. A one way repeated measures analysis of variance (ANOVA) was conducted for means of the function for Conditions 4, 5, and 6. There was a significant difference between means for Condition 5 (PI 40 s) and Condition 4 (PI 100 s), $F(2, 10) = 13.067$, $p = 0.002$. There was a significant difference between means for Condition 5 (PI 40 s) and Condition 6 (PI 300 s), $F(2, 10) = 13.067$, $p = 0.007$.

1.3 Discussion

The aim of this study was to use a similar procedure to that used by Church et al. (1991) in their second experiment, with possums as subjects, to investigate response resurgence on the Peak Procedure. Results from this study showed that responding increased to a peak around the time of reinforcement (20 s) on peak trials for all seven conditions. This result is similar to that found by Roberts (1981). Two different types of PI schedules were used in the first four conditions of the present study. One was fixed and the other was variable. The hypothesis was that responding following the initial peak would decrease when the PI was variable and increase when it was fixed. The procedure for Condition 1 included a variable PI with a mean of 80 s; Condition 2 included a fixed PI 100 s. These conditions were repeated for Conditions 3 and 4 respectively to give an ABAB experimental comparison. The results support Church et al.'s (1991) theory that when the PI is fixed, responding following the initial peak will resurge, and that when the PI is variable, responding will decrease to a minimum just above zero. The results using the ABAB experimental design showed the predicted fall and rise of response rates at the end of the PI, as conditions changed from having a fixed PI to a variable PI duration were reliable.

Condition 5 of this experiment investigated whether responding would resurge when the fixed PI was shortened from 100 s to twice that of the FI (Fixed PI 40 s). Responding started to resurge following the initial peak for two of the subjects (Subject 3 and 6). However when averaged across all animals, this initial resurgence was not evident. This result was similar to that found by Taylor et al. (2002). Taylor et al. used the peak procedure with a PI length 1.5 times the FI duration. Their results found that responding increased to the time of reinforcement, and decreased to a minimum at the end of the trial. Sanabria and Killeen (2007) also found that when the length of the PI was less than twice that of the FI, no resurgence in responding was evident. The fact that responding does not resurge when the PI is twice the FI duration may be due to there not being enough time to do so. If the PI was longer than twice the FI duration, then there is a chance for responding resurge. This can be seen in the results for Conditions 2 and 4 of this study, which used a PI duration of 100 s. Results from PI trials showed that, following the initial peak, responding increased towards the end of the trial. This finding is similar to that of Church et al. (1991), who exposed rats

to a peak procedure with an FI 20 s and a PI 120 s, and also found that responding increased towards the end of the trial.

The PI in Condition 5 was increased to a duration 15 times that of the FI (300 s). Sanabria and Killeen (2007) used a peak procedure with a PI duration 16 times that of the FI (FI 15 s, PI 240 s). In their study the authors found that there was no second peak at this extreme PI duration; rather responding decreased to a low level and remained constant through to the end of the trial. The present experiment found that responding increased towards the end of the trial; which is not consistent with the results reported by Sanabria and Killeen. Condition 7 of this experiment returned to a variable PI with a mean of 80 s as used in Conditions 1 and 3. Responding did not resurge, but rather decreased to a minimum just above zero. This result is consistent with that of Church et al. (1991), that when the PI is fixed, responding will resurge, and when the PI is variable, responding will decrease to a low level. The fact that responding resurged when the PI trial was fixed, and did not resurge when the PI trial was variable as conditions changed, shows just how robust this effect is.

Response resurgence in the present experiment did not include a secondary peak as reported by Kirkpatrick-Steger et al. (1996). *Figure 7* shows normalised response rates, averaged over all animals for Conditions 1, 2, 3, and 4. These averaged results show no secondary rise in responding. Subject 4 shows a noticeable peak in responding at about twice the FI during Conditions 1, 3, and 4. This can be seen in *Figure 6*. Kirkpatrick-Steger et al. (1996) found resurgence in the form of a second peak occurs only when the length of PI trials was four times that of FI trials (FI/PI=4). None of the conditions in this experiment used a PI trial four times the length of the FI. With the exception of Subject 4, the subjects as a whole did not show a secondary rise in responding. This is consistent with Kirkpatrick-Steger et al.'s results. Zeiler and Powell (1994) analysed data for each individual PI trial on the peak procedure. Their results showed that there were few distinct peaks on individual trials, and that usually, responding occurred at a steady rate; Zeiler and Powell's conclusion being that the observable peak is an artefact of averaging responses from a number of PI trials. Kirkpatrick-Steger et al.'s results and that of Subject 4 for this experiment, that show a secondary rise in responding may be accounted for by the responses being averaged over many PI

trials. An analysis of individual trials may not show this unique pattern of responding.

To look at how long it took for response resurgence to decrease and increase when the PI was variable and fixed respectively, results for the first four conditions of this experiment were graphed in a similar way to Kirkpatrick-Steger et al. (1996, *Figure 2*, p. 450). Response rates, averaged over all animals are shown for first trial, first day, first third, second third and last third of each condition in *Figure 12*. Following Condition 1 with a variable PI, resurgence in response rates towards the end of the PI trial is obvious after only one day's exposure to a fixed PI in Condition 2. Similarly, after one day's exposure to a variable PI (Condition 3) and fixed PI (Condition 4), resurgence can be seen to decrease and increase respectively. While there is very little in the research literature to compare these results with, a study by Balci et al. (2008) provides some insight into how response resurgence seen in this study can increase and decrease so rapidly as conditions change. The authors used an algorithm to measure the start and stop times of responding by mice on the peak procedure. They found that temporal precision was mediated by the stop times (decrease in responding following the initial peak) shifting closer to the peak, rather than the start times (increase in responding towards the peak) on peak trials. Stop times appeared, or rather were *acquired* after only three to five sessions for individual animals. Balci et al.'s findings give an insight into how responding by animals in the present study resurged when the PI trial was fixed and did not resurge when the PI trial was variable, after exposure to only one session of each of these trials.

As the duration of the PI increases, the rate of reinforcement, or reinforcer magnitude, decreases. BeT suggests that reinforcement rate controls the rate of an animal's internal clock, as the rate of an animal's internal pacemaker is proportional to the rate of reinforcement (Killeen & Fetterman, 1988). MacEwan and Killeen (1991), using pigeons as subjects, showed that if they reduce the rate of reinforcement by offering less reinforced trials on the peak procedure, they could slow down the animals' internal pacemaker. Their results from PI trials show that the peak at the time of reinforcement shifted to the left. This is because the pigeons internal pacemaker speeds up and they overestimate time. BeT in the present experiment would predict that as the PI interval increases, the rate of reinforcement would decrease; this would result in lower peak function means,

and a shift of these means to the left. Results showed that when reinforcement rate increased (from a PI 300 s and PI 100 s to a PI 40 s) there was a peak shift to the right, and that this shift was significant. This can be seen in *Table 3*, where means for individual animals can be compared for Condition 5 (PI 40 s), Condition 4 (PI 100 s) and Condition 6 (PI 300 s). This is the opposite of what would be expected by BeT.

Weber fractions when related to timing are otherwise known as coefficients of variation; where the standard deviation of the peak function is divided by the mean of the peak function. This is given in Equation 1. Weber fractions were calculated for the first 40 s, or for the initial peak of PI trials. This is in accordance with other studies (Lejeune et al., 1998; Sanabria & Killeen, 2007), and made comparisons of the different conditions easy. SET (Gibbon, 1997) would predict that Weber fractions would remain constant for each condition of this study. *Table 3* shows Weber fractions for each condition of this experiment. Results show that Weber fractions remain constant throughout all conditions. When changing the PI schedule in the present study, be it variable or various fixed lengths, there is no significant effect on FI performance, and therefore the animals timing accuracy. This gives support for Gibbon's (1997) SET. The average Weber fraction for all animals for Condition 1 is slightly higher than those for the remaining conditions, but this difference is not significant, and may be explained by the fact that data for Subject 5 was not included in Weber fractions for all animals in Condition 1 as it was for subsequent conditions. Since Subject 5 had much lower Weber fractions than other animals for Condition 2 onwards (as can be seen in *Table 3*), we can assume that if Subject 5 was included when calculating the average Weber fraction for Condition 1, then the result would be similar to that of other conditions.

The top axis of *Figure 7* shows that response rate at 40 s into the trial is higher for Condition 1 than Condition 2. The bottom axis shows that responding at 40 s for Condition 3 and Condition 4 occurred at a similar rate. This convergence of response rate for Conditions 3 and 4, following on from the earlier conditions may be put down to the animals' prolonged exposure to the peak procedure. Kaiser (2008) found that the descending slope, following the usual time of reinforcement on the non-reinforced PI trials, steepened as training with PI trials continued. Previous experience with the peak procedure in the present

study may have affected the shape of the curve, leading to the similar rates of responding at 40 s for Condition 3 and 4, as seen in the bottom axis of *Figure 7*. The subjects used in this experiment had been exposed to the peak procedure in another study at this laboratory two years ago (Lockhart, 2011). That the subjects were not naïve to the peak procedure may have had an effect on the results. But this can be accounted for by the fact that it was the first time the subjects were exposed to the peak procedure with a variable PI in Conditions 1, 3, and 7. Also, Subject 5 was brought in at the beginning of Condition 2 as an experimentally naïve animal, and her individual results are similar to the other animals for Condition 2 onwards. Therefore any effect of pre-exposure to the peak procedure on results can be accounted for by the naivety of the subjects to variable PI trials, and the similarity of results of experienced animals to Subject 5, who was experimentally naive.

Church et al.'s (1991) anticipation theory explains that an animal exposed to the peak procedure learns to time the duration of fixed probe trials. An increase in responding to the end of the trial suggests that an end to a long trial without reinforcement may be negatively reinforcing. This is supported by the results of Whitaker et al. (2003). The authors used concurrent FI schedules of varying ratios. When one compares performance at a ratio of 1:4 and 1:8 (FI 30:FI 120, and FI 30:FI 240 respectively) as shown in the two bottom axes of *Figure 4*, graphed results look almost identical to performance on fixed PI trials of this experiment (Conditions 2, 4, and 6), and that found by those using a peak procedure with FI:PI ratios of similar lengths (Church et al., 1991; Sanabria and Killeen, 2007).

The decrease in responding when the PI is variable (Conditions 1, 3, and 7) may be partly due to less PI trials occurring at later durations; a factor not mentioned by Church et al. (1991). The trial durations in this study were generated randomly. This meant that there were fewer trials, and therefore fewer opportunities to respond at greater PI durations. However, responding can be seen to decrease immediately following the time of reinforcement (20 s) for Conditions 1 and 3 (Variable PI 80 s) in the top and bottom axes of *Figure 7*. This shows that when the variable PI trials were shorter and offered more opportunity for responding, response rates still decreased.

It may not be the end of the PI trial that acts as a discriminative stimulus, and is therefore reinforcing. It may be the end of the ITI and beginning of the next

reinforced trial that is reinforcing. Further research should explore the effect of a peak procedure with a variable ITI on response resurgence. Resurgence may also be due, in part to the simple fact that there is only one stimulus with which to engage behaviour. That is, there is nothing else for the animal to do but press the lever on offer. Future research could introduce a means for other behaviour during the PI. For example, offering a second lever that becomes active following the FI duration on peak trials should hypothetically reduce responding on the first key. This may in turn eliminate response resurgence.

Sanabria and Killeen (2007) found that responding did not resurge when the PI duration was 16 times that of the FI, but rather decreased to a low level towards the end of PI trials; a result similar to that of Church et al.'s (1991) second experiment where responding did not resurge as the PI trial was variable. This study found a second rise in responding when the PI duration was increased to 15 times that of the FI. Future research could look into extending the PI length further than 15 times the FI duration. This may result in either a decrease of responding, or perhaps a flattening response rate following the initial peak. There were no distinct procedural differences between the present study and that by Sanabria and Killeen that may hint at the difference in the results of each.

In conclusion, results from the present study support Church et al.'s (1991) anticipation theory that escape from a non-reinforced PI trial is negatively reinforcing. As long as the animals can track the end of the PI trial, responding will resurge; if it is variable, animals cannot predict the end of the trial and so response resurgence does not occur. Future research should look at providing a means for other behaviour during the PI trials. It may also be that PI lengths that are greater than 15 times the FI duration can cause responding to flatten following the initial peak. Future research could increase PI lengths to durations greater than 15 times the FI.

Appendix A

Excel files with raw data are attached on accompanying CD

Appendix B

Possum weights and post feed amounts during experimentation are attached on accompanying CD

Appendix C

Ethics approval is attached on accompanying CD

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