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Stimulus Control by Timing in Pigeons

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STIMULUS CONTROL BY TIMING IN PIGEONS

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by

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ABSTRACT

Timing has been widely studied in humans and animals across a variety of different timescales. The concept of time as a stimulus dimension, and how it is processed relative to other stimulus dimensions, has only recently been scrutinized. In the current work I present a review of interval timing as it relates to stimulus control, and discuss the role of attention in timing in the context of three sets of studies in pigeons.

In the first set of studies, I analyzed whether the presence of a non-reinforced timed stimulus would disrupt timing of a stimulus reinforced on a fixed-interval schedule. In Experiment 1, half of the pigeons were trained on a 60-s fixed interval schedule of reinforcement signaled by onset of a sidekey; the other half of the birds had those same reinforced trials interspersed among trials in which the onset of a different sidekey signaled 60-s followed by non-reinforcement. Groups were reversed in the second phase of experimentation. Obtained peak-time curves showed flattened responding to the reinforced stimulus for birds which also received non-reinforced trials, suggesting that control by interval timing was overshadowed by the presence of a food/no food cue. Experiment 2 ruled out the possibility that this effect was caused by differences in reinforcement. Pigeons' responding on this task was not controlled by timing because the visual discrimination based on food vs. no food was more salient than the temporal discrimination.

In the second set of studies, I examined the ability of pigeons to track the identity of multiple stimuli presented in order across a temporal interval terminating in reinforcement. In Experiment 1A, pigeons responded to the final stimulus in a three-item sequence regardless of the preceding order of stimuli, or even if previous stimuli had not

been presented, suggesting that the birds attended only to the reinforced stimulus and not to the order of stimuli. In Experiment 1B, pigeons were presented with baseline non-reinforced trials in which the order of the first two stimuli was reversed, and results showed that they responded differently to the third stimulus based on the order of stimuli. Experiment 2 extended these results with a five-stimulus sequence. Though birds showed only a weak appreciation of order, they nonetheless responded differentially based on temporal order.

In the final study, I observed the tendency of pigeons to anticipate or perseverate after a mid-session reversal of response contingencies. The birds tended to make errors around the reversal point when the discrimination was a visually-based (red vs. green) task, and these errors were conclusively shown to be due to interval timing from the start of the session. However, when presented with a visual-spatial version of the same task, pigeons no longer made timing-induced errors and instead used a reinforcement-maximizing approach. The dimension of discrimination affected the strength of memory for the response and outcome of the previous trial, and in turn affected the tendency of birds to base their responding on an error-prone interval timing strategy.

Co-Authorship Statement

Chapters 2, 3, and 4 are separately published as papers with the Candidate (Neil McMillan) as first author and the Supervisor (Dr. William A. Roberts) as co-author. The Candidate independently designed and performed the experiments described, analyzed the results, and wrote the papers as presented herein. The Supervisor was consulted on best methods for designing the experiments and edited the papers. Copyright licenses for all papers are included in Appendix B.

Acknowledgments

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My Ph.D. committee members, Drs. Scott Macdougall-Shackleton and David Sherry, have likewise been stalwartly supportive across my graduate degrees and have always provided thoughtful insight and questions. That they have served as examiners for my Master's defense, comprehensive exam, and Ph.D. defense speaks to the level of effort and interest they have placed in my academic career, and I appreciate all the work they have contributed to my successes.

I would also like to thank Drs. Martin Kavaliers and Mark Cole for serving on my defense committee. Special thanks to Dr. Angelo Santi for not only serving as my external examiner, but also being the driving force behind my application to graduate school. His early training is the foundation for all of my current and future work in the field.

I thank my funding sources, the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Ontario Graduate Scholarship program (OGS). With their funding, I have contributed to psychological knowledge, and this is a testament to the fundamental support for scientific advancement in Canada.

I thank my labmates, Chelsea Kirk and Krista Macpherson, as well as my pseudo-labmate Caroline Strang, for their help in running my animals as well as maintaining operation of the lab in general. Moreover, they have been great friends at work and outside of it, and I do not take lightly the contribution they have made to the maintenance of my sanity over the years.

I thank my pigeons, just in case one day they learn to read.

Finally, I dedicate this thesis to my parents, whose endless support is best exemplified by the way in which they shamelessly pretend to understand why I do what I do. Knowing that they are proud of my accomplishments has been the best reinforcer I could have hoped for.

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Chapter 1

General Introduction to Interval Timing

Interval timing is the timing of stimulus durations of seconds to minutes (or even hours) and has been of great interest to researchers in a wide variety of behavioral and cognitive neuroscience disciplines (Buhusi & Meck, 2005). Whereas circadian timing is coordinated by the suprachiasmatic nucleus and is concerned with regulating daily (24-h) patterns such as the sleep cycle and feeding, and millisecond timing is localized to the cerebellum and assists mostly in motor coordination, interval timing is possibly distributed over a complex striato-thalamo-cortical pathway and is useful over a huge range of timescales and for different purposes. Timing is pervasive across species (Richelle & Lejeune, 1980), interval timing is considered in the literature to be an obligatory, automatic process (e.g., W. A. Roberts, Coughlin, & S. Roberts, 2000; Sutton & W. A. Roberts, 1998; Tse & Penney, 2006), and timing is prevalent wherever the environment features temporal regularities (Macar & Vidal, 2009). All events occur at some place within some time, so it is perhaps not surprising that animals seem to rely heavily upon timing to best predict the occurrence of salient events.

Interval timing in animals is frequently measured through the use of the peak procedure (Catania, 1970; S. Roberts, 1981), in which subjects are trained on a fixed-interval (FI) reinforcement schedule and then unreinforced peak probe trials are introduced, typically of double or triple the length of the contingent FI. Curves showing rate of response over the course of peak trials typically show a normal distribution of responses over the interval, with the peak at or around the expected point of food reinforcement (see Figure 1.1a). The width of the curve around the peak, the response duration spread, represents noise in the representation of time and exhibits scalar properties (Gibbon, 1977). Peak-trial responding is thus consistent with Weber's
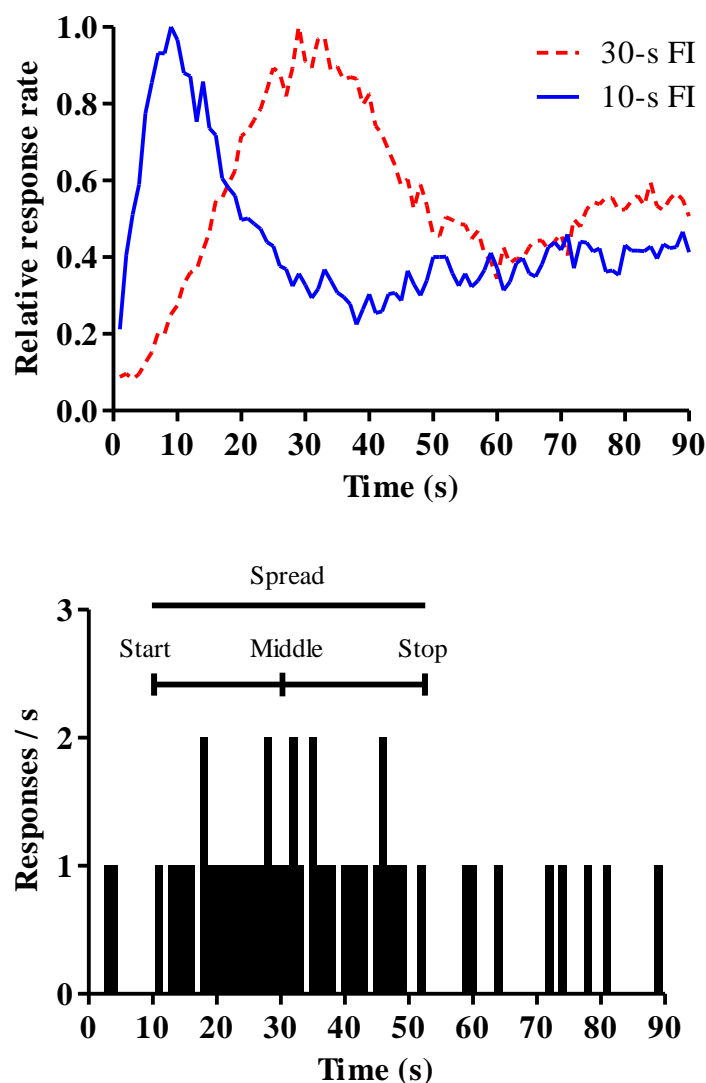
Figure 1.1. (A; Upper Panel) Example of a typical peak-time curve, generated from previous data in our lab by averaging data gathered on empty peak trials for birds trained on 10-s or 30-s FIs. Response data relativized to a maximum of 1 response per second.

(B; Lower Panel) Example of responding on a single empty peak interval trial from a bird trained with a 30-s FI in a previous study in our lab. This illustrates the characteristic break-run-break function in responding, which when averaged across trials and subjects produces a graded response curve similar to that in Panel A. Start time reflects the shift from low to high states of responding, and stop time the change from high to low states of responding; middle time is presumed to reflect the expected time of reinforcement.

Law, wherein the degree of error (i.e., response spread) is proportional to the length of the interval timed. Scalar variability is one of the primary findings in the peak procedure that all models of timing must account for.

Theories of Interval Timing

Several theories have been developed to explain the data obtained with the peak procedure. In the most studied of these theories, scalar expectancy theory (SET), the internal clock consists of a neural pacemaker that emits pulses, a switch that closes when a signal indicates the beginning of an interval to be timed, and an accumulator that sums pulses from the pacemaker (Gibbon & Church, 1984, 1990; Gibbon, Church, & Meck, 1984). The numbers of pulses accumulated at the moment of reinforcement on training trials are stored in reference memory and randomly retrieved as criterion values on subsequent trials. A comparator mechanism continually compares accumulated pulses with the criterion value and initiates responding when the difference between the accumulator and criterion drops below a threshold. Because the difference between the accumulator and criterion is recorded as an absolute value, the comparator also stops responding when the difference threshold is exceeded. Although individual trials tend to involve break-run-break periods of all-or-nothing responding (Cheng & Westwood, 1993; Gibbon & Church, 1990; see Figure 1.1b for an example), averaging trials that start and stop at different times yields smooth Gaussian-like curves. Because SET uses the same comparator process to start and stop responding, the symmetry of peak-time curves is predicted.

In alternative theories of timing, behavioral judgments of time have been more closely related to traditional associative processes. The behavioral theory of timing

(Killeen & Fetterman, 1988) suggests that a pacemaker initiated at the beginning of an FI advances an animal through successive adjunctive behavioral states, and that the behavioral state present at the moment of reinforcement will be conditioned to elicit responding. Because the pacemaker advances according to a Poisson process, a gradient of responding should be found around the FI on peak timing probe trials. However, one of the issues facing the behavioral theory of timing is that there has been little success in showing these deterministic patterns of behavior during the temporal interval (Lejeune, Cornet, Ferreira, & Wearden, 1998). Machado (1997) offered a similar dynamic behavioral model based on real time, called the learning-to-time model, in which a stimulus that initiates an FI activates a series of behavioral states. Each state becomes associated to some extent with the reinforced operant response, but responding during non-reinforced states is weakened through extinction. Importantly, because time is based on the diffusion of activation across many states, this model does not experience the same problems as standard behavioral timing theory when faced with non-monotonic behavior as subjects time.

Contrary to behavioral state-based clocks, trace-based clocks measure time based on continuous neural traces. For example, in Staddon and Higa's (1999) multiple-time-scale model, timing is based on the formation of associations between the reinforced response and the strength of a memory trace of a signal that began the interval to be timed. These traces decay, and traces with strengths near those of previously reinforced intervals will evoke more responding than those that are either stronger (shorter intervals) or weaker (longer intervals). In the conceptually similar spectral timing model (Grossberg & Schmajuk, 1989), different spectra of gated neurons are active at different

times after the onset of a conditioned stimulus, providing a cascade of different timing signals with the peaks in these traces becoming differentially associated with the unconditioned stimulus.

Finally, recent theories of timing have focused on neural oscillators as the foundation of the clock process, such as the multiple-oscillator model (Church & Broadbent, 1990). Oscillating neurons fluctuate back and forth from -1 to 1 states sinusoidally, such as seen in the neurons (or neural networks) guiding heart rate, breathing rate, and circadian rhythms. Theories of time involving oscillators generally suggest that the onset of the conditioned stimulus synchronizes the period of many oscillators, which then beat at different rates. At the time of reinforcement, the current set of states across the oscillators is stored, and this stored state serves as the measure of time. The striatal beat-frequency model (Matell & Meck, 2000, 2004) similarly suggests that timing results from detection of coincident oscillator states by spiny neurons in the striatum. Like the trace models discussed previously, oscillator clocks are biologically plausible because they make use of actual features of neural networks (as opposed to the more conceptual/metaphorical framework of SET). Recent evidence has also suggested that animals have a nonlinear sensitivity to time, which is consistent with oscillator models (see Crystal, 2012). The striatal beat-frequency model, in particular, is attractive because of its combination of the biologically-grounded beat frequency model (Miall, 1989) with principles from the well-studied SET.

Many timing models presume the interval clock to be an internal neural process which is not affected by outside stimulation other than the initial CS (i.e., the cue to start) and the US (the cue to stop). While these models thus tend to be variably successful at

predicting results of more complex timing experiments (e.g., timing multiple stimuli simultaneously), they also tend to be silent on how time might be processed in competition with non-temporal processes. Typical models of timing do not generally include explicit parameters for signal characteristics (e.g., different modalities of stimuli to be timed), attention sharing, or reward value effects, and instead tend to assume that time is automatically processed by the internal clock. A wealth of literature has shown various effects of non-temporal aspects of stimulus presentation on the timing of intervals or gaps in intervals, with accuracy affected by stimulus modality (Meck, 1984; W. A. Roberts, Cheng, & Cohen, 1989), stimulus intensity (Wilkie, 1987), and filled vs. empty intervals (Miki & Santi, 2005; Santi, Miki, Hornyak, & Eidse, 2005; Santi, Keough, Gagne, & Van Rooyen, 2007). Common theories of timing typically must be amended in a post-hoc manner to account for attentional or stimulus dimension effects. For example, attentional models of timing in humans (Block & Zakay, 1996) explicitly stated that the 'switch' mechanism represents attentional control, and fluctuations in the switch lead to 'loss' of accumulated pulses and a tendency to underestimate interval duration.

Alternative theories of timing account for non-temporal effects on timing by omitting the clock process altogether. Ornstein (1969) suggested that timing is simply a deduction of elapsed duration by the amount of information processed: shorter intervals naturally allow for less processing, while long intervals allow for a greater amount of processing. According to this theory, filled intervals and high-intensity stimuli are predicted to be timed as longer than empty intervals or low-intensity stimuli because more information-processing occurs and thus time is perceived as subjectively longer; this effect is commonly observed in data (e.g., Santi et al., 2005; Wilkie, 1987).

Likewise, a number of recent theories have attempted to fit clockless associational

models (Arcediano & Miller, 2002; Dragoi, Staddon, Palmer, & Buhusi, 2003), with the

general suggestion that interval timing can arise simply through the competition between

reinforced and non-reinforced behaviors across an interval and the memory for recent

reinforcement. In essence, the operant response is emitted not because the time of

reinforcement is predicted, but rather because the operant response is consistently more

successful as the interval elapses. Clockless models are attractive because they integrate

seamlessly into existing information processing or learning theory without the need to

conjure an independent timing mechanism.

Learning in the Peak-Time Procedure

Regardless of the type of clock (or lack thereof) used in timing models, each

model must account for the observed data in peak-time procedures. Recent evidence now

suggests that different learning processes may be responsible for the pre- and post-peak

limbs of the peak-time curve. For example, Matell and Portugal (2007) found that rats

trained to make a nose-poke response at an FI of 15 s showed a narrowing of the peak-

time curve on extended test trials compared to brief initial test trials. This effect was

asymmetrical, however, because rats stopped earlier on later trials than on earlier trials

but showed no difference in start times between earlier and later trials. Kirkpatrick-

Steger, Miller, Betti, and Wasserman (1996, Experiment 1) also showed a similar effect

in pigeons, wherein birds were trained on 30-s FI discrete trials, followed by testing with

120-s peak trials. Responding increased rapidly toward the 30 s expected FI across all

peak trials, but on the first peak trial, responding decreased only very gradually after 30 s,

and peaks only narrowed by the end of the first six-trial block. A mostly symmetrical peak was noted on days 25-30, and did not change substantially thereafter.

Even more dramatic effects were reported by Kaiser (2008) who trained rats to press a lever for food reinforcement on signaled FI 30-s trials. The peak-time curve found when non-reinforced probe trials were introduced gradually changed from a flat curve to a more symmetrical Gaussian-like curve over 10 blocks of testing. This change in the peak-time curve was primarily caused by an initially shallow right limb of the curve that became progressively steeper over sessions. Interestingly, this dramatic change in the shape of the peak-time curve was most marked when non- reinforced probe trials were introduced on 10% or 25% of the training trials but not when they were introduced on 50% of the training trials. If one assumed that the increased steepness of the right-limb of the peak-time curve results from extinction of post-FI responding, this finding is puzzling because a higher percentage of non-rewarded trials should lead to faster extinction.

One final example is found in a study of C3H mice trained to press a lever for milk reinforcement on a light-signaled FI 30-s schedule (Balci, Gallistel, Allen, Frank, Gibson, & Brunner, 2009). Responding on non- reinforced probe trials showed a consistent rise in responding over the first 30 s that changed little over 16 days of testing. On the other hand, mice showed no cessation of responding after 30 s on Day 1. Over successive test days, the right limb of the curve declined until it looked like the typical Gaussian peak-time curve by the final days of testing. Analysis of individual trials suggested that individual mice abruptly adopted stop behavior at different points during testing.

These new findings suggest that the typical FI scallop seen in the left limb of the peak-time curve may develop early in FI training as a consequence of reward expectation and continue to be shown on non-rewarded probe trials. The right limb of the peak-time curve, however, may be controlled by extinction or learned inhibition of responding that occurs mainly through experiencing non-rewarded trials during the test phase. Such findings indicate the importance of associative learning in studies of timing and suggest that other learning processes might be involved in the study of behavioral timing. This is of particular interest given observations of cue competition effects in timing (McMillan & Roberts, 2010). When pre-trained with a 'short' (10 s) stimulus interval, pigeons failed to show accurate timing of a 'long' (30 s) stimulus trained later in compound with the short stimulus. In this experiment, pigeons appeared to attend only to the most temporally-proximal stimulus onset, and failed to time a longer-duration stimulus despite pigeons in other conditions showing no such deficit with timing the 30-s stimulus. An outstanding question is whether similar competition effects can cause failure to show accurate timing in the presence of highly salient non-temporal stimuli.

Though interval timing has been extensively studied using tasks such as the peak-time procedure and the temporal bisection task (Church & Deluty, 1977), timing is less frequently the explicit subject of study in other learning tasks, despite many of these procedures having temporal components. Two examples of such procedures are serial pattern learning and serial reversal, which will be independently discussed in the following sections.

Serial Pattern Learning and Ordinal Timing

Animals' ability to represent order has been studied in a number of tasks, such as the delayed sequence-discrimination (DSD) procedure, where subjects are serially presented a number of stimuli in different sequences followed by a test stimulus, pecks in the presence of which are reinforced. Pigeons peck more on the test stimulus after the correct sequence than after incorrect sequences, showing successful discrimination on DSD tasks (e.g., Weisman, Wasserman, Dodd, & Larew, 1980; Weisman, Duder, & von Konigslow, 1985).

Though timing has never been specifically invoked as part of the explanation in sequence learning procedures such as the DSD, solving these tasks could utilize an implicit temporal representation of the sequence. For instance, if presented with the sequence *red-green-blue* in successive order, knowing that red precedes blue is a temporal judgment; the subject must represent when red happens relative to blue (i.e., earlier). Importantly, this judgment need not carry any interval information: whether red occurs 10 s or 100 s before blue in sequence is irrelevant to its order so long as the order is always red followed by green and then blue. Thus, if pigeons are capable of representing time ordinally, they should be able to track both the identity of the sequence based on order of the stimuli across time (e.g., *red-green-blue* vs. *green-red-blue*) and the current position in the sequence relative to food (e.g., blue is proximal to food reward, green is less proximal, and red is least proximal).

In their discussion of different types of timing, Carr and Wilkie (1997) described a little-researched cognitive representation of time they referred to as ordinal timing. Ordinal timing was defined as the representation of events in a certain sequence over a period of time; for example, a bee may visit a particular sequence of flowers for the

duration of each foraging bout (traplining). This concept is interesting because it is possible for ordinal and interval timing mechanisms to be separate representations of time with overlapping purposes of anticipating events using short-time temporal information (i.e., using either an ordinal sequence or interval timer to anticipate a particular future event). Most of the evidence Carr and Wilkie pointed to for this phenomenon was from field observation, with a single study in rats' time-place learning as the lone laboratory example. Ordinal timing has not been explored in pigeons, nor in the operant chamber using conditions more typical of interval timing and serial pattern learning studies.

Reversal Learning

Where sequence discrimination tasks require attending to stimuli serially presented across time, reversal tasks involve flexibly altering behavior to static stimuli with changing task contingencies over time. In the serial reversal procedure, animals are trained on a simultaneous discrimination task (e.g., reinforcement for responding to blue and not to yellow) with a reversal of contingencies occurring once the task is acquired (e.g., reinforcement for response to yellow and not to blue), with a reversal following each successive acquisition of the new discrimination (Mackintosh, McGonigle, Holgate, & Vanderver, 1968). With successive reversals, a variety of animals show improved speed to re-acquisition relative to baseline, suggesting that behavioral flexibility is adaptively valuable (Shettleworth, 1998).

Very recent research has examined comparative reversal performance on a variant of serial reversal, the mid-session reversal procedure. In this task, a subject is presented with two stimuli; responding to one is correct for the first half of trials, and responding to the other is correct on the second half of trials. Pigeons make a large number of

anticipatory errors (i.e., responding to the second-correct stimulus before the reversal) and perseverative errors (i.e., responding to the first-correct stimulus after the reversal) as compared to performance by humans (Rayburn-Reeves, Molet, & Zentall, 2011) and rats (Rayburn-Reeves, Stagner, Kirk, & Zentall, in press). As in the typical reversal procedure, the optimal strategy in the midsession reversal task is to respond based on the outcome of the last trial: if the response on the last trial was reinforced then the animal should make the same response on the next trial, and if the response was non-reinforced then the subject should shift and respond to the other stimulus on the next trial (referred to as win/stay, lose/shift). However, pigeons appear to rely on an alternate strategy to predict the occurrence of the reversal, rather than remembering the response and outcome from the previous trial to obtain optimal reinforcement.

There are only two obvious means by which the pigeons could predict the reversal point. One strategy is to track the approximate number of trials (or reinforcers) until the change in contingencies ("The reversal occurs after 40 trials"). Alternatively, the pigeons could be tracking the interval time since the start of the session ("The reversal occurs after about 300 seconds"). Anticipatory and perseverative errors subsequently occur because the representations of number and time in animals are noisy estimates. Previous research has not conclusively shown which of time or number pigeons are primarily using in the midsession reversal task, and no previous work has closely examined whether the type of discrimination used could affect pigeons' tendency to exhibit optimal win/stay-lose/shift behavior on the task.

Organization of the Present Work

The current thesis was broadly concerned with how the exact presentation of stimuli and reinforcement could affect the use of timing in peak procedure, serial pattern learning, and mid-session reversal tasks. The goal of this research was to more closely examine how interval time competes with other stimulus dimensions for control over behavior, and to understand how interval timing integrates with other forms of learning.

The rationale of Chapter 2 of this thesis was to study explicitly the competition for stimulus control between temporal and non-temporal cue dimensions using the peak procedure. Half of the pigeons were trained and tested with timed reinforcement occurring on a 60-s fixed interval, while the other half of the pigeons were trained with a green stimulus reinforced on a 60-s fixed interval and pecks to a red stimulus not reinforced after 60 s. Overshadowing occurs when a salient conditioned stimulus inhibits learned responding to a less salient stimulus presented in compound (Pavlov, 1927). In varying the relative validity of temporal vs. non-temporal dimensions of cues for predicting reward, I examined whether interval timing could be overshadowed by a non-temporal cue dimension, in this case the visual identity of the stimulus. If timing is a truly automatic process driven by an internal clock independent of other learning processes, then no overshadowing of time would have been expected; conversely, if time is processed in a fashion similar to how other stimulus dimensions are processed, subjects would have been expected to show poor stimulus control by elapsed time when trained with a highly salient visual cue that distinguishes reinforced and non-reinforced trials.

In Chapter 3, pigeons were trained on particular orders of stimuli presented sequentially across a variable interval. By reinforcing responding only after certain orders, I examined the tendency of pigeons to respond more to the reinforced order than

to non-reinforced order, and also to stimuli more temporally proximal to reward than to stimuli located earlier in the order. The goal of this research was to determine how temporal information integrates to allow pigeons to solve cognitively demanding ordering tasks.

In Chapter 4, I examined the peculiar errors pigeons make on the mid-session reversal task and illustrated that these errors result from the tendency to predict the reversal point using interval timing. I also studied how this interval timing strategy was affected by changing the task from a visual discrimination to a confounded visual-spatial discrimination. By allowing pigeons to use either or both of two stimulus dimensions (visual and spatial), I examined whether decreasing working memory load for the response and outcome of the last trial would reduce stimulus control by interval time, and that pigeons would show fewer errors due to timing. Such a result would indicate that stimulus control by time is sensitive to the quality of memory for non-temporal information.

Though each of these chapters used markedly different procedures to observe timing in pigeons, they all share the theme that interval timing is not simply a mechanistic internal process, but rather a functional component of learning which competes for attentional resources and interacts with other elements of behavior. This interactivity between timing and non-temporal learning processes will be the focus of Chapter 5.

References

Arcediano, F. & Miller, R. R. (2002). Some constraints for models of timing: A temporal coding hypothesis perspective. *Learning & Motivation, 33,* 105–123.

Balci, F., Gallistel, 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.

Block, R. A. & Zakay, D. (1996). Models of psychological time revisited. In H. Helfrich (Ed.), *Time and mind* (pp. 171-195). Bern: Hogrefe & Huber.

Buhusi, C. V. & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience, 6,* 755.

Carr, J. A. R. & Wilkie, D. M. (1997). Ordinal, phase, and interval timing. In C. M. Bradshaw & E. Szabadi (Eds.), *Time and Behaviour: Psychological and Neurobehavioural Analyses* (pp. 265-327)*. Amsterdam, The Netherlands: North-Holland/Elsevier Publishers.

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

Cheng, K. & Westwood, R. (1993). Analysis of single trials in pigeons' timing performance. *Journal of Experimental Psychology: Animal Behavior Processes, 19*, 56-67.

Church, R. M. & Broadbent, H. A. (1990). Alternative representations of time, number, and rate. *Cognition, 37,* 55-81.

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

Crystal, J. D. (2012). Sensitivity to time: Implications for the representation of time. In T. R. Zentall & E. A. Wasserman (Eds.), *Oxford Handbook of Comparative Cognition* (pp. 434-450). New York: Oxford University Press.

Dragoi, V., Staddon, J.E.R., Palmer, R.G., & Buhusi, C.V. (2003). Interval timing as an emergent learning property. *Psychological Review, 110,* 126-144.

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

Gibbon, J., & Church, R. M. (1984). Sources of variance in an information processing theory of timing. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds), *Animal cognition* (pp. 465-488). Hillsdale, NJ: Erlbaum.

Gibbon, J., & Church, R. M. (1990). Representation of time. *Cognition, 37*, 23-54.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In J. Gibbon and L. Allan (Eds). *Timing and time perception (Annals of the New York Academy of Sciences*) (Vol. 423, pp. 52-77). New York: New York Academy of Sciences.

Grossberg, S. & Schmajuk, N. A. (1989). Neural dynamics of adaptive timing and temporal discrimination during associative learning. *Neural Networks, 2,* 79-102.

Kaiser, D. H. (2008). The proportion of fixed interval trials to probe trials affects acquisition of the peak procedure fixed interval timing task. *Behavioural Processes, 77*, 100-108.

Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological*

Review, 95, 274-295.

Kirkpatrick-Steger, K., Miller, S. S., Betti, C. A., & Wasserman, E. A. (1996). Cyclic

responding by pigeons on the peak timing procedure. *Journal of Experimental*

Psychology: Animal Behavior Processes, 22, 447-460.

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, 325–334.

Machado, A. (1997). Learning the temporal dynamics of behavior. *Psychological*

Review, 104, 241-265.

Macar, F. & Vidal, F. (2009). Timing processes: An outline of behavioural and neural

indices not systematically considered in timing models. *Canadian Journal of*

Experimental Psychology, 63, 227-239.

Mackintosh, N. J., McGonigle, B., Holgate, V., & Vanderver, V. (1968). Factors

underlying improvement in serial reversal learning. *Canadian Journal of*

Psychology, 22, 85-95.

Matell, M. S. & Meck, W. H. (2000). Neuropsychological mechanisms of interval timing

behavior. *BioEssays, 22,* 94-103.

Matell, M. S. & Meck, W. H. (2004). Cortico-striatal circuits and interval timing:

Coincidence detection of oscillatory processes. *Cognitive Brain Research, 21,*

139-170.

Matell, M. S. & Portugal, G. S. (2007). Impulsive responding on the peak-interval

procedure. *Behavioural Processes, 74*, 198-208.

McMillan, N. & Roberts, W. A. (2010). The effects of cue competition on timing in pigeons. *Behavioural Processes, 84*, 581-590.

Meck, W. H. (1984). Attentional bias between modalities: Effect on the interval clock, memory, and decision stages used in animal time discrimination. In J. Gibbon & L. G. Allan (Eds.), *Timing and time perception* (pp. 528-541). New York: New York Academy of the Sciences.

Miall, R. C. (1989). The storage of time intervals using oscillating neurons. *Neural Computation, 1,* 359-371.

Miki, A. & Santi, A. (2005). The perception of empty and filled time intervals by pigeons. *Quarterly Journal of Experimental Psychology, 58,* 31-45.

Ornstein, R. E. (1969). *On the experience of time*. New York: Penguin.

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

Rayburn-Reeves, R. M., Molet, M., & Zentall, T. R. (2011). Simultaneous discrimination reversal learning in pigeons and humans: Anticipatory and perseverative errors. *Learning & Behavior, 39,* 125-137.

Rayburn-Reeves, R. M., Stagner, J. P., Kirk, C. R., & Zentall, T. R. (in press). Reversal learning in rats (*Rattus norvegicus*) and pigeons (*Columba livia*): Qualitative differences in behavioral flexibility. *Journal of Comparative Psychology.*

Richelle, M. & Lejeune, H., Eds. (1980). *Time in animal behavior.* Oxford: Pergamon Press.

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

Roberts, W. A., Cheng, K., & Cohen, J. (1989). Timing light and tone signals in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 20,* 66-78.

Roberts, W. A., Coughlin, R., & Roberts, S. (2000). Pigeons flexibly time or count on cue. *Psychological Science, 11,* 218-222.

Santi, A., Keough, D., Gagne, S., & Van Rooyen, P. (2007). Differential effects of empty and filled intervals on duration estimation by pigeons: Test of an attention-sharing explanation. *Behavioural Processes, 74,* 176-186.

Santi, A., Miki, A., Hornyak, S., & Eidse, J. (2005). The perception of filled and empty time intervals by rats. *Learning & Motivation, 34*, 282-302.

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior.* New York: Oxford University Press.

Staddon, J. E. R., & Higa, J. J. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior, 71*, 215-251.

Sutton, J. E. & Roberts, W. A. (1998). Do pigeons show incidental timing? Some experiments and a hierarchical framework for the study of attention in animal cognition. *Behavioural Processes, 44,* 263-275.

Tse, C-Y. & Penney, T. B. (2006). Preattentive timing of empty intervals is from marker offset to onset. *Psychophysiology, 43,* 172-179.

Weisman, R. G., Duder, C., & von Konigslow, R. (1985). Representation and retention of three-event sequences in pigeons. *Learning and Motivation, 16,* 239-258.

Weisman, R. G., Wasserman, E. A., Dodd, P. W. D., & Larew, M. B. (1980).

Representation and retention of two-event sequences in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 6,* 312-325.

Wilkie, D. M. (1987). Stimulus intensity affects pigeons' timing behavior: Implications for an internal clock model. *Animal Learning & Behavior, 15,* 35-39.

Chapter 2

Interval Timing under Variations in the

Relative Validity of Temporal Cues

Neil McMillan and William A. Roberts

Abstract

Two groups of pigeons were trained to respond on a white center key on a fixed interval 60-s schedule of reinforcement signaled by the onset of a sidekey cue (S+ training). In additional training sessions, S+ trials alternated between S- trials in which a different sidekey cue signaled non-reinforcement after 60 s (S+/S- training). For one group, S+/S- training sessions followed S+ training, and for the other group, S+/S- training preceded S+ training. Peak-time curves obtained from extended non-rewarded probe trials inserted among training trials showed loss of control by time during S+/S- training relative to S+ training. A follow-up experiment showed that this result was not caused by a difference in probability of reinforcement. We suggest that attention to time was weakened by the introduction of visual cues that were more valid predictors of trial outcomes.

Keywords: pigeons, timing, peak procedure, overshadowing, attention

Interval Timing under Variations in the

Relative Validity of Temporal Cues

Timing is frequently measured through the use of the peak procedure (Catania, 1970; S. Roberts, 1981), in which subjects are trained on a fixed-interval (FI) reinforcement schedule before extended non-rewarded probe trials are introduced. Rate of responding curves plotted over time intervals during the duration of probe trials yield a roughly symmetrical Gaussian distribution, with the peak near the expected point of reinforcement. The individual-trial performance on timed trials has been suggested to be best-described as a "break-run-break" function, with abrupt switches from low rates of responding to high rates, and an abrupt switch back to a low rate of responding later in the trial (Gibbon & Church, 1990); while the underlying performance on individual trials is not Gaussian-shaped (Cheng & Westwood, 1993), the averaging of 'start' and 'stop' times across many trials creates a distribution which is Gaussian-shaped. The width of the curve around the peak is proportional to the duration of the FI (scalar property) and represents noise in the representation of time (Gibbon, 1977).

Recent studies indicate that motivational variables clearly affect timing performance. Galtress and Kirkpatrick (2009) trained rats on an FI 60-s schedule followed by testing with non-rewarded probe trials. The amount of reward on FI trials was 1 or 4 food pellets delivered over different blocks of training and testing trials. It was found that the 4-pellet reward shifted the peak-time curve to the left of the curve found with 1 pellet. When the reward was devalued by pairing it with lithium chloride, subsequent tests showed that the peak-time curve shifted to the right of baseline tests. In another set of studies, Galtress and Kirkpatrick (2010) trained rats to press different bars

after 2 s or 8 s of houselight duration. Correct responses to both durations were rewarded with 1 pellet in a 1-1 control group. In two other groups, the rewards varied for correct responses after 2 s and 8 s between 1-4 and 4-1 pellet groups. Once stable discrimination performance was established, rats were tested at a number of signal durations intermediate between 2 and 8 s. The interesting finding reported was that the psychophysical curves generated by the 1-4 and 4-1 groups were flatter than those generated by the 1-1 control group. Variation in reward thus hindered the precision of timing. In both sets of experiments, Galtress and Kirkpatrick argued that variation in reward magnitude may affect attentional processes in timing. Within the framework of scalar expectancy theory (SET), they suggested that in the peak time experiment (Galtress & Kirkpatrick, 2009) smaller reward led to more fluctuation in the closed-open setting of the accumulator switch than larger reward. The flatter psychophysical curves found by Galtress and Kirkpatrick (2010) were attributed to more fluctuation in the switch when reward varied (1-4 or 4-1) than when it was consistent (1-1).

Pertinent to the discussion of associative learning in timing, there have been mixed results in studying cue competition effects on interval timing. Overshadowing is the phenomenon in which a salient conditioned stimulus (CS) can inhibit learned responding to a less salient stimulus presented in compound (Pavlov, 1927). Jennings, Bonardi and Kirkpatrick (2007) found no evidence for overshadowing of one time interval over another in rats. Recently, we looked for cue competition effects in pigeon timing (McMillan & W. A. Roberts, 2010, Experiment 1) using the peak-time procedure. Pigeons were trained to peck a white center key while red and green sidekeys signaled different FI schedules of reinforcement. For example, a control bird would be presented

with a left green key signaling a 10-s FI on some trials and with a right red key signaling a 30-s FI on other trials. Birds in an overshadowing group were always presented with 20 s of the right red key followed by 10 s of the red and green sidekeys before reinforcement was enabled. Non-rewarded probe trials were periodically introduced that presented only the red key or the green key. Although rates of responding were affected by the overshadowing manipulation, peak times were not affected. That is, pigeons timed 10-s and 30-s FI signals as well when they had been presented in compound as when they had been presented in isolation.

A closely-related topic to overshadowing is blocking, wherein pre-exposure to one CS inhibits responding to another stimulus later presented in compound (Kamin, 1969). Jennings and Kirkpatrick (2006) showed in rats that a long stimulus could block a shorter one, though only when CS1 was noise and CS2 was light. McMillan and W. A. Roberts (2010, Experiment 2) used similar procedures to study blocking. Two different groups of pigeons were initially trained to time either a 10-s FI or a 30-s FI, each signaled by a green or red sidekey. Both groups then were transferred to training with the two FIs put in compound. A control group was trained only with the compound FIs. Peak-time curves obtained from non-rewarded probe trials, on which only the 10-s or only the 30-s sidekey cue was presented, showed that initial training with the 30-s FI had no influence on timing the 10-s FI learned during compound training. Initial training with the 10-s FI, however, completely blocked timing of the 30-s FI later trained in compound. In other words, learning to time a short interval blocked subsequent learning to time a long interval, but learning to time a long interval did not block subsequent learning to time a short interval. Due to the limited number of studies in this area, it is difficult to say if the

results of Jennings and Kirkpatrick (2006) and McMillan and W. A. Roberts (2010)

conflict due to species differences or methodological differences (as discussed in

McMillan and W. A. Roberts, 2010). Regardless, there is preliminary evidence to

suggest that timing may be susceptible to associative processes such as blocking and to

motivational variables; a remaining question is whether a timed cue dimension can be

overshadowed by a non-timed cue dimension. In the present research, we examined the

effects of a non-rewarded stimulus on timing a rewarded fixed-interval stimulus; we were

interested in whether a salient visual cue dimension could overshadow learning to time.

Presently, we report two experiments in which pigeons were trained and tested

with a standard peak-time procedure. On control sessions, the onset of a key containing a

color or pattern signaled the beginning of an FI 60-s schedule on discrete trials (S+

sessions), and non-rewarded probe trials were introduced to examine the peak-time

function. During experimental sessions, pigeons were trained on exactly the same

procedure, with an S+ stimulus signaling the FI 60-s schedule. However, on additional

trials, pigeons were presented with an S- color or pattern that signaled the absence of

reinforcement after 60 s (S+/S- sessions). Thus, pigeons in experimental sessions had to

attend to two dimensions, time and color or pattern. The question of interest was whether

presenting pigeons with visual cues that reliably predicted trial outcomes would affect

control by the less-reliable time cue. Temporal control was assessed by examining the

shapes of peak-time curves obtained during S+ and S+/S- training. In a second

experiment, overall probability of reinforcement was controlled for by a group which saw

both red and green stimuli, and had both stimuli reinforced on 50% of the trials on an FI

60-s schedule and non-reinforcement on the other 50% of the trials.

Experiment 1

Two groups of pigeons were trained and tested. One group was initially trained over sessions with the S+/S- procedure described above. To anticipate the results, this procedure had a marked effect on the peak-time curve. This group then was given control training on the temporal dimension alone to determine if the typical peak-time curve would appear. A second group of pigeons was trained first on the S+ procedure and then on the S+/S- procedure. The second group was trained to find out if two-dimensional training would affect the peak-time curve after pigeons had learned to time the 60-s FI accurately.

Method

Subjects.

Ten naïve adult White Carneaux pigeons (*Columba livia*) were used. Birds were maintained at approximately 85% of free-feeding weight throughout the experiment, with constant access to water and health grit. They were individually housed in cages in a room kept environmentally controlled at 22 degrees C. Fluorescent lights were turned on at 8:30 a.m. and off at 10:30 p.m. each day. Testing was performed between 9 a.m. and 4 p.m. for 5 days each week.

Apparatus.

Three enclosed, sound-attenuating operant chambers measuring 31 x 35.5 cm (floor) x 35.3 cm (height) were used. The front wall of each chamber held three pecking keys, 2.5 cm in diameter and level with the pigeon's head, in a row, spaced 8 cm apart. Projectors behind each key projected filtered light, presenting different colors or patterns on the keys. Grain reinforcement was delivered by an electromechanical hopper through

a 6 x 6 cm opening in the front wall located near the floor, directly below the center key. Presentation of stimuli, reinforcement, and recording of responses were carried out by microcomputers, in another room, interfaced to the operant chambers.

Procedure.

The following procedures were conducted between groups of subjects.

Group S+/S- →S+. Five birds in this group were first trained and tested with S+ and S- stimuli appearing on alternate trials and then were trained and tested with only the S+ stimulus. Within a session containing 44 trials, S+ and S- stimuli each appeared on 22 trials in random order. On both types of trials, the center key was lit white to start the trial, and pecks on the center key were recorded in 1-s bins. On S+ trials, the left sidekey also was lit with green light for three pigeons or with a white circle on a black background for the other two pigeons. The first peck made on the center key after a 60-s FI yielded 5 s of access to grain reinforcement. The center key and the S+ sidekey stayed on until either the first reinforced peck to the center key or 120 s had elapsed since the start of the trial. On S- trials, the center key appeared with the left sidekey lit red for the three birds that saw green as the S+ and lit with a white triangle for the two birds that saw circle as the S+. Pecking the center key was never reinforced on S- trials, and the keys turned off after 60 s. After a reinforced keypeck on S+ trials or the end of 60 s on S- trials, the chamber was darkened for an intertrial interval that varied randomly between 40-80 s. After birds completed 10 sessions of training with S+ and S- stimuli, they were given 10 further sessions in which probe trials were introduced. Four non-rewarded probe trials were randomly interspersed among the 44 training trials. On probe trials, the S+ stimulus was presented for 120 s, and pecks were recorded throughout this period.

During 20 further sessions, the pigeons were transferred to training and testing with only S+ trials presented. Thus, the S+ stimulus was presented on each of 44 training trials, and pecking the white center key was reinforced on an FI 60-s schedule. Each session contained an additional four probe trials on which the S+ stimulus was presented for 120 s and no reinforcement was delivered.

Group S+$\rightarrow$S+/S-. Five birds were trained and tested in the reverse order of the conditions used with Group S+/S-$\rightarrow$S+. These birds received 20 sessions with only the S+ stimulus present on every trial and then were transferred to 20 further sessions in which S+ and S- trials alternated randomly. Four non-rewarded probe trials containing the S+ stimulus were interjected randomly during each session; the only difference between groups was that probe trials were presented during all 40 sessions in Group S+$\rightarrow$S+/S-, and thus were not excluded from the initial sessions as they were for Group S+/S-$\rightarrow$S+.

Data analysis.

Unless otherwise noted, only data from sessions 11-20 from each phase were analyzed, to remove early development effects. Each pigeon's average distribution of responses was relativized to a response rate of 1 and was fit using the log Gaussian function in GraphPad Prism 5.0 software. The log normal was used rather than a typical Gaussian function to allow for the right skew often inherent in peak time responding, generally caused by random or renewed responding toward the end of the probe interval. The center (geometric mean) of each curve was used as an approximation of peak responding, with spread of one geometric standard deviation calculated and used as a measure of accuracy of timing.

Results

Data from one pigeon in Group S+→S+/S- were removed from the results because the bird failed to show any evidence of timing during the experimental procedure, with flat responding throughout the duration of probe trials.

All birds showed increasing peck rates over the FI on S+ trials. By the third session of training and thereafter, responding on S- trials was negligible. Figure 2.1 shows relative response rates plotted over 120 s of S+ presentation on non-rewarded probe trials. Note that narrower peak-time curves were found during S+ training than during S+/S- training. Particularly noticeable is that the right limb of curves for S+/S- training phases show little decline in response rate past the FI (60 s), whereas the curves for S+ training phases show a clear decline in response rate. Furthermore, it appears that the effect of S+/S- training did not depend on whether it preceded or followed S+ training, as the curves for Groups S+/S-→S+ and S+→S+/S- appear to be highly similar.

Separate analyses of variance (ANOVA) were performed on the left limb and right limb of the curves shown in Figure 2.1. The factors in the analyses were 2 x 2 x 60 (Group [Group S+/S- →S+, Group S+ →S+/S-] x Condition (S+/S-, S+) x Time Bin). The main effects of the time-bin factor are not reported because they were highly significant in all analyses. The analysis of the left limbs (bins 1-60 s) yielded a significant effect of condition, $F(1, 7) = 6.68$, $p = 0.036$, and a significant interaction of Condition x Time Bin, $F(59, 413) = 3.61$, $p < .001$. Similarly, the analysis of the right limbs (bins 61-120 s) yielded a significant effect of condition, $F(1, 7) = 11.99$, $p = 0.011$, and of the condition x time bin interaction, $F(59, 413) = 7.11$, $p < .001$. The effect of group and none of the interactions with group were significant. Thus, the introduction of
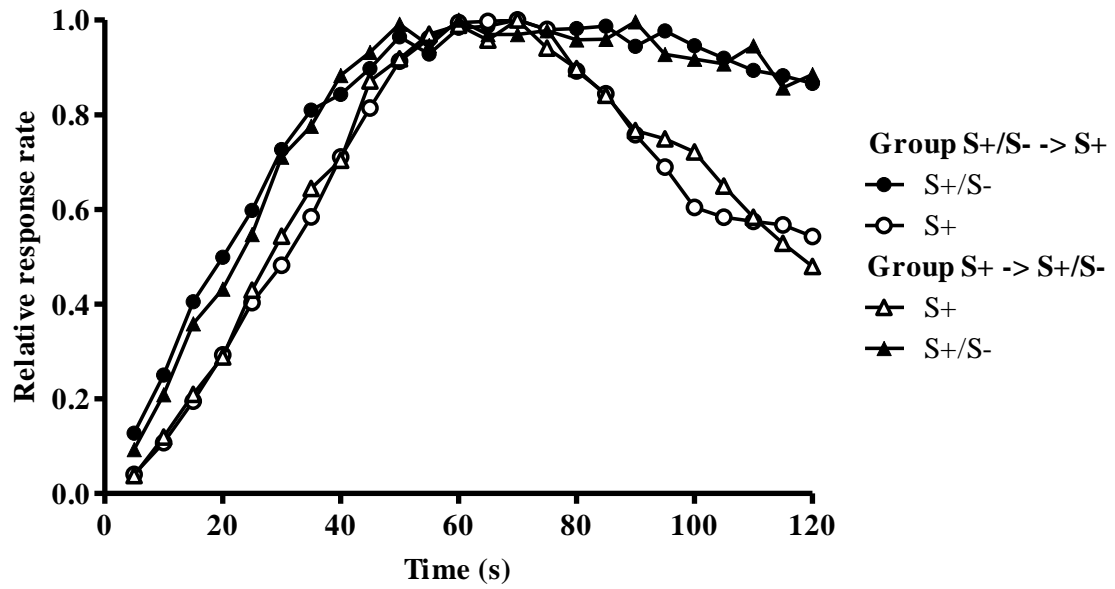
Figure 2.1. Peak-time curves generated by S+/S- and S+ training in Group S+/S- →S+ and in Group S+→S+/S-. The data have been relativized to a peak rate of 1.0 and are plotted as a function of 5-s time bins.

S+/S- training interfered with timing equally in both groups before and after the 60-s FI was reached.

The mean peak times (geometric means) and widths (geometric standard deviations) of the response curves for pigeons in each group on S+ and S+/S- probe trials were computed from log-normal curves fit to the data. On S+ sessions, both groups' mean peaks were close to the 60-s training FI. Mean peaks on S+/S- sessions clearly overestimated the FI, being over 10 s longer. The widths of the response curves also show considerably more noise during S+/S- sessions than during S+ sessions. An ANOVA performed on peak times yielded no significant effects of group or condition. The failure to find an effect of condition (S+ versus S+/S-) is attributable to considerable variation between subjects in peak times during S+/S- training. When the absolute differences between peak time and 60 s were calculated for each condition, the means were 6.5 s for S+ training and 17.5 for S+/S- training. The difference between these means fell just short of significance, $t(8) = 2.11$, $p = .07$. The greater error in timing under S+/S- training is found more clearly in an analysis of the widths of peak-time curves. A 2 x 2 Group x Condition ANOVA performed on the mean widths yielded a significant effect of condition, $F(1, 7) = 30.47$, $p < .001$. The increase in error of timing in the S+/S- condition (geometric SD: 1.2 and 1.2 in Groups S+/S- →S+ and S+ →S+/S-, respectively) relative to the S+ condition (0.6 and 0.7 in Groups S+/S- →S+ and S+ →S+/S-, respectively) was equivalent between groups.

The effects of training sessions and of transfer between conditions were examined within each group. Figure 2.2 shows data from Group S+/S- →S+ (top panel) for Sessions 11-20 of S+/S- testing and for Session 1-10 and Sessions 11-20 of S+ training

and testing. The right limbs of the S+ curves drop relative to the more flat S+/S- curve, as seen in Figure 1. However, the S+ curve for Sessions 11-20 drops more steeply to a lower level of responding than the curve for Sessions 1-10. Note also that the slopes of the left-limb curves appear to differ. The S+/S- curve is steeper than the S+ curves, suggesting more accurate timing on S+ sessions than on S+/S- sessions. However, the steepness of the left limb for S+ trials does not appear to vary over sessions.

These observations were supported by statistical analyses. The effect of S+ training sessions was examined in a 2 x 60 (Session Block [Sessions 1-10, Sessions 11-20] x Time Bins) ANOVA for each limb of the peak time curves (i.e., time bins 1-60 and 61-120, respectively). This analysis yielded no significant effect of block of sessions or of the block of sessions x time bin interaction, Fs < 1.0, for the left limbs of these curves. A similar analysis of the right limbs of these curves, however, showed significant effects of block of sessions, $F(1, 236) = 8.69$, $p = .042$, and of the block of sessions x time bin interaction, $F(59, 236) = 1.40$, $p = .041$.

A 2 x 60 (Condition [S+/S-, S+] x Time Bins) ANOVA examined the effects of S+/S- training compared to sessions 1-10 of S+ training shown in the top panel of Figure 2. Analysis of the left limb of these curves revealed significant effects of condition, $F(1, 7) = 17.85$, $p = .013$, and of the Condition x Time Bin interaction, $F(59, 236) = 4.28$, $p < .001$. Analysis of the right limbs also yielded significant effects of condition, $F(1, 7) = 8.58$, $p = .043$, and of the Condition x Time Bin interaction, $F(59, 236) = 2.05$, $p < .001$.
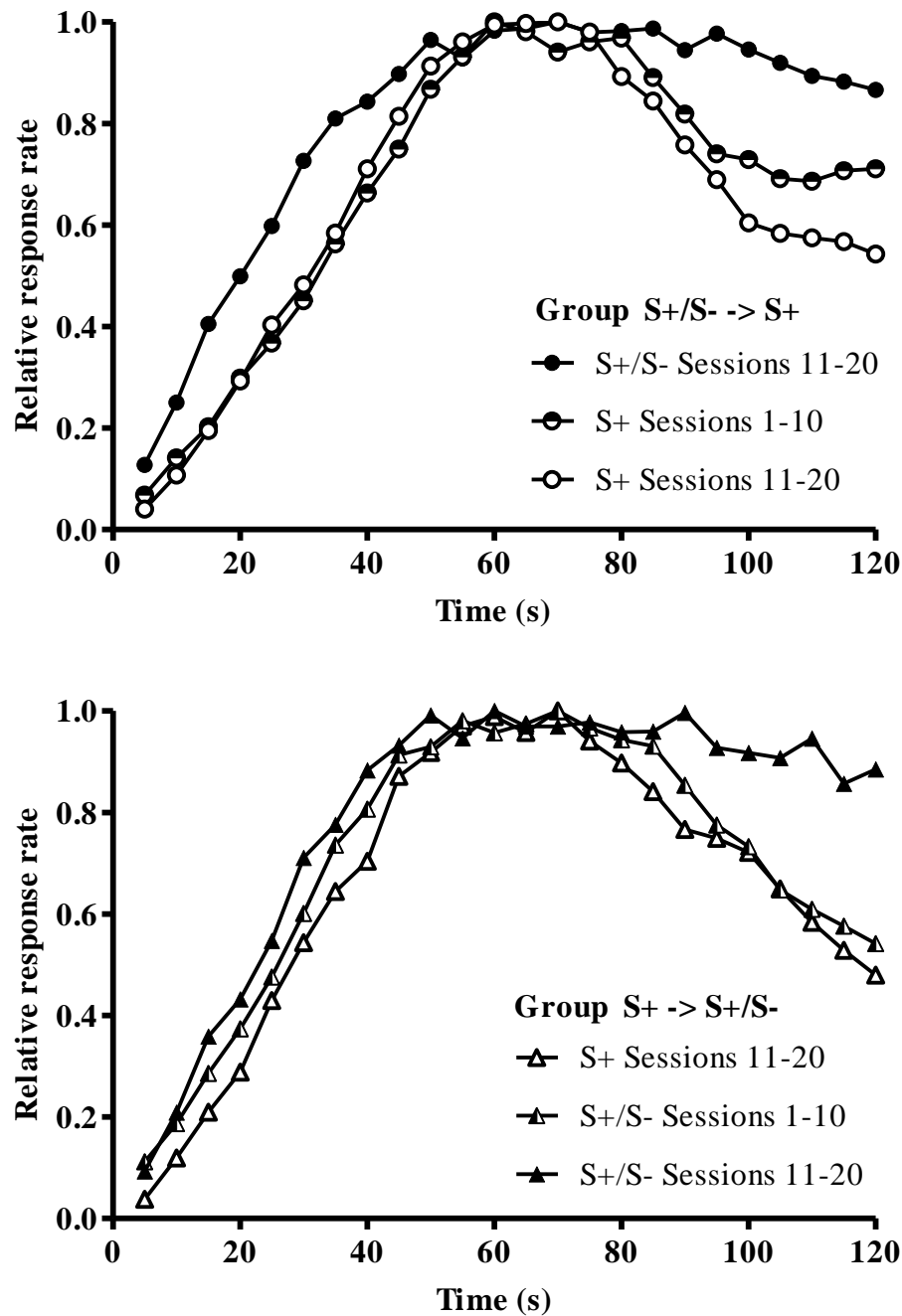
Figure 2.2. Peak-time curves generated by S+/S- and S+ training in Group S+/S- →S+ (top panel) and Group S+→S+/S- (bottom panel), with the effects of training shown separately for Sessions 1-10 and Sessions 11-20 in each second phase. The data have been relativized to a peak rate of 1.0 and are plotted as a function of 5-s time bins.

Probe trial response curves for Group S+ →S+/S- are shown in the bottom panel

of Figure 2 for Sessions 11-20 of S+ testing and Sessions 1-10 and 11-20 of S+/S-

testing. The S+ curve shows the declining rate of responding in the right limb, as seen in

Figure 1. The striking finding seen in the figure is that the S+/S- curves show the same

declining right-limb curve on Sessions 1-10 but then flatten out on Sessions 11-20. It

appears that the symmetrical timing curve learned during initial S+ training carried over

to the first 10 sessions of S+/S- training and testing. The effect of the additional S- trials

then took hold on the second set of 10 sessions, and accurate timing was lost. Note that

the S+/S- curves on the left limbs of the functions are somewhat steeper than the S+

curve, but this difference is not marked.

Two ANOVAs were performed on the data shown in the bottom panel of Figure

2. First, the S+ curve obtained on Sessions 11-20 was compared with the S+/S- curve

obtained on Sessions 1-10. As suggested by the curves, these analyses yielded no

significant effects of condition or Condition x Time Bin, Fs $\leq$ 1.0, for either limb of the

curves. A second analysis examined the effect of S+/S- training by comparing Sessions

1-10 versus 11-20. Analysis of the left limb showed no effect of block of sessions or the

Session Block x Time Bins interaction, Fs < 1.0. Analysis of the right limb yielded a

non-significant effect of block of sessions, F < 1.0, but a significant interaction of

Session Block x Time Bins, $F(59, 177) = 1.63$, $p = .008$. Thus, the slope of the right limb

of the S+/S- peak-time curve became significantly flatter between blocks of sessions.

Discussion

Pigeons in two groups were trained to peck a white center key on an FI 60-s

schedule signaled by onset of a sidekey cue. Occasional non-rewarded probe trials were

introduced within sessions in order to obtain peak-time curves. When peak-time curves were examined on early and late sessions of probe testing, it was found that the right limb became steeper as test sessions progressed (top panel of Figure 2). Pigeons thus showed increased sharpening of peak-time curves over successive sessions of probe testing, produced primarily by a decline in responding after the FI. This finding replicates similar observations recently made with pigeons (Kirkpatrick-Steger, S. S. Miller, Betti, & Wasserman, 1996) and with rodents (Balci et al., 2009; Kaiser, 2008; Matell & Portugal, 2007).

In addition to cued FI training on one block of sessions in Experiment 1, cued FI S+ trials were intermixed with cued S- trials that always ended in non-reinforcement after 60 s on another block of sessions. The introduction of S- trials led to a marked flattening of the right limb of the peak-time curve and loss of accurate timing of the FI on probe trials when the S+ was presented. Furthermore, the extent of this loss of timing control was equivalent when S- training followed standard S+ training (Group S+ →S+/S-) or preceded S+ training (Group S+/S- →S+). The observation that the peak time curve became flatter after 10 sessions of S+/S- training in Group S+→S+/S- (Sessions 11-20 in the bottom panel of Figure 2) is particularly important. This finding shows that after learning to time the FI accurately during S+ training, control by timing can be subsequently lost by the introduction of S+/S- training. If precise timing during the S+ training simply involved lowering the right limb of the peak-time curve through extinction, as suggested by the top panel of Figure 2, the introduction of S- trials should not have led to a loss of timing control. Some additional process introduced by the presentation of S- trials must have been responsible for this effect.

In a classic experiment on stimulus validity, Wagner, Logan, Haberlandt, and Price (1968) reinforced one group of rats with 50% reinforcement of a compound houselight + Tone 1 stimulus and 50% reinforcement of a compound houselight + Tone 2 stimulus (Group Uncorrelated). Another group always had one houselight-tone compound reinforced and the other houselight-tone compound non-reinforced (Group Correlated). When response to the houselight was tested in each group, houselight controlled strong responding in Group Uncorrelated but little responding in Group Correlated. It was suggested that stronger relative validity of the tone cues in Group Correlated overshadowed control by the light cue. We suggest that in the present study, the relative validity of the visual cues in S+/S- training overshadowed attentional control by the 60-s time cue, leading to flatter peak-time curves.

One caveat to explaining our data on the basis of the results in Wagner et al. (1968) is that our control condition received only S+ trials, whereas the control group used by Wagner et al. (Group Uncorrelated) had two stimulus conditions each reinforced on a 50% reward schedule. Our S+ control varied from the S+/S- experimental group on both the relative validity of the visual and temporal stimuli and on the probability of reinforcement across trials. In a follow-up experiment, we sought to disentangle these two possible explanations by more closely emulating the design used by Wagner et al. (1968) in the context of the peak procedure.

Experiment 2

In this experiment, there were two conditions: Correlated, which was identical to the S+/S- condition from Experiment 1, had 100% reinforcement on an FI-60 s for one timed stimulus and 0% reward following a 60-s presentation of the other (and thus the

identities of the stimuli are correlated with food reinforcement and nonreinforcement);

and Uncorrelated, with identical stimulus presentations but reward presented after a 60-s

FI on 50% of both trial types (thus the identities of the stimuli are not correlated with

food reinforcement and nonreinforcement). Since probability of reinforcement is

controlled for in this experiment, the only difference between the conditions is the

predictive validity of the stimuli.

Method

Subjects and apparatus.

Ten naïve adult White Carneaux pigeons (*Columba livia*) were used. All aspects

of animal husbandry and apparatus were otherwise identical to Experiment 1.

Procedure.

The following procedures were conducted between groups of subjects.

Group Correlated. Five birds in this group were trained and tested over 50

sessions with S+ and S- stimuli appearing on alternate trials. Within a session containing

44 trials, S+ and S- stimuli each appeared on 22 trials in random order. On both types of

trials, the center key was lit white to start the trial, and pecks on the center key were

recorded in 1-s bins. On S+ trials, the left sidekey also was lit with green light. The first

peck made on the center key after a 60-s FI yielded 5 s of access to grain reinforcement.

The center key and the green sidekey stayed on until either the first reinforced peck to the

center key or 120 s had elapsed since the start of the trial. On S- trials, the center key was

lit white with the left sidekey lit red. Pecking the center key was never reinforced on S-

trials, and the keys turned off after 60 s. After a reinforced keypeck on S+ trials or the

end of 60 s on S- trials, the chamber was darkened for an intertrial interval that varied

randomly between 40-80 s. Four non-rewarded probe trials were randomly interspersed among the 44 training trials. On each of four probe trials, either the S+ stimulus or the S- stimulus was presented for 120 s, and pecks to the lit center key were recorded throughout this period.

Group Uncorrelated. Five birds received 50 sessions with either the red or green stimulus presented on every trial similarly to Group Correlated, but reinforcement was available 50% of the time on both stimuli. Thus, the green stimulus and the red stimulus each was presented on 22 training trials, and pecking the white center key was reinforced on an FI 60-s schedule for half of the trials for each stimulus, and met with non-reinforcement and the ITI after 60 s for the other half of the trials. Each session contained an additional four probe trials on which the white center key and either the red or green stimulus was presented for 120 s and no reinforcement was delivered.

Data analysis.

Unless otherwise noted, only data from sessions 31-50 in each phase were analyzed, to remove early development effects. Each pigeon's average distribution of responses was relativized to a response rate of 1 and was fit using the log Gaussian function in GraphPad Prism 5.0 software. The center (geometric mean) of each curve was used as an approximation of peak responding, with spread of one standard deviation calculated and used as a measure of accuracy of timing.

Results

Figure 2.3 shows relative response rates plotted over 120 s of S+ presentation on non-rewarded probe trials. To equate number of probes per condition, each Uncorrelated bird had one stimulus chosen at random to be the arbitrary "S+" to match with the

Correlated pigeons. A flatter peak-time curve was found in the Correlated group than was found in group Uncorrelated.

Separate ANOVAs were performed on the left limb and right limb of the curves shown in Figure 3. The factors in the analyses were 2 x 60 (Group (Correlated, Uncorrelated) x Time Bin). The main effects of the time-bin factor are not reported because they were highly significant in all analyses. The analysis of the left limbs (bins 1-60 s) yielded a significant interaction of group x time bin, $F(59, 472) = 1.56$, $p = .007$. Similarly, the analysis of the right limbs (bins 61-120 s) yielded a significant group x time bin interaction, $F(59, 472) = 1.42$, $p < .027$. The data suggest that the slopes of responding in the first 60 s and the last 60 s of each trial were sharper in birds on an Uncorrelated contingency than on a Correlated contingency.

Log-gaussian curves could not be generated for two of the five birds in the Correlated group: one bird showed a flat response distribution while the other had two distinct peaks. As a result, the peak data could not be analyzed in this experiment.

Two ANOVAs were performed on the probe trial response curves for the Correlated group, examining the effect of training by comparing the first 50 probe trials versus the last 50 probe trials. Analysis of the left limbs of these curves showed an effect of block of sessions [$F(1,4) = 18.64$, $p = .012$] and effect of time bin [$F(59,236) = 5.22$, $p < .001$], but no significant interaction. The block of sessions effect was caused by a higher relative response rate throughout the first block of probe trials compared to the
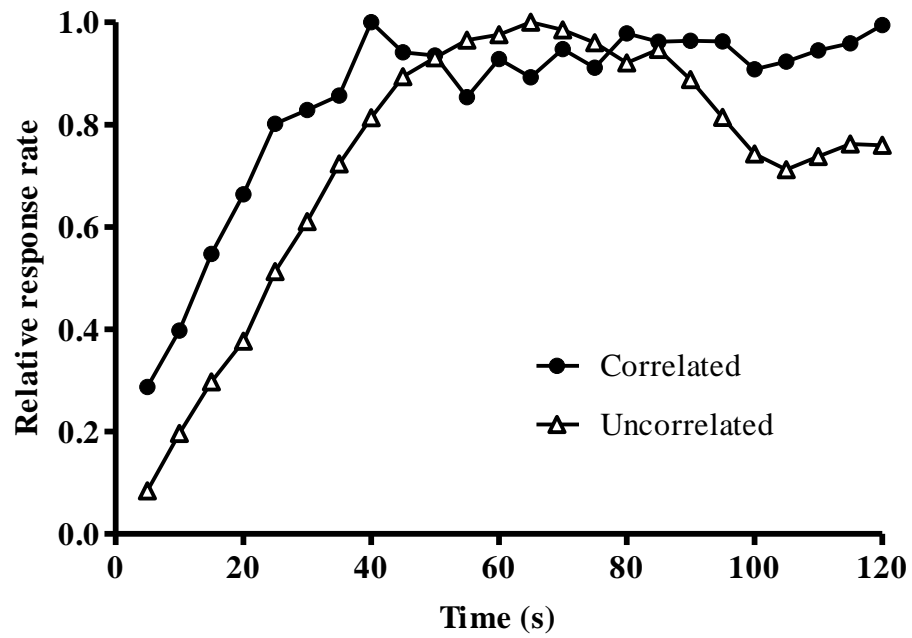
Figure 2.3. Peak-time curves generated by Correlated and Uncorrelated groups. The data have been relativized to a peak rate of 1.0 and are plotted as a function of 5-s time bins.

later probe trials. Analysis of the right limb yielded no significant main effect or interaction.

A similar comparison was made for the probe trial response curves for the Uncorrelated group, examining the effect of training by comparing the first 50 probe trials versus the last 50 probe trials. Analysis of the left limbs of these curves showed an effect of time bin [$F(59,236) = 5.22$, $p < .001$], and a significant interaction of block by time bin [$F(59,236) = 1.93$, $p < .001$]. The block by time bin interaction was the result of a change in the slopes of responding leading up to 60 s, with a sharper curve seen in the last 50 probe trials compared to the first 50. Analysis of the right limb yielded a significant main effect of time bin [$F(59,236) = 4.02$, $p < .001$] but the interaction between block and time bin did not reach significance [$F(59,236) = 1.35$, $p = .064$].

We collected the data in Experiment 2 such that individual trials could also be analyzed using a low-high-low analysis function in MATLAB, provided to us by Kimberly Kirkpatrick. The purpose of this procedure is to isolate the break-run-break responding on individual trials, such that start, peak, and stop times can be computed. This algorithm was implemented as reported in Church, Meck and Gibbon (1994) and Galtress and Kirkpatrick (2009). The only constraints on the analysis were that the start time had to precede the end time, and the ω^2 had to be greater than 0.05. There was a critical asymmetry in the number of trials which were excluded from the analysis on this basis. In the first phase, though Group Uncorrelated had a moderate percentage of trials excluded ($M = 14.5\%$, $SD = 2.09$), this was significantly less than the percentage of trials excluded in Group Correlated ($M = 41.0\%$, $SD = 9.78$), $t(4.36) = 5.93$, $p = 0.003$. A large proportion of trials on Correlated probes did not meet the criteria for the low-high-

low analysis, which generally means there was not a single discrete break-run-break function of responding on these trials, which indicates poor temporal control over behavior (Church et al., 1994; Galtress & Kirkpatrick, 2009). The large difference in number of trials excluded precludes reliable statistical analysis of start and stop times in this experiment, because of the resultant differences in the underlying distributions.

Discussion

Experiment 2 replicated the primary result of Experiment 1, with group Correlated showing flatter response curves on both the left and right limbs compared to birds in the Uncorrelated condition. This finding is comparable to the results of Wagner et al. (1968) and provides evidence that the disruption in temporal control over responding seen in Experiment 1 was not caused by a difference between conditions in the probability of reinforcement. The results suggest that the relative predictive validity of the visual cues in the Correlated condition (as with the S+/S- condition in Experiment 1) overshadowed control by the timing cue dimension; that is, the identity of the visual stimulus predicts reward vs. non-reward, and thus is a more salient dimension to the pigeon than the time interval to reward.

General Discussion

Most dimensions studied in animal learning experiments are sensory dimensions produced by differences in energy emanating from the environment. Interval timing, on the other hand, has been conceptualized as a more internal dimension produced solely by neural changes. Previous research has suggested that temporal control can be affected by motivational factors (e.g., Galtress & Kirkpatrick, 2009, 2010) or by other time cues (McMillan & Roberts, 2010). Here, we consider the possibility that time is a dimension

that interacts with sensory dimensions such as wavelength or line orientation, just as they interact with one another. In Experiment 1 S+ training, the onset of a sidekey cue (e.g., green) initiated an interval timing process and remained during the FI until reinforcement was delivered. Thus, a compound of two cues was present when reinforcement occurred, a time cue near 60 s and a green sidekey cue. As the 60-s time cue was reinforced over sessions, progressively greater control by time was shown by steeper peak-time curves on non-rewarded probe trials. When an S- cue was introduced (e.g., red), it was placed in compound with the 60-s time cue, and both were non-reinforced. The outcome of S+/S- training was that color became a highly relevant predictor of trial outcome (reinforcement or non-reinforcement), but time became a relatively invalid predictor of trial outcome. Thus, control by time was lost, as shown by flattening of the peak-time curve. This result was also evident in Experiment 2, providing evidence that relative predictive validity of the stimuli, and not overall rates of reinforcement, can explain the results.

Recall that in the Wagner et al. (1968) studies of relative cue validity, differential reinforcement of tone cues put in compound with a houselight weakened conditioned responding to the houselight. The more valid tone cues overshadowed control by the light cue. We suggest that in a similar manner, the relative validity of the visual cues in S+/S- training overshadowed control by the 60-s time cue, leading to flatter peak-time curves. The relative validity effect seen in Wagner et al. (1968) has been previously explained in the context of the Rescorla-Wagner Model (Rescorla & Wagner, 1972) and the same explanation can be applied to the results of the S+/S- procedure here. In the current AX, BX discrimination, the value of the λ parameter (i.e., the asymptotic strength that the unconditioned stimulus supports) is 1.0 in cases of reinforcement and 0 in cases

of nonreinforcement, and the β parameter (i.e., the learning rate parameter associated

with the unconditioned stimulus) is assumed to be greater in cases of reinforcement than

nonreinforcement. Although this predicts that the associative strength of the visual cue

dimension associated with reinforcement (A) should increase relative to the visual

dimension associated with nonreinforcement (B), it also predicts that the associative

strength of A should outpace learning of the temporal dimension (X) which occurs in

cases of both reinforcement and nonreinforcement. This lack of associative strength for

time would result in a lack of temporal control over behavior, such as that seen in the

current studies via the flattening of response curves and the greater number of individual

trials without discrete break-run-break functions. This account also raises the interesting

question about whether the effect seen in the current research would be replicated if the

reinforced FI and the non-reinforced interval were not the same duration, essentially

making the procedure an AX, BY discrimination.

   Theories of attention also describe the flattening of response curves found in the

present studies. In the two-stage model of Sutherland and Mackintosh (1971), a

dimension (analyzer) was more strongly attended to as its outputs (cues) consistently

predicted trial outcomes. Importantly, as one analyzer was strengthened, other analyzers

were weakened (the inverse hypothesis). Mackintosh (1975) rejected the inverse

hypothesis in favor of the idea that the relative salience or validity of cues would affect a

learning rate parameter, α, associated with each cue. If one cue, tone frequency,

consistently predicted reinforcement and non-reinforcement while another cue, light,

failed to predict trial outcome, α should increase for tone cues and decrease for the light

cue. Both of these theories readily account for the loss of control by the time cue seen in

the current experiment. Introduction of S+/S- training in which sidekey cues were perfectly correlated with reinforcement and non-reinforcement should decrease the analyzer strength of the time dimension (Sutherland & Mackintosh, 1971) or lower the α value associated with the time cue (Mackintosh, 1975). Both theories predict a loss of control by the time dimension as a consequence of S+/S- training. This would have the effect of less inhibition of non-timed responding, as seen in the present studies in the form of greater tail responding and fewer trials with timed break-run-break response peaks. Lejeune and Wearden (1991) suggested that at least part of observed between-species differences in timing may be due to different levels of non-timing responding (rather than due to time sensitivity), and the present results suggest the same effect within-species caused by varying attention to the temporal dimension.

It should be noted that the flattening effect on the curves in the S+/S- condition in both of the current experiments is not exactly symmetrical. Though significant effects were observed on both sides of the response curves, the post-60-s curves appear flatter. Part of this is likely an artifact of responding starting at 0; S. Roberts (1981) showed that the roughly Gaussian curves generated by the peak procedure are often best fit by a ramp plus a Gaussian function, with responding fit by the ramp function hypothesized as not related to timing. However, recent research suggests that different learning processes are responsible for pre- and post-peak performance (Balci et al., 2009; Kaiser, 2008; Kirkpatrick-Steger et al., 1996; Matell & Portugal, 2007). Because pre-peak responding reaches asymptote much faster than does post-peak responding, the asymmetry in response curve flattening in the current research might be due to differential effects on learning.

A common question of cue competition and relative validity studies is whether the difference in behavior to the overshadowed stimulus reflects a learning deficit or a performance deficit (e.g., Kasprow, Cacheiro, Balaz, & R. R. Miller, 1982; Kaufman & Bolles, 1981; Matzel, Schachtman, & R. R. Miller, 1985). In the present research, the animal might fail to learn the temporal cue dimension because it does not provide substantial information (or 'surprisingness': Rescorla & Wagner, 1972) or it may learn the timing of the stimulus but simply opt not to temporally control its behavior. The common test of this distinction is to devalue the stimulus which has monopolized associative strength and observe the change in responding to the overshadowed stimulus. In the current paradigm, however, it is not feasible to devalue a visual stimulus while presenting the temporal cue on its own. Whether the lack of temporal control is a learning or performance deficit thus remains unclear, although the gradual changes shown in Figure 2.3 may suggest the former.

In conclusion, we argue on the basis of our findings that time may be treated as a dimension similar to sensory dimensions studied in learning experiments. Thus, time cues may enter into cue competition effects not only with other time cues (McMillan & Roberts, 2010), but also with other cue dimensions, such as color, line orientation, and sound frequency, with the relative control exerted by time dependent upon the extent to which it overshadows or is overshadowed by the saliency or validity of these cues from other dimensions.

References

Balci, F., Gallistel, 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.

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

Cheng, K., & Westwood, R. (1993). Analysis of single trials in pigeons' timing performance. *Journal of Experimental Psychology: Animal Behavior Processes, 19*, 56-67.

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,* 135-155.

Galtress, T., & Kirkpatrick, K. (2009). Reward value effects on timing in the peak procedure. *Learning and Motivation, 40*, 109-131.

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

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

Gibbon, J., & Church, R. M. (1990). Representation of time. *Cognition, 37*, 23-54.

Jennings, D. J., Bonardi, C., & Kirkpatrick, K. (2007). Overshadowing and stimulus duration. *Journal of Experimental Psychology: Animal Behavior Processes, 33,* 464-475.

Jennings, D. J., & Kirkpatrick, K. (2006). Interval duration effects on blocking in appetitive conditioning. *Behavioural Processes, 71,* 318-329.

Kaiser, D. H. (2008). The proportion of fixed interval trials to probe trials affects acquisition of the peak procedure fixed interval timing task. *Behavioural Processes, 77*, 100-108.

Kamin, L. J. (1969). Predictability, surprise, attention, and conditioning. In Campbell, B. A. & Church, R. M. (Eds.). *Punishment and aversive behavior* (pp. 279-296). New York: Appleton-Century-Crofts.

Kasprow, W. J., Cacheiro, H., Balaz, M. A., & Miller, R. R. (1982). Reminder-induced recovery of associations to an overshadowed stimulus. *Learning & Motivation, 13,* 155-166.

Kaufman, M. A. & Bolles, R. C. (1981). A nonassociative aspect of overshadowing. *Bulletin of the Psychonomic Society, 18,* 318-320.

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

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

Mackintosh, N. J. (1975). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review, 82*, 276-298.

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

Matzel, L. D., Schachtman, T. R., & Miller, R. R. (1985). Recovery of an overshadowed
association achieved by extinction of the overshadowing stimulus. *Learning &
Motivation, 16,* 398-412.

McMillan, N., & Roberts, W. A. (2010). The effects of cue competition on timing in
pigeons. *Behavioural Processes, 84*, 581-590.

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

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

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

Sutherland, N. S., & Mackintosh, N. J. (1971). *Mechanisms of animal discrimination
learning*. New York: Academic Press.

Wagner, A. R., Logan, F. A., Haberlandt, K., & Price, T. (1968). Stimulus selection in
animal discrimination learning. *Journal of Experimental Psychology, 76*, 171-
180.

Chapter 3

Pigeons Rank-Order Responses to Temporally Sequential Stimuli

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Abstract

We explored pigeons' ability to learn a particular sequence of stimuli in which the durations of each stimulus varied among trials with the first response at the end of the sequence was reinforced. In Experiment 1A, we found that pigeons failed to use the whole sequence of three stimuli to predict food reinforcement, and instead responded only to the third 'rewarded' stimulus. When rewarded (123) and nonrewarded (213) sequences were used in a go/no-go procedure in Experiment 1B, however, pigeons showed a tendency to rank-order responding, with higher response rates to the second stimulus than the first, as well as lower response rates to the third stimulus on nonrewarded sequence trials. In Experiment 2, pigeons showed rudimentary rank-ordering of five stimuli in sequence, with lower responding to the final stimulus on nonrewarded trials, even when the sequence presented differed from the rewarded sequence only in a reversal of the second and third stimuli. Pigeons were capable of using ordinal information in a temporal task, but only when that information was easily discriminable and led to explicit consequences (rewarded sequences vs. nonrewarded sequences).

Keywords: pigeons, timing, ordinal, interval, serial pattern learning

Pigeons Rank-Order Responses to

Temporally-Sequential Stimuli

In a typical environment over the course of a day, animals are required to produce multiple complex behaviors in response to a complicated array of spatiotemporally-graded stimuli. Because animals cannot produce all behaviors at all times, and stimuli are not available at all times, efficient performance requires organizing behavior in some manner in order to maximize reward. Although the laws of conditioning may explain responses made to single stimuli by animals in lab experiments, those explanations often do not extend to the ability to organize behaviors when more complex organizations of stimuli are encountered in a natural environment. For example, if an array of foraging patches replenish on temporally distinct schedules, how does an animal organize its foraging behavior to maximize its reward while minimizing effort and predation risk?

Sequence Discrimination

Animals have previously been shown in a wide variety of tasks to be able both to discriminate and to produce sequences of stimuli in particular orders. Shimp (1976) presented pigeons with a sequence of three white Xs on left and right sidekeys in random order. After the sequence was presented, the pigeon was presented with one of three hues on the center key to peck, and once it had done so it was presented with that same hue on both sidekeys. The subjects were reinforced for pecking the side key on which one white X had been presented in the sequence, according to the positional cue provided by the hue: first in sequence for red, second for blue, and third for white. For example, the initial sequence *left-right-left* would correspond to pecking left on a red test cue, right on a blue test cue, or left on a white test cue. Although pigeons' accuracy in this task was

modulated by the retention interval and the duration of the stimulus presentations, Shimp found that birds were sensitive to the ordinal position of the stimuli, which he described as remembering "the temporal structure, or organization, or pattern, of events in its recent past" (p. 55).

Another example of a procedure which has examined animals' ability to represent the order of events is the delayed sequence-discrimination (DSD) task. In this procedure, a number of stimuli (e.g., red and yellow) are presented in different sequences, each for a fixed duration, followed by a test stimulus. Pecking on the test stimulus is only reinforced after one particular sequence (e.g., red-yellow in a two-event DSD, or red-yellow-red in a three-event DSD). Pigeons showed successful discrimination by pecking more on the test stimulus after the correct sequence than after incorrect sequences on both the two-event (Weisman, Wasserman, Dodd, & Larew, 1980) and three-event (Weisman, Duder, & von Konigslow, 1985) DSD tasks.

The procedures discussed thus far were primarily concerned with whether an animal is capable of remembering a succession of events or responding correctly on a test based on working memory trial-to-trial. These experiments may be compared to other procedures wherein an animal is shown an array of stimuli on one screen and required to respond to individual stimuli in the correct order based on reference memory. Using a simultaneous-chaining paradigm, it has been found that pigeons, Capuchin monkeys, and Rhesus macaques can learn to respond to as many as five stimuli (colors or patterns) in a correct (reinforced) order (D'Amato & Colombo, 1988, 1989; Swartz, Chen, & Terrace, 1991; Terrace, 1986, 1987, 1991). Tests that required the ordering of non-adjacent subsets of items from a learned list suggested that monkeys, but not pigeons, formed an

overall representation of the list (Terrace & McGonigle, 1994). However, recent research, using a more sensitive test controlling for contextual changes in subset testing, has revealed evidence suggesting that pigeons form an overall representation of 4- and 5- item lists (Scarf & Colombo, 2010). After training on four- or five-item lists, pigeons in this study were faster to learn pairs of internal stimuli that were presented in the same sequence as in list training rather than in a reversed sequence, showing that they represented the order of the internal pairs and not just the terminal items. In a second experiment, birds trained with four-item lists responded correctly to presentations of internal pairs above chance, even on initial probe trials, so long as training on the four-item list continued on the remainder of trials.

Recently, Scarf and Colombo (2011) used a procedure similar to that previously used in monkeys (Chen, Swartz, & Terrace, 1997), in which pigeons were trained on three different four-item lists. During testing, pigeons were presented with derived lists composed of the previously-trained items, with items placed either in the same ordinal positions as in training or in changed ordinal positions. Subjects performed much better on position-maintained derived lists during testing than on changed lists, including on the first session of testing. It was ruled out that pigeons were simply forming item-item associations because adjacent items were taken from different lists and the pattern of errors made in changed lists was different from maintained lists. These findings suggest that pigeons are capable of ordinal knowledge of lists of items, even with lists greater than three items long.

Pfuhl and Biegler (2012) studied ordinal representation in jackdaws using a hybrid paradigm of reference and working memory procedures. Subjects were trained to

respond in the correct order to 14 different three-item 'triplets', with each stimulus always correct at the same position within each triplet. On working memory tests, birds viewed the triplet presented sequentially, and then were tested with four items presented simultaneously: the three stimuli presented as that trial's triplet, plus a distractor item from another list. Birds were rewarded for pecking the correct sequence at test, and the trial was terminated when a bird made any error. Birds showed many more intrusion error responses to distractors with the same ordinal position as the correct sequence item. Over a series of experiments, the researchers found that the pattern of intrusion errors could best be explained by assuming that jackdaws had learned the ordinal position of items. In the final experiment, jackdaws "deduced" the ordinal position of a novel item presented with two familiar items. When three novel items were presented, each belonging to different ordinal positions, birds chose them in the correct order significantly above chance.

Ordinal Timing

Although ordinal representation of stimuli presupposes attending to a temporal succession of events, it is rarely discussed in the context of timing. A number of different timing mechanisms has been described recently (Buhusi & Meck, 2005; Carr & Wilkie, 1997a), including circadian timing (24-hr entrainable clock), interval timing (seconds to minutes to hours), and millisecond timing (up to one second). Along with these more commonly-accepted phase and interval timers, Carr and Wilkie suggested that animals possess a discrete 'ordinal timing' mechanism, a timer which 'counts up' from a particular position p through a series of events with n elements. By forming a representation of its position in a sequence of temporally-organized events, such as in

serial pattern learning as discussed previously, or following a fixed daily foraging circuit ('traplining': Gill, 1995), Carr and Wilkie suggested that animals can then predict the next event in time. By defining timing as solving a particular problem in the temporal domain (i.e., predicting when an event will occur), the authors stated that this ability for maintaining ordinal information constituted a timing mechanism.

To study this hypothesis, Carr and Wilkie (1997b) tested rats on a daily time-place task. Rats were trained to lever press at two different locations in an operant chamber, with one being correct during morning sessions and the other correct during afternoon sessions. During testing, select morning or afternoon sessions were omitted, and thus the next session would be out of phase. Whether the morning or afternoon session was omitted, on the next afternoon or morning session (respectively) rats chose the location correct for the morning session, and thus the rats were visiting the 'first' daily location in both cases. The researchers interpreted this as evidence that rats were using an ordinal timer which was reset each day.

Recent studies have challenged the suggestion that animals use ordinal timers in daily time-place learning tasks. Pizzo and Crystal (2002) reasoned that an ordinal timer should be insensitive to the relative interval location of each item; to borrow their example, knowing who finished first, second, or third in a race does not provide information about how close their race times were. The researchers trained rats to search four food troughs across three daily sessions, either two in the morning and one in the afternoon (Group AB-C) or one in the morning and two in the afternoon (Group A-BC), with each of sessions A, B, and C differentially rewarded across spatial locations. On probe sessions, the time of bout B was shifted later in the AB-C group and earlier in the

A-BC group. Rats in both groups performed at chance on these probes, suggesting they were not using an ordinal timer on this task and were instead using interval or circadian temporal information (subsequent tests suggested they were using both interval and circadian timing). Further, Pizzo and Crystal (2004) suggested that the rats in a time-place task will use a non-temporal alternation strategy (similar to Carr & Wilkie, 1997b) when non-temporal cues, such as handling before each session, are available. Crystal (2006) noted that animals can simultaneously use circadian and interval timing mechanisms for anticipating food in time-place tasks but omitted the possibility that animals might also simultaneously process temporally-ordered information (i.e., an ordinal timer).

Rationale for Present Research

There are several limitations to interpreting the results of previous work in daily time-place conditioning as evidence for or against the existence of ordinal timers in animals. Firstly, Carr and Wilkie (1997b) showed that rats would visit the 'first' daily location after an omission of either a morning or afternoon testing session, while Pizzo and Crystal (2002) varied the temporal location of the 'middle' foraging bout of three daily trials in testing. Pigeons (Straub & Terrace, 1981) and bees (Collet, Fry, & Wehner, 1993) have been shown to learn the order of first and last ordinal elements relatively easily compared to middle elements, and if rats have a similar difficulty with learning the middle elements of temporal sequences then this may account for the difference in ordinal ability in rats between Carr and Wilkie (1997b) and Pizzo and Crystal (2002). These studies also vary from other work in the sequence learning literature in a number of key ways, largely due to their presentation outside the operant

chamber, including fewer training trials and less discrete ordinal stimuli. Using ordered time of day instead of discrete stimuli (such as different colors and shapes used in operant procedures) could lead to overshadowing of order by more-salient interval cues.

Conversely, the literature focused on ordinal timing in daily time-place tasks also highlights questions left unanswered in typical sequencing research. Since many tasks which show successful sequence learning utilize simultaneous presentation of stimuli, it is difficult to apply a timing concept to the behaviors observed in these studies. Even in research which has found that pigeons will respond accurately to sequences of stimuli presented over time, such as in the DSD task (e.g., Weisman et al., 1980; 1985), animals usually observe passively the presentation of stimuli over a short interval and respond to a separate stimulus if the observed sequence was the 'correct' (rewarded) order of stimuli. These gaps make it difficult to ascertain how animals represent stimuli in a temporal sequence. Ordinal timing is defined as the ability to "anticipate events that reliably occur in a certain order within a period of time" (Carr & Wilkie, 1997a), yet there is little direct evidence in the studies reviewed here that animals maintain their current position within a temporal sequence to anticipate what will happen next in sequence.

In the present experiments, we examined whether pigeons are capable of tracking the identity of a particular sequentially-presented sequence of colors and respond based on their temporal location within each sequence. By using an operant chamber and a procedure more typical of interval timing studies, we determined whether pigeons were capable of rank-ordering their responses based on a particular order of stimuli in time. In Experiment 1A, pigeons were presented with three-stimulus sequences that varied in

length from 30 to 90 s (variable interval; VI) throughout training; on test trials, pigeons were presented with fixed interval (FI) probes of different presentations of the same three stimuli. We expected that if pigeons track the order of stimuli presented in training, they should respond more to the final stimulus in the sequence on probe trials identical to baseline and less on probe trials whose presented sequence differed from baseline. A secondary prediction was that pigeons may respond more to the second stimulus in the sequence than to the first but less than to the third, due to its relative proximity to reward in the sequence. In other words, pigeons were expected to rank-order their responding based on the positional identity of stimuli within the sequence presented. Experiment 1B was procedurally identical to 1A, except that a nonreinforced order was presented during training on separate trials from the previously-rewarded order. We expected that presenting a 'No Go' sequence during baseline would enhance discrimination of 'incorrect' order of stimulus presentations, with concomitant decreases in responding to the third stimulus when presented out of order. Finally, in Experiment 2, we presented pigeons with various sequences of five stimuli, with only one particular order rewarded for the first peck after 30-90 s, to study the ordinality of pigeons' responding on a more complex sequence of stimuli.

<p align="center">**Experiment 1A**</p>

Method

      Subjects.

Six adult White Carneaux pigeons (*Columba livia*) were used. Pigeons had previous experience with operant procedures. Birds were maintained at approximately 85% of free-feeding weight throughout the experiment, with constant access to water and

health grit. They were individually housed in cages in a room kept environmentally controlled at 22 degrees C. Fluorescent lights were turned on at 8:00 a.m. and off at 8:00 p.m. each day. Testing was performed between 9 a.m. and 4 p.m. for 5 days each week.

Apparatus.

Three enclosed, sound-attenuating operant chambers measuring 31 x 35.5 cm (floor) x 35.3 cm (height) were used. The front wall of each chamber held three pecking keys, 2.5 cm in diameter and level with the pigeon's head, in a row, spaced 8 cm apart. Projectors behind each key projected filtered light, presenting different colors or patterns on the keys. Grain reinforcement was delivered by an electromechanical hopper through a 6 x 6 cm opening in the front wall located near the floor, directly below the center key. Presentation of stimuli, reinforcement, and recording of responses were carried out by microcomputers, in another room, interfaced to the operant chambers.

Procedure.

Each of 40 sessions consisted of 34 baseline trials. On each trial, pigeons were presented with three different colors (red, green, and blue) presented sequentially (i.e., "1-2-3") on the center key, in the same order on each trial. Two birds saw a red-green-blue order, two saw a green-blue-red order, and two saw a blue-red-green order. Each color was presented for a 10-30 s variable interval (VI; uniform distribution). After the contingent interval had elapsed for the third presented stimulus, the first peck to that stimulus ended the trial and resulted in 3 s of access to hopper grain. A 40-80 s darkened inter-trial interval (ITI; uniform distribution) followed food access. Pecks to the center key were recorded throughout each trial in 1-s time bins.

Non-reinforced probe trials were interspersed randomly among baseline trials from sessions 11-40. Two each of five types of probe trials were used, for a total of ten per session. All probe trials used fixed intervals (FIs) rather than VIs. The five probe trial types were:

- Identical to baseline (i.e., 1-2-3 order), with the exception that the three stimuli were presented for 20 s each;

- First ordinal stimulus (i.e., 1-only) presented for 60 s;

- First and second stimulus (i.e., 1-2 order) presented for 30 s each;

- Third stimulus (i.e., 3-only) presented for 60 s; and

- Reordered stimuli (i.e., 2-1-3 order), with stimuli presented for 20 s each. For example, a pigeon whose baseline rewarded order was 'red-green-blue' would see the stimuli presented in the order 'green-red-blue' on these trials.

The "1-only" and "1-2 order" conditions were included as controls for interval timing (i.e., that responding may increase with increasing interval durations regardless of stimulus presentation), while the remainder of the probe trials were included to illustrate pecking to the typically-rewarded third stimulus in a variety of sequences. All probe trials were followed by a 40-80 s darkened ITI (uniform distribution). Pecks to the center key were recorded throughout each probe trial in 1-s time bins.

Results and Discussion

Probe trial data from the final 10 sessions were analyzed to eliminate training effects. Figure 3.1 illustrates the data from each of the five probe trial types from this
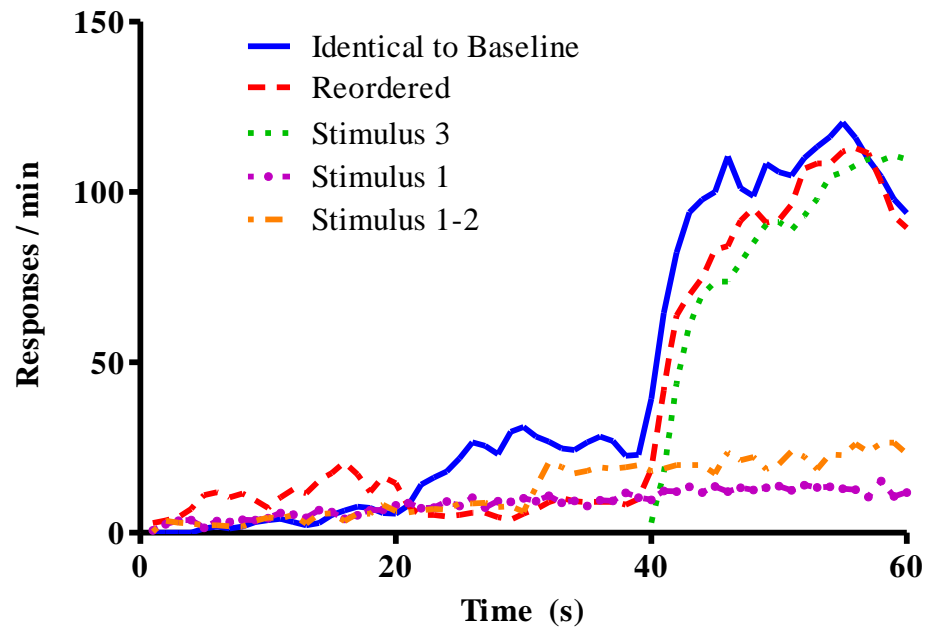
Figure 3.1. Experiment 1A: Mean responses per min across 60-s probe trials. Each stimulus was presented for 20 s, except in the Stimulus 1 and Stimulus 3 conditions (presented for 60 s) and stimulus 1-2 condition (each presented for 30 s).

period. In all analyses, the stimulus number (1, 2, or 3) represents the order in which stimuli appeared on baseline trials, and not necessarily the order in which they were presented on a particular probe trial.

We analyzed average data from the last 20 s of three probe trial types to verify that changes in responding were due to the presentation of the different stimuli, and not simply interval timing from the beginning of the trial. A one-way repeated-measures ANOVA comparing the average response rate on three conditions (Identical to Baseline, Stimulus 1, and Stimulus 1-2) in the last 20 s of the probe trial (i.e., the last 20 s of the first stimulus on condition Stimulus 1, the second stimulus on Stimulus 1-2, and the third stimulus on Identical to Baseline) showed a significant effect, $F(2,10) = 34.50$, $p < 0.001$. A Bonferroni-corrected post-hoc test showed a significant difference between responding to the third stimulus in the last 20 s compared to the second stimulus [$t(5) = 9.72$, $p = .001$] and the first stimulus [$t(5) = 6.54$, $p = 0.004$]. There was no significant difference in responding between the first and second stimulus in the final 20 s of the trial [$t(5) = 0.74$, $p = 1.000$]. Birds pecked significantly more to the third, typically-rewarded stimulus than to either of the other stimuli in the last 20 s of probe sessions, indicating that differences between probe-trial conditions cannot be explained by pigeons simply increasing responding using an interval timer from the onset of the first stimulus throughout the 60 s intervals.

A 3 (Stimulus: 1, 2, 3) x 2 (Condition: Identical to Baseline, Reordered) repeated measures ANOVA examining average response rates showed a non-significant interaction, $F(2,10) = 3.79$, $p = 0.060$. The main effect of stimulus was significant, $F(2,10) = 56.139$, $p < .001$, but the main effect of condition was not, $F(1,10) = 3.265$, $p =$

.131. A planned-comparison 2 (Stimulus: 1, 2) x 2 (Condition: Identical to Baseline, Reordered) ANOVA again showed a non-significant interaction, $F(1,5) = 5.704$, $p = .063$. In this comparison, neither main effect was significant, Fs ≤ 1.48, ps $\geq .278$. Pigeons did not peck significantly less in the Reordered condition compared to the condition identical to baseline. Also, a lack of a significant main effect for stimulus when comparing just the first two stimuli suggests that pigeons did not, on average, respond differently to the first and second stimuli, regardless of the order in which they were presented.

In a one-way repeated measures ANOVA comparing average response rates to just the third stimulus, there was no significant difference in responding on baseline, reordered, and third-stimulus-only probe trials, $F(2,10) = 1.41$, $p = .289$. Pigeons did not appear to alter their responding to the third stimulus based on which stimuli preceded it, even on trials in which the third stimulus was presented without any prior stimuli.

Experiment 1B

In Experiment 1A, pigeons did not appear to rank-order stimuli in a sequence ending in food reward, and instead their behavior appeared to be strongly controlled by the mere presence of the third stimulus. Because the third stimulus is the only one to which responding is directly rewarded, and is thus most proximal to reward, it is not surprising that pecking was largely controlled by the ultimate cue. We hypothesized that birds needed a greater basis for comparison among the stimuli in order to attend to cues preceding the highly salient third cue. In Experiment 1B, we trained the same birds from Experiment 1A on a similar procedure, with half of baseline trials presented identically to Experiment 1A. However, on the other half of baseline trials, pigeons viewed the

'reordered' trial type, with the first two stimuli reordered in sequence and no reinforcement available for pecking the third stimulus. We reasoned that with only 50% reward available for attending to the third stimulus alone, pigeons may attend to the order in which stimuli are presented.

Method

Subjects and apparatus.

The subjects used, and all aspects of animal husbandry and experimental apparatus, were the same as in Experiment 1A.

Procedure.

Each session consisted of 17 baseline *Go* trials and 17 baseline *No-Go* trials. Go trials were identical to baseline trials in Experiment 1A, with each of the stimuli red, green, and blue presented for 10-30 s, and each bird was maintained on the same order of stimuli used in Experiment 1A. On No-Go trials, the order of the first two stimuli was reversed in sequence relative to Go trials (e.g., a bird whose Go condition was red-green-blue would have a reordered No-Go condition in the sequence green-red-blue). A 40-80 s darkened ITI followed food access on Go trials, or termination of the third stimulus on No-Go trials. Pecks to the center key were recorded throughout each trial in 1-s time bins.

All probe trials were identical to those used in Experiment 1A and were presented randomly among baseline trials starting from the first session; probe trials consisting of the first stimulus alone (1-only) and the first and second stimuli in order (1-2 order) were included only for consistent testing with Experiment 1A and were not analyzed as part of the present results. Pigeons were run for 33 sessions.

Results and Discussion

Only data from the final 10 sessions were used, to eliminate training effects. Probe trial data from this period are presented in Figure 3.2. In all analyses, the stimulus number (1, 2, or 3) represents the order in which stimuli appeared on Go trials, and not necessarily the order in which they were presented on a particular probe trial.

A 3 (Stimulus: 1, 2, 3) x 2 (Condition: Go, No-Go) repeated measures ANOVA examining average response rates showed a significant interaction, $F(2,10) = 33.178$, $p < 0.001$. The main effect of stimulus was significant, $F(2,10) = 18.66$, $p < .001$, and there was a nonsignificant main effect of condition, $F(1,10) = 3.28$, $p = .130$. A planned-comparison 2 (Stimulus: 1, 2) x 2 (Condition: Go, No-Go) ANOVA again showed a significant interaction, $F(1,5) = 18.67$, $p = .008$. Neither the main effect of stimulus nor that of condition reached significance. Planned comparisons revealed a significant decrease in responding to stimulus 2 out of sequence [$t(5) = 3.02$, $p = 0.029$] but no significant difference in responding to stimulus 1 regardless of when it was located in the sequence [$t(5) = 0.62$, $p = 0.56$]. Pigeons appeared to rank-order stimuli, responding more to the second stimulus than to the first, especially when the second stimulus was presented second in sequence. Given the low responding to stimulus 1, it is possible that a floor effect can account for the lack of a difference in responding.

In a one-way repeated measures ANOVA comparing average response rates to just the third stimulus, there was a significant difference in responding among Go, No-Go, and third-stimulus-only probe trials, $F(2,10) = 10.61$, $p = .003$. Planned comparisons showed that responding to the third stimulus on the Go probe was significantly different from both the No-Go ($t[5] = 2.98$, $p = .031$) and third-stimulus-only probes ($t[5] = 3.65$, p
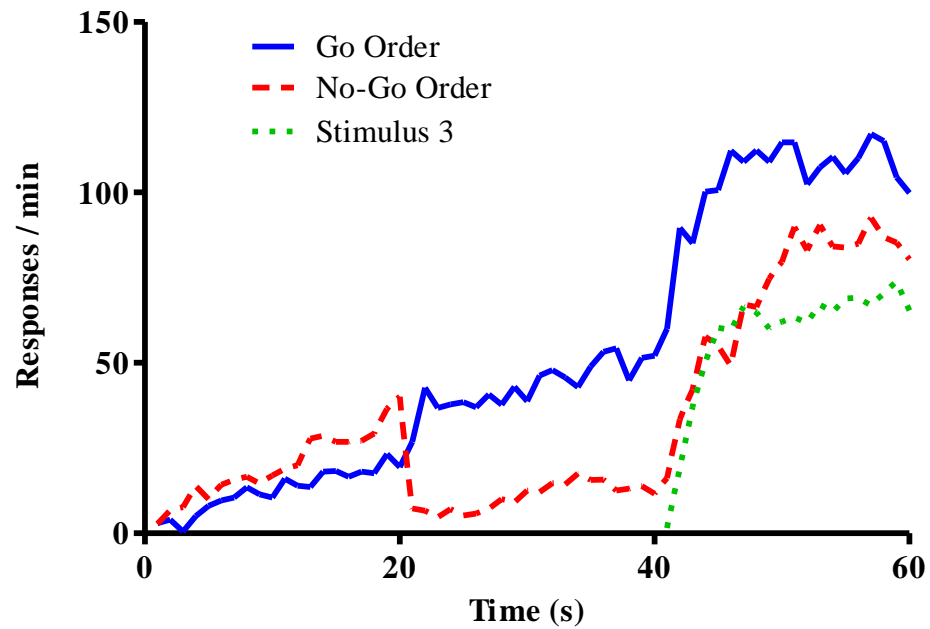
Figure 3.2. Experiment 1B: Mean responses per min across 60-s probe trials. Stimuli presented in sequence contingent with reward in baseline (Go) or in sequence not contingent with reward in baseline (No-Go). Data from first 20 s of 3-only probe trial included for comparison.

= .015). Pigeons responded more when the third stimulus appeared in the Go sequence

than when it appeared out of that sequence, suggesting that pigeons were attending to the

order of the first two stimuli even though responding to them was never directly

reinforced; however, it is possible that pigeons were not directly attending to the first

stimulus, and only to whether the second stimulus preceded the third.

Experiment 2

Experiment 1B showed that pigeons respond less to a typically-reinforced

stimulus if it is presented at the end of a nonreinforced sequence. However, some results

suggested that pigeons may have ignored whether the first stimulus had been presented,

and instead attended only to whether the second stimulus preceded the third. Pigeons

may simply be conditioned to the second stimulus in the Go condition as a higher-order

reinforcer based on its proximity to the third stimulus on reinforced Go trials. This would

explain high pecking rates to the third stimulus and lower (but still high) rates of pecking

to the second stimulus. It could thus be argued that pigeons did not establish a cognitive

ordinal "map" of the ranks of each of the three stimuli, but rather based their response

rates to the third stimulus on their current rate of pecking when the third stimulus came

on. This possibility would explain lower response rates to the third stimulus in both the

2-1-3 condition and in the 3-only probe condition, where the third stimulus appeared

when the pigeon was not pecking at a high rate, compared to the 1-2-3 probe condition

where the pigeon is already pecking at a high rate when the third stimulus comes on.

In Experiment 2, pigeons saw longer five-stimulus sequences, with one particular

sequence being reinforced and the remainder nonreinforced. All sequences started and

ended with the same stimuli, because beginning and end elements have been argued to

have distinct features in addition to ordinality (Terrace, Chen, & Jaswal, 1996), but ordinal position of the second, third, and fourth stimuli varied on nonreinforced trials. By varying the three 'middle' stimuli but not the first or last, we explored the degree to which each stimulus influenced responding on reinforced trials vs. nonreinforced trials where neither the last stimulus nor the stimulus immediately preceding it perfectly predicted reward. We also used geometric VI distributions for stimuli and ITI durations instead of the uniform distributions used in previous experiments, because geometric distributions have been suggested to eliminate subjects' ability to rely on interval timing for rewarded intervals or non-rewarded ITIs (Fleshler & Hoffman, 1962). By using five-stimulus sequences instead of three-stimulus sequences, we sought to examine whether pigeons could learn more about a sequence than simply the order of the last two stimuli.

Method

Subjects and apparatus.

Six new pigeons were used in Experiment 2, and all aspects of animal husbandry and experimental apparatus were the same as in Experiment 1.

Procedure.

Each of 60 sessions consisted of 40 trials. Twenty trials were *Go* trials comprised of yellow, red, green, blue, and white triangle (1, 2, 3, 4, and 5, respectively) stimuli presented in sequence on the center key. Each stimulus was presented for 8-22 s (geometric distribution), meaning that presentation of the entire sequence was a 40-110 s VI. The first peck to the white triangle stimulus after the contingent interval had elapsed was reinforced with 6 s of access to hopper grain, followed by a 32-94 s darkened ITI (geometric distribution). To maintain high rates of responding, a limited hold was used

such that failure to obtain reinforcement before 150 s had elapsed since the beginning of the trial led directly to the ITI. Pecks on the center key were recorded throughout each session as total pecks per stimulus.

The other 20 trials on each session consisted of five of each of four *No-Go* trial types. On each of these trials, yellow (1) was the first-presented stimulus and a white triangle (5) the last-presented stimulus, as in the Go condition. However, the ordinal location of the three intervening stimuli (2, 3, 4) was varied from the Go condition, with sequences of green-blue-red (3-4-2), green-red-blue (3-2-4), blue-red-green (4-2-3), and blue-green-red (4-3-2) represented. Each of the five stimuli were presented for 8-22 s (geometric distribution) as in the Go condition, but after the contingent interval had elapsed for the white triangle, the stimulus turned off and led directly to the 32-94 s (geometric distribution) ITI. Pecks on the center key were recorded throughout each session as total pecks per stimulus, and all data were separated such that each of the stimuli on each of the four No-Go trial types could be analyzed separately.

Results and Discussion

Only data from the final 30 sessions were used, to eliminate training effects. Trial response averages for Go trials and each of four No-Go trial types, as well as an average of all four No-Go trial types, are presented in Figure 3.3.

A one-way ANOVA comparing average response rates to each of the five stimuli on Go trials alone showed a significant difference, $F(4,20) = 18.10$, $p < .001$. This effect was characterized by a significant linear trend [$F(1,5) = 40.66$, $p = .001$] and a quadratic trend [$F(1,5) = 9.57$, $p = .027$]. This effect suggests that on average pigeons responded more to each stimulus in order, but much more to the final stimulus, as expected based on
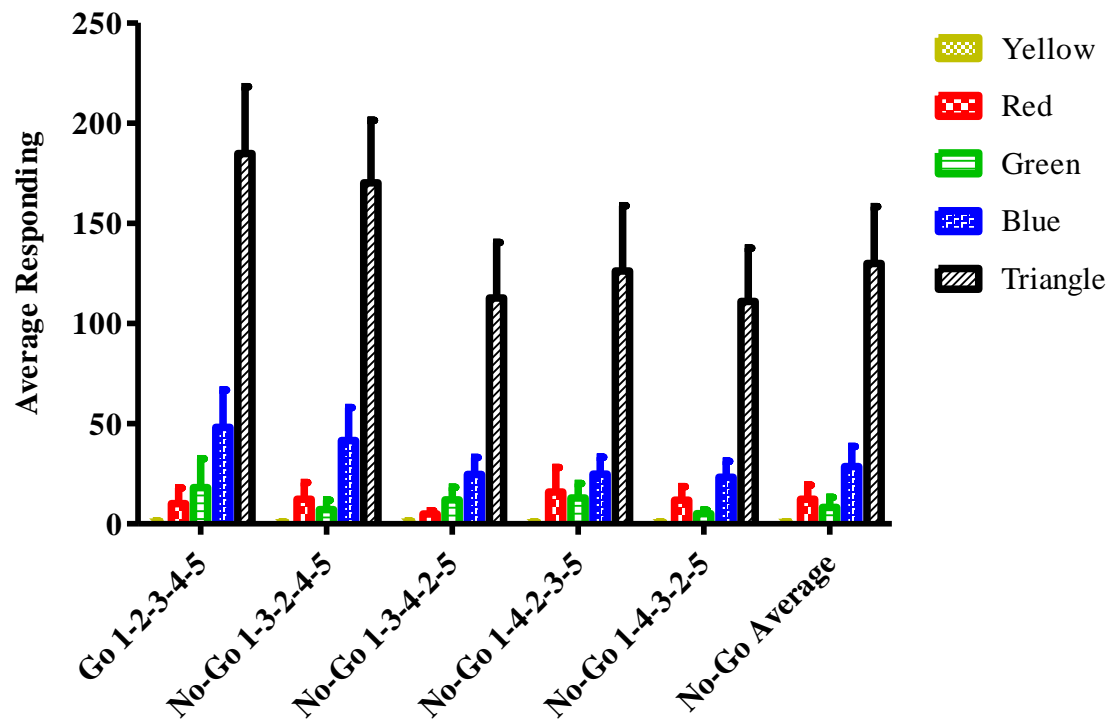
Figure 3.3. Experiment 2: Mean responses to each of five colored stimuli presented in sequence on sessions 31-60, either rewarded (Go) or not rewarded (No-Go). Numbers (1, 2, 3, 4, 5) are color numbers (Yellow, Red, Green, Blue, and Triangle, respectively) relative to Go condition.

previous experiments presented here. Planned comparisons showed no significant differences between response rates to stimuli 1 and 2 or between stimuli 2 and 3, ts $\leq$ 1.24, ps $\geq$ .268. There was a marginally significant difference between responding to stimulus 3 and to stimulus 4, $t(5) = -2.55$, $p = .051$, and a significant difference between responding to stimulus 4 and stimulus 5, $t(5) = -3.26$, $p = .023$.

A 3 (Stimulus: 2, 3, 4) x 2 (Condition: Go, No-Go averages) planned-comparison repeated measures ANOVA showed a marginally significant interaction, $F(2,10) = 4.07$, $p = .051$. The main effect of stimulus was significant, $F(2,10) = 6.88$, $p = .013$, but there was no main effect of condition, $F(1,10) = 2.19$, $p = .199$.

In a one-way repeated measures ANOVA comparing average response rates to just the fifth stimulus across each of the five trial types, there was a significant main effect in responding even after correcting the degrees of freedom with Greenhouse-Geisser, $F(1,6) = 9.44$, $p = .021$. A simple contrast of responding to the fifth stimulus on Go trials compared to averaged responding to the fifth stimulus across all No-Go trials showed a significant difference, $t(5) = 3.55$, $p = .016$. A further planned comparison between responding to the fifth stimulus on Go trials to the same stimulus on just 1-3-2-4-5 No-Go trials (i.e., Go and No-Go trials in which the fifth stimulus was immediately preceded by the fourth) also showed a significant difference, $t(5) = 5.55$, $p = .003$. Though examination of Figure 3 suggests that responding to the fifth stimulus was very similar between the 1-2-3-4-5 and the 1-3-2-4-5 conditions (with a relatively high degree of between-subjects variability), in fact all six pigeons showed decreased pecking to the fifth stimulus in the No-Go condition, with relatively low within-subject variability. Finally, a planned contrast showed a significant difference between responding on the

fifth stimulus of the 1-3-2-4-5 condition compared with the average of the three other No-Go trials, $t(5) = 2.80$, $p = 0.038$. Overall, pigeons responded more when the fifth stimulus appeared in the Go sequence than when it appeared in a No-Go sequence, including when it was preceded by the same stimulus as in the Go condition. This result suggests that pigeons were attending to the order of stimuli, even though stimuli other than the white triangle were never directly reinforced. Moreover, it suggests that pigeons responded to the final stimulus based on more information than the mere presence of blue as the penultimate stimulus; however, pigeons still responded more to the fifth stimulus on trials with blue (compared to other stimuli) as the penultimate stimulus.

General Discussion

Birds showed behavior suggesting they were sensitive to the temporal order of a number of stimuli, though only when non-rewarded sequence alternatives were also presented on separate trials. In Experiment 1B, birds showed decreased responding to the third, often-reinforced stimulus when it was presented in a non-rewarded sequence, despite previous experience in Experiment 1A where they ignored the sequence and pecked only the third stimulus. The only difference between the two procedures was the presence of baseline "no-go" sequence trials. With presentation of sequences of five stimuli in Experiment 2, pigeons pecked significantly more to the fifth stimulus when it was in the reinforced rather than non-reinforced sequence, even relative to a very similar arrangement of stimuli. This suggests that pigeons were not simply chaining behaviors by responding to the fifth stimulus only when it followed the usually-correct fourth, but rather were tracking the positional identity of stimuli within the full sequence, or at least a greater subsection of it than just the final two stimuli.

One important caveat to claiming the current studies show ordinal timing is that although our results showed significant differences in response rates between rewarded and non-rewarded sequences, the differences were not large. Birds responded at high rates to the final stimulus even at the end of non-reinforced sequences, which is likely a result of the associative strength of the final stimulus coupled with poor inhibitory control. It is also true that without a non-reinforced "no-go" baseline for comparison, birds did not organize their responding sequentially. In simple terms, although birds were capable of ordinal timing in the current experiments, they did not appear to be very good at it. Finally, though birds pecked the final stimulus more on Go trials than on No-Go trials with the same penultimate stimulus (sequence 13245), they also pecked the final stimulus more on those No-Go trials than on other No-Go trials. These results suggest that although birds have some capacity for temporally ordering their behavior based on sequentially-presented stimuli, the mechanism by which they accomplish this does not appear to have automatic control over behavior as has been suggested of the internal interval timer (Roberts, W. A., Coughlin, & Roberts, S., 2000; McMillan & Roberts, W. A, 2010). It may be that the mechanism underlying this temporal sequencing ability may not be 'wired' specifically for ordinal timing, compared to how we might describe interval timing as directly resulting from an automatic and obligatory endogenous timing mechanism such as a pacemaker-accumulator or oscillator. Instead, temporally sequenced behavior may result from co-opting a number of other mechanisms available to the animal in response to a highly complex and dynamic environment.

Ordinal timing is based on the ordinal level of measurement, compared to phase and interval timing which are based on the interval and ratio levels of measurement,

respectively (Carr & Wilkie, 1997a). An important feature of Stevens' (1946; 1951) levels of measurement is that ordinal information is relatively impoverished compared to interval information, and ratio information (interval information with a true zero point) is least impoverished. Ratio information, such as that derived from timing intervals, has a large number of valid operations (=, <, >, +, -, *, /) while the number of valid operations for ordinal information is comparably small (=, <, >). For example, in Experiment 1A reported here, the wait time from the onset of the first stimulus to food reward is (on average) three times the duration (a mean of 60 s) compared to the wait to food reward from the onset of the third stimulus (a mean of 20 s); however, it is not meaningful to measure the first stimulus as three times "earlier" or three times "worse" than the third stimulus. Ordinal information may be derived from ratio information, however, because of the nested nature of operations: the first stimulus is earlier than the third stimulus (thus predicting increased levels of responding to later stimuli). In the present experiments, the pigeons may have been ordinally representing each stimulus in long-term memory based on its average interval delay to food reward (as shown in Olthof & Santi, 2007), and separately organizing its behavior on a current trial based on how closely the present order of stimuli matched the overall order of previously-rewarded sequences (as shown in previous serial pattern learning studies). By leveraging both of these two previously-evidenced mechanisms, pigeons would be expected to produce roughly the results found here, with high rates of responding to temporally-proximal stimuli even on non-reinforced sequence trials, yet lower rates compared to trials in which the 'correct' sequence is shown.

If what Carr and Wilkie (1997a, 1997b) described as ordinal timing were in fact an amalgamation of several underlying processes, it would not pose a great threat to its existence as a 'timing system' per se. All timing mechanisms by definition allow organisms to predict when an event will occur. The breadth of this problem-based definition allows it to encompass multiple processes so long as it still allows the organism to accomplish a temporally-based task. It makes sense that ordinal timing may be a high-level cognitive representation relying on multiple low-level processes if only because it is required to track a theoretically infinite number of stimuli over a large continuum of timescales.

The concept of ordinal timing presents an interesting contrast with traditional models of timing, such as those described by Buhusi and Meck (2005). Ordinal timing does not map on to any one time scale as in the case of circadian, interval, and millisecond timers. Instead, an ordinal timer might approximate time on any number of scales by cognitively organizing the stimuli and/or behaviors within that scale. It is already well known that many species array their foraging behaviors in particular ordered patterns throughout each 24-hr cycle, such as in the traplining of bees (Janzen, 1970) and birds (Gill, 1995). Ordinally-organized behavior has also been used as an explanation for interval timing; for example, the behavioral theory of timing (Killeen & Fetterman, 1988) suggests that a pacemaker initiated at the beginning of an FI advances an animal through successive adjunctive behavioral states and that the behavioral state present at the moment of reinforcement will be conditioned to elicit responding. Finally, though it would be difficult for organisms to track sequences of stimuli in the under-a-second range typical of millisecond timing, many complex behaviors are the result of temporally

organized behavior on the millisecond scale. In humans, playing a guitar or piano requires not only coordinating one's fingers from one note or chord to the next, but also smoothly transitioning between a number of notes (sometimes very rapidly) within the constraints of an oscillating time scale (rhythm). Where millisecond, interval, and circadian timers are low-level processes which automatically entrain oscillators based on relatively non-overlapping time scales (Buhusi & Meck, 2005), an ordinal timer might be called upon to organize behavior based on representations from any of (or across) the three scales. It may be that temporally-sequenced behaviors result from an integration of information from more conventional cognitive systems of categorization and timing mechanisms.

References

Buhusi, C. V. & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience, 6,* 755.

Carr, J. A. R. & Wilkie, D. M. (1997a). Ordinal, phase, and interval timing. In Bradshaw, C. M. & Szabadi, E. (Eds.), *Time and Behaviour: Psychological and Neurobehavioural Analyses* (pp. 265-327)*.* Amsterdam, The Netherlands: North-Holland/Elsevier Publishers.

Carr, J. A. R. & Wilkie, D. M. (1997b). Rats use an ordinal timing system in a daily time-place learning task. *Journal of Experimental Psychology: Animal Behavior Processes, 23,* 232-247.

Chen, S., Swartz, K. B., & Terrace, H. S. (1997). Knowledge of the ordinal position of list items in rhesus monkeys. *Psychological Science, 8,* 80-86.

Collet, T. S., Fry, S. N., & Wehner, R. (1993). Sequence learning by honeybees. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology, 172,* 693-706.

Crystal, J. D. (2006). Time, place, and content. *Comparative Cognition & Behavior Reviews, 1,* 53-76.

D'Amato, M. R., & Colombo, M. (1988). Representation of serial order in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes, 14*, 131-139.

D'Amato, M. R., & Colombo, M. (1989). Serial learning with wild card items by monkeys (*Cebus apella*): Implications for knowledge of ordinal position. *Journal of Comparative Psychology, 15*, 252-261.

Fleshler, M. & Hoffman, H. S. (1962). A progression for generating variable-interval

    schedules. *Journal of the Experimental Analysis of Behavior, 5,* 529-530.

Gill, F. B. (1995). *Ornithology*. New York: W. H. Freeman & Co.

Janzen, D. H. (1970). Euglossine bees as long-distance pollinators of tropical plants.

    Science, 171, 203-205.

Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological*

    Review, 95, 274-295.

McMillan, N. & Roberts, W. A. (2010). The effects of cue competition on timing in

    pigeons. *Behavioural Processes, 84,* 581-590.

Olthof, A. & Santi, A. (2007). Pigeons (*Columba livia*) associate time intervals with

    symbols in a touch screen task: Evidence for ordinality but not summation.

    Journal of Comparative Psychology, 121, 82-94.

Pfuhl, G. & Biegler, R. (2012). Ordinality and novel sequence learning in jackdaws.

    Animal Cognition, 15, 833-849.

Pizzo, M. J. & Crystal, J. D. (2002). Representation of time in time-place learning.

    Animal Learning & Behavior, 30, 387-393.

Pizzo, M. J. & Crystal, J. D. (2004). Evidence for an alternation strategy in time-place

    learning. *Behavioural Processes, 67,* 533-537.

Roberts, W. A., Coughlin, R., & Roberts, S. (2000). Pigeons flexibly time or count on

    cue. *Psychological Science, 11,* 218-222.

Scarf, D., & Colombo, M. (2010). Representation of serial order in pigeons (*Columba*

    livia). *Journal of Experimental Psychology: Animal Behavior Processes, 36*, 423-

    429.

Scarf, D. & Colombo, M. (2011). Knowledge of the ordinal position of list items in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 37,* 483-487.

Shimp, C. P. (1976). Organization in memory and behavior. *Journal of the Experimental Analysis of Behavior, 26,* 113-130.

Stevens, S. S. (1946). On the theory of scales of measurement. *Science, 103,* 677-680.

Stevens, S. S. (1951). Mathematics, measurement, and psychophysics. In S. S. Stevens (Ed.), *Handbook of experimental psychology* (pp. 1-49). New York: John Wiley & Sons, Inc.

Straub, R. O. & Terrace, H. S. (1981). Generalization of serial learning in the pigeon. *Animal Learning & Behavior, 9,* 454-468.

Swartz, K. B., Chen, S., & Terrace, H. S. (1991). Serial learning by rhesus monkeys. I. Acquisition and retention of multiple four-item lists. *Journal of Experimental Psychology: Animal Behavior Processes, 17*, 396-410.

Terrace, H. S. (1986). A non-verbal organism's knowledge of ordinal position in a serial learning task. *Journal of Experimental Psychology: Animal Behavior Processes, 12,* 203-214.

Terrace, H. S. (1987). Chunking by a pigeon in a serial learning task. *Nature, 325*, 149-151.

Terrace, H. S. (1991). Chunking during serial learning by a pigeon: I. Basic evidence. *Journal of Experimental Psychology: Animal Behavior Processes, 17*, 81-93.

Terrace, H. S., Chen, S., & Jaswal, V. (1996). Recall of three-item sequences by pigeons. *Animal Learning and Behavior, 24,* 193-205.

Terrace, H. A., & McGonigle, B. (1994). Memory and representation of serial order by

children, monkeys, and pigeons. *Current Directions in Psychological Science, 3*,

180-185.

Weisman, R. G., Duder, C., & von Konigslow, R. (1985). Representation and retention of

three-event sequences in pigeons. *Learning and Motivation, 16,* 239-258.

Weisman, R. G., Wasserman, E. A., Dodd, P. W. D., & Larew, M. B. (1980).

Representation and retention of two-event sequences in pigeons. *Journal of

Experimental Psychology: Animal Behavior Processes, 6,* 312-325.

Chapter 4

Pigeons Make Errors as a Result of Interval Timing in a Visual, but not Visual-Spatial, Midsession Reversal Task

Neil McMillan and William A. Roberts

Abstract

It has been shown previously that pigeons make surprising errors on a visually-based mid-session reversal task (Cook & Rosen, 2010; Rayburn-Reeves, Molet, & Zentall, 2011). We trained birds with red and green sidekeys, with one color rewarded in the first 40 trials (S1) and the other color rewarded in the latter 40 trials (S2). Importantly, in Phases 1 and 3, red and green were always presented on the same side, while in Phase 2 sidekeys were presented on the left and right equally often. In Phases 2 and 3, probe sessions with inter-trial intervals (ITIs) longer or shorter than the training ITI were interjected among baseline sessions. Results showed that pigeons presented with visual-only cues used interval duration since the beginning of the session to predict when the reversal of reward contingency would occur, but pigeons presented with color and spatial dimensions confounded for predicting reward tended to use a more optimal reward-following strategy of choice based on local reinforcement.

Keywords: pigeons, interval timing, reversal learning, simultaneous discrimination, reward-following

Pigeons Make Errors as a Result of Interval Timing in a Visual,

but not Visual-Spatial, Midsession Reversal Task

Cognitive flexibility is the "readiness with which the person's concept system changes selectively in response to appropriate environmental stimuli" (Scott, 1962, p. 405). One of the most common tasks used for studying cognitive flexibility in animals is the reversal procedure, wherein subjects are trained on either a spatial or visual discrimination, and, after acquisition, the reward contingencies are reversed. A wide variety of animals show decreased time to reach criterion with increasing numbers of successive reversals (Shettleworth, 1998), which could be characterized as cognitive flexibility.

Several recent articles have reported on the effects of a modified serial reversal task in which the reversal occurs at the midpoint within each session of training (Cook & Rosen, 2010; Rayburn-Reeves, Molet, & Zentall, 2011; Rayburn-Reeves, Stagner, Kirk, & Zentall, in press). Cook and Rosen trained birds in a task with matching-to-sample being correct for the first half of an 80-trial session, and nonmatching-to-sample correct after trial 40. Rayburn-Reeves et al. (2011; also see Rayburn-Reeves et al., in press) simplified this procedure, with a simultaneous discrimination procedure in which one stimulus was rewarded for the first half of the session (S1) and the other stimulus was rewarded only in the second half of the session (S2). In these types of experiment, to optimize reinforcement, subjects should ideally attend to local reinforcement on the last trial; that is, they should continue to choose S1 (or match to sample) until it is no longer rewarded, and then switch to responding only to S2 (or choose the nonmatching simulus). This strategy is referred to as win-stay/lose-shift, or alternatively, reward-following

(Graf, Bullock, & Bitterman, 1964). This appears to be the strategy used by humans (Rayburn-Reeves et al., 2011) and rats (Rayburn-Reeves et al., in press). It was observed with pigeons, however, that a decrement in performance occurred around the reversal point, with responding to S1 declining before the reversal (anticipatory errors) and also continuing after the reversal (perseverative errors).

Both types of errors are interesting because they indicate that (1) birds are using less optimal mechanisms for directing choice than those used by humans and rats and (2) pigeons are using either interval timing or trial/reinforcer number to predict the approaching mid-session reversal, and choosing incorrectly at the midpoint due to error in timing or number estimation. In peak-time and peak-number experiments, pigeons typically show Gaussian-like curves around the peak, indicating anticipatory and perseverative responding (Roberts & Boisvert, 1998; Roberts, Coughlin, & Roberts, 2000). Also, pigeons have been shown to perseverate in other tasks, choosing to lose/stay rather than lose/shift (Zentall, Steirn, & Jackson-Smith, 1990), which could explain the tendency to continue choosing S1 after the reversal. However, both errors require the animal to have largely ignored local reinforcement rates, especially in the case of perseverative errors: no pigeon is ever reinforced within-session for responding to S1 after the first trial on which S1 is not reinforced (or after being reinforced for responding to S2), whereas a pigeon may occasionally be reinforced for 'anticipating' the reversal by responding on S2 on trial 41.

One important aspect of previous research is that the mid-session reversal effect in pigeons has been replicated with different stimulus discriminations: Cook and Rosen (2010) originally used color alternatives in a matching/nonmatching reversal, Rayburn-

Reeves et al. (2011) used red and green keys presented spatially randomly in a simultaneous discrimination, and Rayburn-Reeves et al. (in press) used spatial alternatives with both keys illuminated with white light. This is important not only for the simple purpose of replication of an effect across procedures, but also because pigeons show asymmetric learning and reversal depending on procedures and stimuli used. Sutherland and Mackintosh (1971) suggested that associative strength was greater for spatial than that for visual stimuli, and Bitterman (1965) argued for phylogenetically earlier appearances of advanced behaviors (which cognitive flexibility might be included in) for spatial over visual discrimination. Perhaps most importantly, pigeons tend to match responding to reward contingencies on visual tasks (Bullock & Bitterman, 1962a) but tend to maximize (or reward-follow) in spatial tasks (Graf et al., 1964). Thus it would seem that the use of spatial location as the discriminative dimension in Rayburn-Reeves et al. (in press) rules out the possibility that birds produce errors on the mid-session reversal task due simply to the stimulus dimension used affecting their probability-matching behavior throughout the session.

One outstanding question from previous research is exactly what mechanism pigeons are using to direct responding in the mid-session reversal procedure, if not a reward-following strategy utilizing local reinforcement. Cook and Rosen (2010) used a single large empty delay interval (10 or 20 min) prior to the reversal to artificially lengthen sessions without affecting trial number, and interpreted their results as evidence that pigeons used interval time to direct their choice behavior. This procedure not only poses the problem of how the pigeons may have interpreted such a long delay (e.g., instructional ambiguity: Zentall, 2006), but also precluded shortening the session duration

for comparison with the original duration. As Cook and Rosen state in their second experiment, an increased tendency to pick the nonmatching sample prior to reversal could also indicate a loss of stimulus control; while they did not find this to be the case when an 'irrelevant' cue was introduced in this experiment, they did not include delayed testing with the third cue. Rayburn-Reeves et al. (2011) showed in their third experiment that pigeons would make errors even when the reversal point was unpredictable, but by varying the trial number of the reversal point, time and number were confounded for answering which mechanism the pigeons were using to choose between S1 and S2.

In the present experiment, we replicated the procedure of Rayburn-Reeves et al. (2011) with minor procedural modifications. In Phase 1, pigeons responded on a mid-session reversal procedure with red always presented on the left, and green always presented on the right, such that the visual and spatial dimensions of the stimuli were equally useful for predicting reward. In Phase 2, red and green stimuli were presented randomly on either side as in Rayburn-Reeves et al., such that color was the only contingent dimension for reinforcement. After training with a 6-s ITI, probe sessions were inserted after every third baseline test session, wherein the ITI length was either doubled to 12 s or halved to 3 s, with the effect of lengthening or shortening the session duration without changing the number of trials before the reversal. In this procedure, pigeons would be expected to make more anticipatory errors with a longer session and more perseverative errors with a shorter session if they were using interval time, but not trial number, since the beginning of the session to predict the reversal point. Finally, in Phase 3, visual and spatial discriminative stimulus dimensions were confounded as in

Phase 1, and after acquisition, ITI length was manipulated in probe sessions as in Phase 2.

Method

Subjects

Nine experimentally naïve adult White King pigeons (*Columba livia*) were used. Birds were maintained at approximately 85% of free-feeding weight throughout the experiment, with constant access to water and health grit. They were individually housed in cages in a room kept environmentally controlled at 22 degrees C. Fluorescent lights were turned on at 8:30 a.m. and off at 8:30 p.m. each day. Testing was performed between 9 a.m. and 11 a.m. for 5 days each week.

Apparatus

Three enclosed, sound-attenuating operant chambers measuring 31 x 35.5 cm (floor) x 35.3 cm (height) were used. The front wall of each chamber held three pecking keys, 2.5 cm in diameter and level with the pigeon's head, in a row, spaced 8 cm apart. Projectors behind each key projected filtered light, presenting different colors on the keys. Grain reinforcement was delivered by an electromechanical hopper through a 6 x 6 cm opening in the front wall located near the floor, directly below the center key. Presentation of stimuli, reinforcement, and recording of responses were carried out by microcomputers, in another room, interfaced to the operant chambers.

Procedure

During each experimental training session in Phase 1, birds were presented with 80 trials separated by 6-s darkened ITIs. On each trial, the left sidekey was illuminated with a red hue, and the right sidekey was illuminated with a green hue. For five of the

subjects, pecking the red sidekey (S1) was correct for the first 40 trials (S1+/S2-) and pecking the green sidekey (S2) was correct for the final 40 trials (S2+/S1-); these contingencies were reversed for the four other birds. Correct responses turned off both sidekeys and were reinforced with 2 s of access to grain followed by the ITI, while incorrect responses led directly to the ITI. Subjects were trained for 20 sessions.

In Phase 2, all aspects of training were identical to Phase 1, with the exception that the red and green sidekeys were each presented on either the left or right equally often, with spatial location varied randomly across trials. Pigeons were trained for 20 sessions. During testing, three out of every four sessions were identical to training (i.e., baseline sessions). Every fourth session was an ITI probe session, with all experimental procedures identical to baseline but with 12-s ITIs (test sessions 1-20) or 3-s ITIs (test sessions 21-40). Training and testing thus equaled a total of 60 sessions in Phase 2.

In Phase 3, all aspects of training were identical to Phase 1, including maintaining the spatial location of red and green sidekeys across trials. Pigeons were trained for 20 sessions. As in Phase 2, during testing, three out of every four sessions were identical to training (i.e., baseline 6-s ITI sessions). Every fourth session was an ITI probe session, with all experimental procedures identical to baseline but with 12-s ITIs (test sessions 1-20) or 3-s ITIs (test sessions 21-40). Training and testing thus equaled a total of 60 sessions in Phase 3.

Results

The data from the first five sessions of training in each Phase were removed from all analyses; data pooled over five-session blocks suggested that only the first block of responding appeared qualitatively different from the other blocks. The average
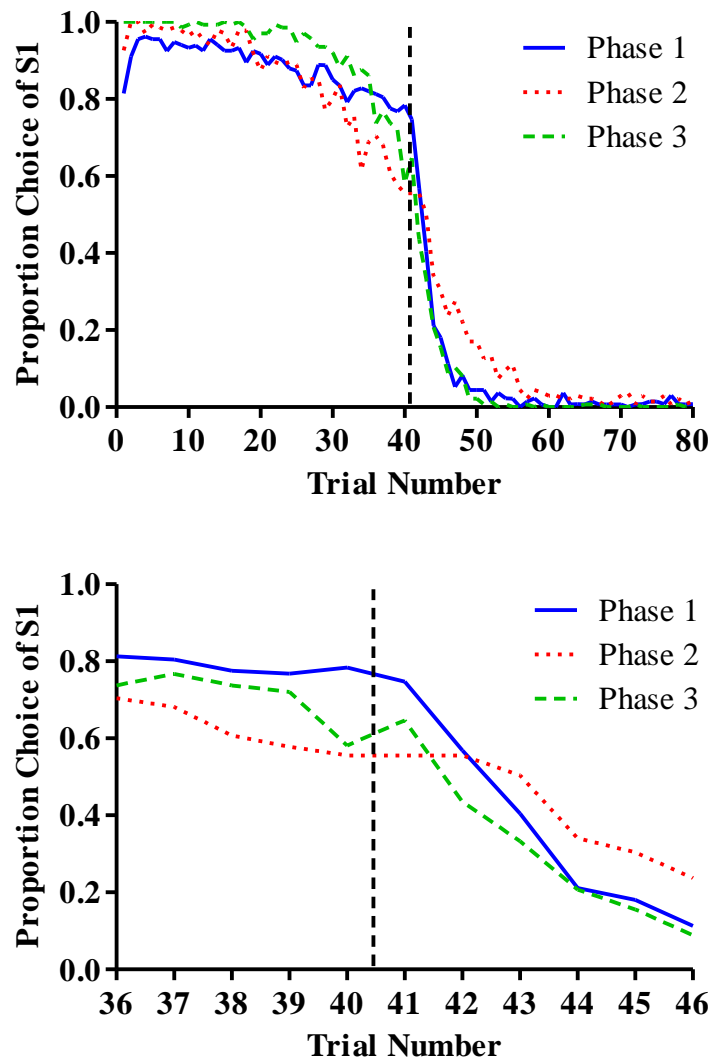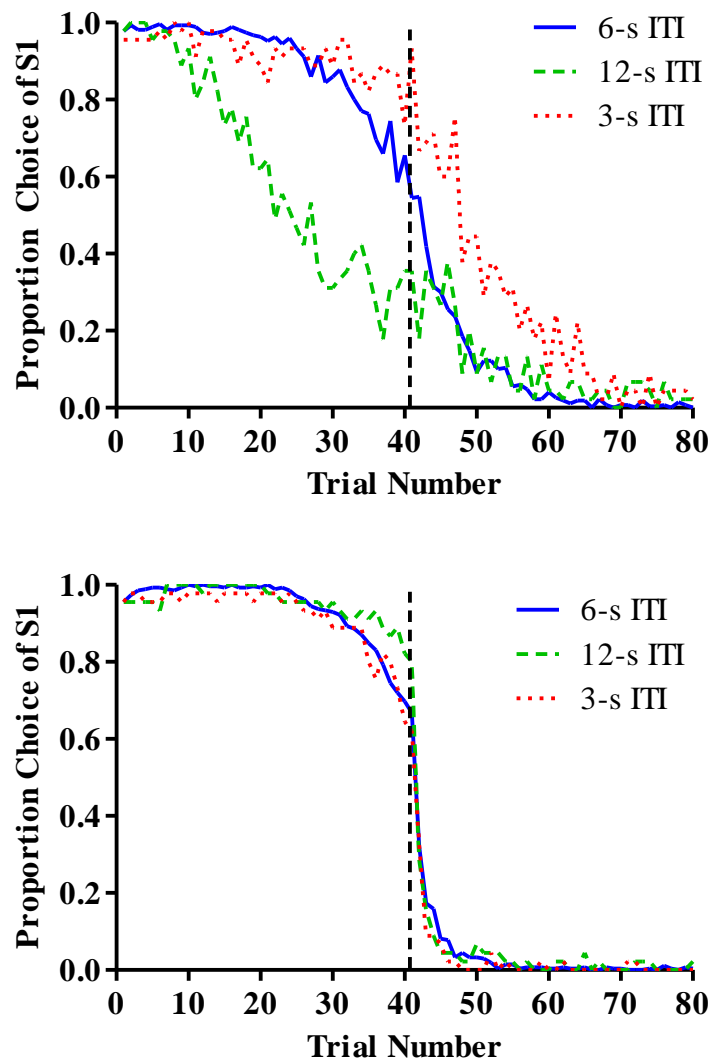
Figure 4.1. (A; Upper Panel) Mean proportion of choice of first-correct stimulus (S1) across 15 training sessions for each of the three experimental Phases. Mid-session reversal point is indicated with vertical dashed line.

(B; Lower Panel) Mean proportion of choice of first-correct stimulus (S1) in the five trials preceding the reversal (Trials 36-40), the trial immediately following the reversal (Trial 41), and the five trials after (Trials 42-46) for each of three training phases. Mid-session reversal point is indicated with vertical dashed line.

Figure 4.2. (A; Upper Panel) Phase 2: Mean proportion of choices of the first-correct stimulus (S1) in each of three testing conditions: 34 sessions of baseline (6-s ITI), and 5 sessions each of 12-s and 3-s ITI probe trials. Mid-session reversal point is indicated with vertical dashed line.

(B; Lower Panel) Phase 3: Mean proportion of choices of the first-correct stimulus (S1) in each of three testing conditions: 34 sessions of baseline (6-s ITI), and 5 sessions each of 12-s and 3-s ITI probe trials. Mid-session reversal point is indicated with vertical dashed line.

proportion of responses to S1 on each trial across the remaining 15 sessions for each of the three Phases of training is presented in Figure 4.1a, with mean proportion of S1 responses across the five trials before and after trial 41 presented in Figure 4.1b to better illustrate sensitivity to local reinforcement around the reversal trial. Figure 4.2a illustrates the testing data from Phase 2, while Figure 4.2b illustrates testing data from Phase 3.

Phase 1

The most striking feature of the Phase 1 training distribution compared to previous mid-session reversal data is the sharper decline in S1 choices immediately following trial 41 compared to the preceding trials. These data look qualitatively different from the more continuous distribution seen in previous work (Cook & Rosen, 2010; Rayburn-Reeves et al., 2011, in press). Pigeons showed flat S1 responding averaging 80% from trials 36-41, and S1 responding dropped over trials 42-46 to an average of only 30%. The comparison of the average drop in S1 responding from trials 36-41 with the average drop in S1 responding between trial 41 and 42 was statistically significant [$t(8) = 3.16$, $p < .013$] showing that pigeons were sensitive to the change in reinforcement on trial 41 and significantly decreased S1 responding on trial 42 compared to previous trials. There was no significant difference between the drop in S1 responding from trial 41 to 42 and the average drop in responding from 42-46, $t(8) = 1.34$, p = .218. This finding suggests it often took several perseverative errors after the reversal on trial 41 before pigeons primarily chose S2. Nonetheless, pigeons reliably waited until the first nonreinforced response to begin to change responding from S1 to S2. This use of local

reinforcement by pigeons in the mid-session reversal procedure is novel compared to previous work (Cook & Rosen, 2010; Rayburn-Reeves et al., 2011, in press).

Phase 2

A 3 x 3 (ITI length [3 s, 6 s, 12 s] x Trials [36-41, 41-42, 42-47]) ANOVA multivariate test (Wilk's Lambda) examined the average drops in S1 responding from each of trials 36-41 and 42-47 with the average drop in responding between trials 41 and 42, across each of the three ITI conditions. There was a significant interaction between ITI length and trial condition, $F(4, 5) = 8.50$, $p = .019$, as well as a significant main effect of ITI length, $F(2, 7) = 5.77$, $p = .033$, and trial contrast, $F(2, 7) = 15.79$, $p = .003$. Within the baseline 6-s ITI testing condition, we compared the average drop in S1 responding from each of trials 36-41 with the average drop in responding between trials 41 and 42 and found that the difference was not statistically reliable during either the training or testing 20-session blocks, ts$(8) \leq 1.26$, ps $\geq .243$. There was also no significant difference on the same test in the 12-s ITI condition, $t(8) = 2.09$, $p = 0.07$. In the 3-s ITI condition, there was a significant difference, $t(8) = 4.11$, $p = .003$, though when looking at the graph it appears that this is likely due to a chance increase in S1 responding at trial 41 inflating the apparent decrease at trial 42. We also compared the drop in responding to S1 from trial 41 to 42 with the average S1 response decline in trials 42-47. Again, there was no significant difference in the 12-s ITI condition, $t(8) = 2.06$, p $= 0.073$, but there was a significant difference in the 3-s ITI condition, $t(8) = -3.51$, $p = 0.008$. However, this may also have been due to increased S1 responding on trial 41 as noted previously. Overall, pigeons appeared relatively insensitive to local reinforcement changes with the discrimination reversal on trial 41, suggesting that they instead relied on

the less-optimal strategy of interval timing. There was some evidence that pigeons were more likely to lose/shift with a shorter ITI, but this difference was small.

A 3 x 2 (ITI length [3 s, 6 s, 12 s] x Trials [36-40, 42-46]) ANOVA multivariate test (Wilk's Lambda) examined the average number of errors made immediately before and after 'reversal' trial 41, and showed a significant interaction, $F(2, 16) = 19.03$, $p = .001$. 'Errors' were S2 responses made before trial 41 (anticipatory errors), or S1 responses made after trial 41 (perseverative errors). In pairwise comparisons, pigeons showed more perseverative errors in the 3-s ITI condition relative to the 6-s ITI anchoring condition, $t(8) = 3.42$, $p = .009$, but there was no significant difference in the number of anticipatory errors, $t(8) = -0.59$, $p = .573$. In the 12-s ITI condition relative to the 6-s ITI condition, pigeons showed more anticipatory errors, $t(8) = 15.86$, $p < .001$, and fewer perseverative errors, $t(8) = -5.82$, $p < .001$. The only modification to the procedure on test trials was to lengthen or shorten the ITI, which correspondingly lengthened or shortened the interval time since the start of the session and increased the number of anticipatory or perseverative errors, respectively. Based on these results, it appears that pigeons primarily responded on the visual mid-session reversal task based on the interval time since the beginning of the session.

Phase 3

A 3 x 3 (ITI length [3 s, 6 s, 12 s] x Trials [36-41, 41-42, 42-47]) ANOVA multivariate test (Wilk's Lambda) examined the average drops in S1 responding from each of trials 36-41 and 42-47 with the average drop in responding between trials 41 and 42, across each of the three ITI conditions. There was no significant interaction between ITI length and trial condition, $F(4, 5) = 1.30$, $p = .381$, and no significant effect of ITI

length, $F(2, 7) = 4.08$, $p = .067$; the effect of trial contrast was significant, $F(2, 7) = 23.47$, $p = .001$. We contrasted the average drop in S1 responding across each of trials 36-41 with the average drop in responding between trial 41 and 42 collapsed across each ITI test condition, which yielded a significant difference, $t(8) = 7.27$, $p < .001$. We also contrasted the average drop in S1 responding from trials 41-42 with the average drop in responding between each of trials 42-47 collapsed across each condition in testing, which was also significant, $t(8) = -6.59$, $p < .001$. Finally, the comparison in drop in S1 responding between trials 36-41 and trials 42-47 was not significant, $t(8) = 1.66$, $p = .135$. Overall, pigeons appeared to be attuned to local reinforcement before and after the discrimination reversal on trial 41, with fewer anticipatory or perseverative errors compared to response-switching on trial 42 alone. Importantly, this effect did not appear to vary based on ITI length.

A 3 x 2 (ITI length [3 s, 6 s, 12 s] x Trials [36-40, 42-46]) ANOVA multivariate test (Wilk's Lambda) examining the number of errors on either side of 'reversal' trial 41 showed no significant interaction or main effects, $Fs \leq 1.74$, $ps \geq .244$. There was no significant difference among the ITI conditions in the number of errors subjects made immediately before (i.e., S2 anticipatory responses) or after trial 41 (i.e., S1 perseverative responses). It is apparent that interval duration since the beginning of the session did not heavily influence pigeons' choice of S1 and S2 when the reward-contingent stimulus dimensions were both visual and spatial, compared to the results in Phase 2 where color was the only relevant stimulus cue, and birds primarily relied on interval timing to judge the expected reversal.

Comparison Among Phases

We compared change in responding to S1 from trials 41 to 42 in training across each of the three Phases. This was our primary measure of how comparable birds were in changing their responding after the 'critical' post-reversal trial (i.e., the first trial on which responding to S1 is not reinforced) across the three Phases; only training data were used for this particular test because they were the only data that were equivalent across all three Phases. A one-way repeated-measures ANOVA multivariate test (Wilk's Lambda) comparing the drop in S1 responding between Phase 1 training, Phase 2 training, and Phase 3 training was significant [$F(2,7) = 5.18$, $p = .022$], and a trend analysis showed a significant quadratic contrast [$F(1,8) = 11.51$, $p = .009$]. This suggested that Phases 1 and 3 may have differed from Phase 2; this was upheld by LSD t-tests showing a significant difference between Phases 1 and 2 [$t(8) = -2.60$, $p = 0.032$] and between Phases 2 and 3 [$t(8) = 2.56$, $p = 0.033$] but no difference between Phases 1 and 3 [$t(8) = 0.24$, $p = 0.813$]. This pattern suggests that birds changed responding after their first perseverative error on trial 41 significantly more with a color/spatial compound than with only color stimuli, even early in training with each task. Also, the increased amount of experience with the stimuli did not appear to affect the change in responding from trial 41 to trial 42 across training in otherwise-identical Phases 1 and 3.

Discussion

Here we illustrate that pigeons' performance on the mid-session reversal task is largely controlled by interval timing when a visual simultaneous discrimination is presented, but that pigeons switch primarily to a reward-following or win-stay/lose-shift strategy when a confounded spatial-visual discrimination is used.

It should be noted that the results of Phase 2 do not suggest that pigeons are using only interval timing as the mechanism for moderating their choice behavior; if they were, we would expect greater separation in the S1 response curves. Instead, pigeons seem to use local reinforcement to some degree in the visual discrimination, but are also strongly controlled by an interval timer. This observation corroborates the finding in Phase 3 of Rayburn-Reeves et al. (2011), where there was an asymmetry present between anticipatory and perseverative errors across different within-session trial reversals; the authors interpreted this as evidence that pigeons were at least marginally affected by local reinforcement differences with changing reversal points. Conversely, in the current Phase 3, though the vast majority of their response-switching occurred on trial 42, pigeons still made some anticipatory and perseverative errors. However, these errors do not appear to be due to interval timing, because there were not significantly more switches in the 3-s or 12-s ITI conditions relative to the 6-s ITI baseline. Small numbers of errors could be explained by difficulty inhibiting 'other' behavior near the switch point, even if birds were using an optimal response strategy on many trials. In this case, number of trials may have been a secondary mechanism for pigeons rather than using a simple win-stay/lose-shift strategy. Taken together, the results of Phases 2 and 3 suggest that pigeons use multiple mechanisms to alter their choices between the S1 and S2 stimuli across the session duration, and that the degree to which one mechanism is used over others is strongly affected by the stimulus dimensions used for discrimination.

In some earlier experiments, it was found that pigeons performed differently on visual and spatial discriminations, depending on the problem learned (Bitterman, 1965). Pigeons showed progressive improvement in their ability to learn successive between

session reversals of both visual and spatial discriminations (Bullock & Bitterman, 1962b). When tested on probability learning, however, pigeons showed differences between spatial and visual discriminations. In probability learning, one stimulus was randomly reinforced on a majority of trials (e.g., 70%), and the other stimulus was reinforced on a minority of trials (30% of trials). When the discrimination required choice between right-left spatial positions, pigeons tended to maximize or choose the majority stimulus on almost all the trials. When the discrimination required choice between keys of different color that appeared randomly on the right and left, pigeons tended to match the probability of reinforcement by choosing the 70% reinforced color on 70% of the trials and the 30% reinforced color on 30% of the trials (Graf et al., 1962). Although there is therefore some evidence that pigeons may respond differently to spatial and visual discriminations, the spatial discriminations used in probability learning typically did not involve confounded spatial-visual cues. Also, it should be remembered that Rayburn-Reeves, et al. (in press) found that pigeons showed a pattern of anticipatory and perseverative errors on mid-session reversal of a spatial discrimination with two white keys that was typical of mid-session reversal of a visual discrimination (Rayburn-Reeves et al., 2011). The findings presented here then raise the question of why pigeons appear to use local reinforcement more prominently than interval timing when confounded spatial-visual cues are used than when visual or spatial dimensions alone are used.

It is rare to use multiple stimulus dimensions as contingent cues for reinforcement in discriminative choice tasks. Researchers typically only allow one element of a stimulus to vary as a matter of control; spatial tasks typically use two keys of the same

color in different locations, while visual tasks counterbalance location across trials with different visual stimuli. Riley and Brown (1991) suggested that though animal learning researchers have traditionally viewed the processing of multi-dimensional stimuli as linearly summed (i.e., a compound stimulus is assumed to be processed as separable elements), stimuli which consist of more than one dimension (in their review, visual compounds) may be processed differently compared to either of their elements alone.

One possible explanation is that color and space interact to produce additive summation (see Weiss, 1972) when presented in compound on the mid-session reversal task; in other words, presenting a simultaneous discrimination in both the spatial and visual dimensions somehow potentiates learning to a greater degree than the same task in either dimension alone. It has already been suggested that superimposed spatial and visual information do not interfere with one another for channel capacity, as do dimensions within the visual domain (Kraemer, Mazmanian, & Roberts, 1987). Likewise, non-food-storing birds have been shown to process spatial and color or brightness elements of a compound about equally well, suggesting they attend to or remember both dimensions (Brodbeck & Shettleworth, 1995). A multi-dimensional cue may provide independently-available information; for example, spatial discriminations might elicit prospective orienting behavior during the ITI (Kraemer et al., 1987) while highly discriminable hue dimensions might trigger retrospective coding (Zentall, Urcuioli, Jagielo, & Jackson-Smith, 1989). In effect, pigeons may be able to use multiple sources of information for the previous trial, helping to bridge the 6-s temporal ITI between response/reward contingencies. Also, as Lionello and Urcuioli (1993) suggested that pigeons automatically treat stimuli as compounds of visual and spatial elements, it

may be that making both cue dimensions relevant increases memory relative to presenting only one, or alternatively that presenting only one dimension increases confusion when the other element is irrelevant to reward. For example, when presenting only spatially-relevant white stimuli, as in Rayburn-Reeves et al. (in press), the color element of the compound (white) is equally reinforced for pecking left and right keys, which is obviously in conflict with a spatial discrimination task. This could produce confusion and the animal may use another element of the stimulus compound, in this case the interval time since beginning of the session.

One point to consider is that spatial, visual, and temporal cues are separate sources of information that compete for attentional control (Mackintosh, 1975). Of course, spatial and visual cues are perceived external to the organism, and temporal cues are internal. Nevertheless, recent findings suggest that different temporal cues may overshadow or block one another (McMillan & Roberts, 2010), and unpublished research from our lab suggests that salient visual cues can overshadow temporal cues. It may be that when memory for local response/reinforcer contingencies is poor (here, on visual-only sessions), the pigeon learns to use interval time as its primary cue; when memory for local response/reinforcer contingencies is good (here, on compound spatial/visual sessions), the pigeon learns to ignore interval time and use local reinforcement instead.

Given such a theoretical approach, the comparative implications are interesting. Clearly, humans tend to show control by local reinforcement on both visual and spatial discriminations (Rayburn-Reeves, et al., 2011, in press). Rayburn-Reeves et al. (in press) found that rats, unlike pigeons, showed control by local reinforcement when spatial cues were used. Unlike our Phases 1 and 3, the spatial cues were not visually differentiated

(right and left levers). A question that remains, however, is how rats would perform on mid-session reversal of a visual discrimination. If rats had to discriminate a lit lever from a dark lever, with lit and dark levers switched randomly between left and right locations, how would they respond to mid-session reversal? If visual cues alone do not disrupt short-term memory, as seems to be the case with spatial cues (Rayburn-Reeves et al., in press), then rats should show a sharp mid-session reversal curve indicating control by local cues. On the other hand, the increased difficulty of using visual cues that vary in location from trial to trial might lead temporal cues to dominate local reinforcement history and give rise to the gradual mid-session reversal curves found with pigeons (Rayburn-Reeves et al., 2011; Phase 2 here).

References

Bitterman, M. E. (1965). The evolution of intelligence. *Scientific American, 212,* 92-100.

Brodbeck, D. R. & Shettleworth, S. J. (1995). Matching location and color of a compound stimulus: Comparison of a food-storing and a nonstoring bird species. *Journal of Experimental Psychology: Animal Behavior Processes, 21,* 64-77.

Bullock, D. H. & Bitterman, M. E. (1962a). Probability-matching in the pigeon. *The American Journal of Psychology, 75,* 634-639.

Bullock, D. H. & Bitterman, M. E. (1962b). Habit reversal in the pigeon. *Journal of Comparative and Physiological Psychology, 55,* 958-962.

Cook, R. G. & Rosen, H. A. (2010). Temporal control of internal states in pigeons. *Psychonomic Bulletin & Review, 17,* 915-922.

Graf, V., Bullock, D. H., & Bitterman, M. E. (1964). Further experiments on probability-matching in the pigeon. *Journal of the Experimental Analysis of Behavior, 7,* 151-159.

Kraemer, P. J., Mazmanian, D. S., & Roberts, W. A. (1987). Simultaneous processing of visual and spatial stimuli in pigeons. *Animal Learning & Behavior, 15,* 417-422.

Lionello, K. M. & Urcuioli, P. J. (1998). Control by sample location in pigeons' matching to sample. *Journal of the Experimental Analysis of Behavior, 70,* 235-251.

Mackintosh, N. J. (1975). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review, 82,* 276-298.

McMillan, N. & Roberts, W. A. (2010). The effects of cue competition on timing in pigeons. *Behavioral Processes, 84,* 581-590.

Rayburn-Reeves, R. M., Molet, M., & Zentall, T. R. (2011). Simultaneous discrimination reversal learning in pigeons and humans: Anticipatory and perseverative errors. *Learning & Behavior, 39,* 125-137.

Rayburn-Reeves, R. M., Stagner, J. P., Kirk, C. R., & Zentall, T. R. (in press). Reversal learning in rats (*Rattus norvegicus*) and pigeons (*Columba livia*): Qualitative differences in behavioral flexibility. *Journal of Comparative Psychology.*

Riley, D. A. & Brown, M. F. (1991). In G. R. Lockhead & J. R. Pomerantz (Eds.), *The perception of structure: Essays in honor of Wendell R. Garner* (pp. 227-245). Washington, D.C.: American Psychological Association.

Roberts, W. A., & Boisvert, M. J. (1998). Using the peak procedure to measure timing and counting in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 24*, 416-430.

Roberts, W. A., Coughlin, R., & Roberts, S. (2000). Pigeons time or count flexibly on cue. *Psychological Science, 11,* 218-222.

Scott, W. A. (1962). Cognitive complexity and cognitive flexibility. *Sociometry, 25,* 405-414.

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior.* New York: Oxford University Press.

Sutherland, N. S. & Mackintosh, N. J. (1971). *Mechanisms of animal discrimination learning.* New York: Academic Press.

Weiss, S. J. (1972). Stimulus compounding in free-operant and classical conditioning: A review and analysis. *Psychological Bulletin, 78,* 189-208.

Zentall, T. R. (2006). Timing, memory for intervals, and memory for untimed stimuli: The role of instructional ambiguity. *Behavioral Processes, 71,* 88-97.

Zentall, T. R., Steirn, J. N., & Jackson-Smith, P. (1990). Memory strategies in pigeons' performance of a radial-arm-maze analog task. *Journal of Experimental Psychology: Animal Behavior Processes, 16,* 358-371.

Zentall, T. R., Urcuioli, P. J., Jagielo, J. A., & Jackson-Smith, P. (1989). Interaction of sample dimension and sample-comparison mapping on pigeons' performance of delayed conditional discriminations. *Animal Learning & Behavior, 17,* 172-178.

Chapter 5

General Discussion

Timing has previously been suggested to be an automatic process (W. A. Roberts, Coughlin, & S. Roberts, 2000; J. E. Sutton & W. A. Roberts, 1998; Tse & Penney, 2006). Most theories of interval timing consider the clock as an internal neural mechanism, detached and independent from other learning processes. However, the work described in the present thesis suggests that the interval timing mechanism: (a) fails to control behavior when placed in competition with more salient visual cues for reward vs. non-reward (Chapter 2); (b) can compromise with other serial learning processes to solve a cognitively demanding ordinal task (Chapter 3); and (c) will control reversal behavior on a visual midsession reversal task, but not a confounded visual-spatial task (Chapter 4). Strikingly, the use vs. non-use of interval time throughout these very different procedures was governed by relatively simple modifications of cue dimension and reward vs. non-reward contingencies. Together, these results suggest that timing is much more affected by and integrated with other learning processes than previously believed.

Chapter 2 illustrated that timing can be overshadowed by visual cue dimensions with high relative validity for predicting food; together with previous research showing that 'long' duration temporal cues could be blocked by 'short' duration temporal cues (McMillan & W. A. Roberts, 2010), this evidence suggests that temporal processing is susceptible to cue competition, just as are other learning processes. These findings suggest that processing of time may be subject to attention and competition for stimulus control, similarly to low-level stimulus features such as shape and color.

Perhaps the most intriguing aspect of the overshadowing of temporal control by salient visual stimuli is that while interval time was not a valid predictor of whether food would be available, it was still valid for predicting when reward would be available.

Experiment 2 showed that pigeons would still time stimuli for a 50% chance at eventual reward, suggesting that time was important for efficient use of resources (i.e., reducing peck rate early in each trial, a time when food was not forthcoming). However, the mere presence of visually-predicted non-rewarded trials led to a failure of temporal control over responding on rewarded trials. This suggests that time was treated similarly to visual identity as an attribute of each of the stimuli. This is particularly interesting because time is a stimulus property that is not physically nor immediately apparent; if presented with a 10-s stimulus, it is impossible to determine its exact temporal properties until the 10-s interval has elapsed. Also, like space, time can never be presented as an independent stimulus element: it must always be experienced in compound with visual, auditory, or other perceptual elements of stimuli. These stimulus properties of time have previously led to time being considered as a higher-order cognitive capability of animals, processed separately and automatically in order to drive efficient responding. However, the present research shows that time is nonetheless still processed as a component of stimuli and is subject to attention in the same manner as other stimulus dimensions.

In Chapter 3, pigeons showed a limited capability to rank-order their responding to stimuli presented in particular orders over time, suggesting they attended to both the order of the stimuli and their individual temporal proximity to reward. Importantly, pigeons only attended to the visual identity of the rewarded stimulus with reinforced baseline trials and attended to order only when non-reinforced sequences were introduced. This is superficially the inverse effect noted in Chapter 2, where non-reinforced trials led to poor timing. The important comparison between these studies is the change in validity of stimuli based on the addition of non-reinforced trials: in the

interval example, the basic visual identity of the stimuli was the valid predictor for reward, while in the ordinal example the order of stimuli was the only means of predicting eventual reward. More simply, pigeons altered their use of timing vs. rewarded stimulus identity based on how stimulus presentation predicted reward.

It is also important to note that the results of Chapter 3 are not compatible with interpretation based on interval timing alone. While initial results (Experiment 1A) were consistent with pigeons simply timing from the onset of the third stimulus until reward was presented, other results showed monotonic increases in responding to stimuli across the order rather than a graded response curve across the interval. For example, in a three-stimulus order (Experiment 1B), pigeons responded significantly more to the second stimulus in order relative to the first (and less relative to the last), but did not increase responding to the second stimulus toward the end of its presentation relative to early in its presentation. Interval timing alone also cannot explain why pigeons would respond less to the final stimulus in the order when it was preceded by an 'incorrect' order of stimuli. This was especially apparent in Experiment 2 where statistically significant decreases in 1-3-2-4-5 order showed that pigeons could not have only timed from the onset of the penultimate stimulus. Together, while these results do not rule out that pigeons may have used interval timing to solve an ordinal timing task, they could not have used it exclusively.

Finally, in Chapter 4 pigeons used interval timing since the beginning of the session to predict a midsession reversal of reward contingencies on a visual discrimination but relied on local reinforcement rates (i.e., win/stay-lose/shift strategy) to maximize midsession reversal reinforcement with visual-spatial discrimination. It is

surprising that pigeons would switch strategies from timing to reward-following on this task purely based on presenting the discrimination visual-spatially, especially since previous literature had shown stubborn use of interval timing on both a spatial discrimination midsession reversal (Rayburn-Reeves, Stagner, Kirk, & Zentall, in press) and a visual discrimination with an unpredictable midsession reversal point (Rayburn-Reeves, Molet, & Zentall, 2011).

Subsequent research in our lab (McMillan, Kirk, & Roberts, in prep) has shown near-perfect maximization of reward in pigeons in a visual-spatial, variable-trial midsession reversal procedure. This performance was noticeably better than even the results reported in Chapter 4 here, and the data suggested that several pigeons were no longer compromising between local reinforcement strategy and other strategies such as timing. Individual differences were also noticed in strategy use, with some pigeons still not optimally following reward. In separate experiments, pigeons were trained on a spatial-discrimination midsession reversal, and rats were trained on a spatial-discrimination midsession reversal on a t-maze. The results conflicted with previous work examining midsession reversal with a spatial discrimination (Rayburn-Reeves, Stagner, Kirk, & Zentall, in press). Pigeons showed sensitivity to local reinforcement similar to that reported in Chapter 4 here, and rats showed poor sensitivity to local reinforcement. This suggests that what was previously reported as a species difference on the midsession reversal task is likely due to individual differences and artifacts of memory tasks presented spatially in operant chambers. Some pigeons are capable of reward-following on a spatial reversal, which could be a result of spatially orienting to the left or right sidekey during the inter-trial interval, essentially 'cheating' the memory

component of the procedure (McMillan, Kirk, & Roberts, in prep; Rayburn-Reeves, Laude, & Zentall, 2013). That rats show good reversal performance on a spatial discrimination in the Skinner box (Rayburn-Reeves, Stagner, Kirk, & Zentall, in press) but not in a t-maze (McMillan, Kirk, & Roberts, in prep) – where the choice point is spatially distinct from the start position – corroborates the suggestion that animals are capable of following local reinforcement on the midsession reversal procedure by prospectively orienting during the delay between trials. Broadly, animals will use a win/stay-lose/shift strategy in midsession reversal when working memory load is light, but will instead use interval timing when working memory load is heavy (i.e., when tasked to remember both the response and the consequence of the last trial over a 6-s delay).

Timing and Attention

It is frequently difficult to disentangle attentional effects on timing behavior with actual changes to the clock described in various timing models. For example, dopaminergic agonists have previously been shown to produce peak-curve shifts and time estimates consistent with speeding up of the internal interval clock (and the opposite effects are observed with dopaminergic antagonists), while cholinergic drugs produce effects more consistent with changes to memory for time rather than processing of time (Meck, 1983, 1986). However, other evidence has questioned these explanations of dopaminergic effects on interval timing, suggesting that observed data may be driven by the attentional effects of dopamine rather than only adjustments in the internal clock (Santi, Weise, & Kuiper, 1995; Stanford & Santi, 1998). Consistent with these attentional interpretations of biases in duration estimates, in the human literature,

predictable biases are introduced in timing when participants are required to perform any of a wide variety of non-temporal tasks while simultaneously required to time an interval: in general, the less attention paid to time, the shorter the estimates of elapsed time (Block & Zakay, 1996; Brown, 1997, 2008). Participants are perfectly capable of attention-sharing between concurrent timing and non-temporal processing, but systematically limiting attentional resources to timing produces 'short'-biased estimates of time. This effect has also been shown in animals (Lejeune, Macar, & Zakay, 1999; J. E. Sutton & W. A. Roberts, 2002). These effects are sometimes interpreted as being caused by a switch (in the same language as scalar expectancy theory) that loses accumulated pulses when interrupted, such as by being stopped and restarted (Block & Zakay, 1996).

Compared to other studies observing the effects of attentional control on timing, the primary difference which sets the current thesis findings apart is that rather than showing systematic biases in timing, subtle manipulations in the present experiments affected whether timing controlled behavior at all. Pigeons opted to use salient visual cues that predicted reinforcement (Chapters 2 & 3) or local reinforcement rates (Chapter 4) under some arrangements of stimulus dimension and reinforcement contingencies, where in other conditions pigeons showed control by timing. These disruptions in temporal control could be due to attention shifts; for example, in considering scalar expectancy theory, attentional control could be attributable to the switch process, determining whether the organism times a particular interval. However, this does not specifically explain why a pigeon would fail to accurately time a 60-s interval when presented with non-reinforced intervals (Chapter 2), especially if it has previously been subject to good control by time on 60-s reinforced intervals presented alone. Many

timing theories also assume that intervals are timed based on the onset of a particular

stimulus, an assumption which is challenged both by successful timing of multiple

stimuli presented in sequence (Chapter 3) and by timing an interval from the onset of the

session rather than between stimuli or between reinforcers, as shown in the midsession

reversal procedure (Chapter 4).

Clockless models which consider timing an emergent property of information

processing (Ornstein, 1969) or behavior (Dragoi, Staddon, Palmer, & Buhusi, 2003;

Machado, 1997) are immediately amenable to attentional effects on timing and temporal

control, and more conventional models of timing would benefit from being more closely

integrated with learning models to explain effects like those observed in the present

thesis. Examples of attempts for integrative timing theories include the temporal delay

hypothesis (R. E. Sutton & Barto, 1990), the learning-to-time model (Machado, 1997)

and most recently the behavioral economic model (Jozefowiez, Staddon, & Cerutti,

2009). These theories generally describe how subjects learn about time and its

relationship to reinforcement. Crucially, each theory commonly predicts that particular

behaviors and responses become more closely associated with food as the interval

elapses, essentially making the animal's own behavior the clock rather than necessitating

separate pacemakers. In the general case, behavior-based theories of timing allow for

direct integration of timing with attentional and learning processes by virtue of timing

being treated as an intrinsic property of behavior rather than a separate neural

mechanism.

Traditional models of time (notably scalar expectancy) and strictly neural-based

timers (such as striatal beat-frequency) are not necessarily incompatible with the current

results. Attentional processes are capable of acting on different aspects of these models, though they are not always well-described. Importantly, the results reported here cannot rule out that pigeons failed to time: the S+ in S+/S- training (Chapter 2); the order of stimuli without non-reinforced orders presented (Chapter 3); or the duration from the start of the session to the reversal point in a spatial midsession reversal (Chapter 4). In each of these cases, pigeons could have accurately timed the contingent interval but not shown stimulus control by timing. Lejeune and Wearden (1991) compared interval timing across a variety of species and found that certain species showed greater timing accuracy than others. However, the authors concluded that differences in observed timing ability were in large part due to differences in tasks (e.g., a fish tank is quite different from a rat operant chamber) and the ability to inhibit non-timed behavior (e.g., cats are better able to inhibit random responding than pigeons), rather than species differences in sensitivity to time. In the same manner, the present results could be compatible with the interpretation that pigeons timed the contingent intervals, but that timing failed to control behavior in competition with other non-temporal processes. Control by (or attention to) time appears to be modulated by relative cue validity (Chapter 2), the presence of more proximal predictors for reward (Chapter 3; also see McMillan & Roberts, 2010) and working memory load for other processes (Chapter 4).

In sum, the results reported in this thesis show differences in how pigeons use timing on a variety of procedures with simple manipulations of stimulus and reward presentation. These results are inconsistent with interval timing being purely an automatic contributor to behavior, mechanistically processed internally and not affected by external factors. Instead, time should be considered an important element of the

complex stimulus compounds that comprise all environments, as well as a very important component of standard learning processes. Behavior-based theories of timing may be better situated to explain many of these results, but other models of timing should be integrated with associative approaches to better model the links between learning, timing, and attention.

References

Block, R. A., & Zakay, D. (1996). Models of psychological time revisited. In H. Helfrich (Ed.), *Time and mind* (pp. 171-195). Bern: Hogrefe & Huber.

Brown, S. W. (1997). Attentional resources in timing: Interference effects in concurrent temporal and nontemporal working memory tasks. *Perception & Psychophysics, 59,* 1118-1140.

Brown, S. W. (2008). Time and attention: Review of the literature. In S. Grondin (Ed.), *Psychology of time* (pp. 111-138). Bingley, UK: Emerald Group Publishing.

Dragoi, V., Staddon, J.E.R., Palmer, R.G., & Buhusi, C.V. (2003). Interval timing as an emergent learning property. *Psychological Review, 110,* 126-144.

Jozefowiez, J., Staddon, J. E. R., & Cerutti, D. T. (2009). The behavioral economics of choice and interval timing. *Psychological Review, 116,* 519-539.

Lejeune, H., Macar, F., & Zakay, D. (1999). Attention and timing: Dual task performance in pigeons. *Behavioral Processes, 44,* 127-145.

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

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

McMillan, N., & Roberts, W. A. (2010). The effects of cue competition on timing in pigeons. *Behavioural Processes, 84*, 581-590.

Meck, W. H. (1983). Selective adjustments of the speed of the internal clock and memory processes, *Journal of Experimental Psychology: Animal Behavior Processes, 9,* 171-201.

Meck, W. H. (1986). Affinity for the dopamine D_2 receptor predicts neuroleptic potency in decreasing the speed of an internal clock. *Pharmacological Biochemistry and Behavior, 25,* 1185-1189.

Ornstein, R. E. (1969). *On the experience of time*. New York: Penguin.

Rayburn-Reeves, R. M., Laude, J. R., & Zentall, T. R. (2013). Pigeons show near-optimal win-stay/lose-shift performance on a simultaneous-discrimination, midsession reversal task with short intertrial intervals. *Behavioural Processes, 92,* 65-70.

Rayburn-Reeves, R. M., Molet, M., & Zentall, T. R. (2011). Simultaneous discrimination reversal learning in pigeons and humans: Anticipatory and perseverative errors. *Learning & Behavior, 39,* 125-137.

Rayburn-Reeves, R. M., Stagner, J. P., Kirk, C. R., & Zentall, T. R. (in press). Reversal learning in rats (*Rattus norvegicus*) and pigeons (*Columba livia*): Qualitative differences in behavioral flexibility. *Journal of Comparative Psychology*.

Roberts, W. A., Coughlin, R., & Roberts, S. (2000). Pigeons flexibly time or count on cue. *Psychological Science, 11,* 218-222.

Santi, A., Weise, L., & Kuiper, D. (1995). Amphetamine and memory for event duration in rats and pigeons: Disruption of attention to temporal samples rather than changes in the speed of the internal clock. *Psychobiology, 23,* 224-232.

Stanford, L., & Santi, A. (1998). The dopamine D_2 agonist quinpirole disrupts attention to temporal signals without selectively altering the speed of the internal clock. *Psychobiology, 26,* 259-266.

Sutton, J. E., & Roberts, W. A. (1998). Do pigeons show incidental timing? Some experiments and a hierarchical framework for the study of attention in animal cognition. *Behavioural Processes, 44,* 263-275.

Sutton, J. E., & Roberts, W. A. (2002). The effect of nontemporal information processing on time estimation in pigeons. *Learning & Motivation*

Sutton, R. S., & Barto, A. G. (1990). Time derivative models of Pavlovian reinforcement. In M. R. Gabriel & J. W. Moore (Eds.), *Learning and computational neuroscience: Foundations of adaptive networks* (pp. 497-537). Cambridge, MA: MIT Press.

Tse, C-Y., & Penney, T. B. (2006). Preattentive timing of empty intervals is from marker offset to onset. *Psychophysiology, 43,* 172-179.

Appendix A – Ethics

Nov. 27, 2009

This is the Original Approval for this protocol
A Full Protocol submission will be required in 2013

Dear Dr. Roberts:

Your Animal Use Protocol form entitled:
Information Processing in Animals
Funding Agency NSERC - Grant #7894-2009

has been approved by the University Council on Animal Care. This approval is valid from **November 27, 2009 to November 30, 2013**. The protocol number for this project is **#2009-086 which replaces #2005-083 which has expired.**.

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
   If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

ANIMALS APPROVED FOR 4 Years

SPECIES & SECT D.5.1 GROUP ID#	STRAIN &/or OTHER SPECIES DETAIL For Rodents, Also Provide Vendor Stock #	AGE or WEIGHT & SEX	4-YEAR TOTAL ANIMAL NUMBER
Rat ID#	Long-Evans	Male 350 g	80
Other ID#	White Carneau Pigeons	Male & Female 400-600 g	32

REQUIREMENTS/COMMENTS
Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.
The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

c.c. Approved Protocol   - B. Roberts, J. Majewski
       Approval Letter   - B. Roberts, J. Majewski

The University *of* Western Ontario
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Publications

McMillan, N. & Roberts, W. A. (in press-a). Inhibitory-stimulus interval training disrupts timed responding on excitatory-stimulus peak trials. *Journal of Experimental Psychology: Animal Behavior Processes.*

McMillan, N. & Roberts, W. A. (in press-b). Pigeons rank-order responding to temporally sequential stimuli. *Learning & Behavior.*

McMillan, N. & Roberts, W. A. (2012). Pigeons make errors due to interval timing in a visual, but not a visual-spatial, mid-session reversal task. *Journal of Experimental Psychology: Animal Behavior Processes, 38,* 440-445.

Roberts, W. A., **McMillan, N.**, Musolino, E., & Cole, M. (2012). Information-seeking in animals: Metacognition? *Comparative Cognition & Behavior Reviews, 7,* 85-109.

McMillan, N. & Roberts, W. A. (2010). The effects of cue competition on timing in pigeons. *Behavioural Processes, 84,* 581-590.

Roberts, W. A., Feeney, M. C., **McMillan, N.**, Macpherson, K., & Musolino, E. (2009). Do pigeons study for a test? *Journal of Experimental Psychology: Animal Behavior Processes, 35,* 129-142.

Roberts, W. A., Feeney, M. C., Macpherson, K., Petter, M., **McMillan, N.**, & Musolino, E. (2008). Episodic-like memory in rats: Is it based on when or how long ago? *Science, 320,* 113-115.

Van Rooyen, P., **McMillan, N.**, & Santi, A. (2008). Rats' memory for event duration in delayed matching-to-sample with nonspatial comparison response alternatives. *Behavioural Processes, 78,* 1-9.

Conference Presentations

McMillan, N. & Roberts, W. A. (2013, May). Pigeons rank-order responding to temporally ordered stimuli. Presented at the Ontario Ecology, Ethology & Evolution Colloquium, London, ON.

McMillan, N., Kirk, C. R., & Roberts, W. A. (2013, March). Pigeons make few errors on a variable mid-session reversal task with visual/spatial cue dimensions. Presented at the International Conference for Comparative Cognition, Melbourne, FL.

McMillan, N. & Roberts, W. A. (2012, May). Pigeons make errors due to interval timing in a visual, but not visual-spatial, mid-session reversal task. Presented at the Ontario Ecology, Ethology & Evolution Colloquium, Hamilton, ON.

McMillan, N. & Roberts, W. A. (2012, March). Mid-session reversal in pigeons on visual and spatial discrimination tasks. Presented at the International Conference for Comparative Cognition, Melbourne, FL.

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McMillan, N., Hamat, S., & Roberts, W. A. (2010, March). Obtaining information in pigeons. Presented at the International Conference for Comparative Cognition, Melbourne, FL.

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