Simultaneous temporal and spatial processing

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Rats searched for food that was contingent on time and place in an open field. One location was active at a time, the active location moved in a clockwise direction after each reward, and each location was repeated several times on each daily session. When a location was active, the first response after a fixed interval produced food. The intervals associated with each of the four locations were consistently 60, 30, 30, and 60 sec. For independent groups, inspecting an inactive location had no consequence ($n = 7$) or reduced the amount of food delivered at the active location ($n = 6$). The rates of inspecting active and inactive locations increased before the associated intervals elapsed, with preferential responding at the active locations. Rates of anticipation at active locations failed to superimpose when plotted as a function of proportional time. Simultaneous temporal and spatial processing contributed to the failure of proportional timing.

Animals are able to exploit temporal and spatial regularities that occur in the environment by organizing behaviors in time and space. These abilities are particularly important for foraging in situations in which food is available at different locations at regular intervals. For example, hummingbirds adjust the rate of revisiting flowers in a foraging circuit to the accumulation rate of floral nectar (Gill, 1988).

Most research on temporal and spatial information processing focuses on each domain independently, with some notable exceptions (e.g., Cheng, 1992b; Cheng, Spetch, & Miceli, 1996). Consequently, there is a considerable amount of information known about time perception (e.g., Gibbon, 1991) and spatial perception (e.g., Cheng, 2000). Recently, experiments have been designed to study time-place learning that use tasks in which time and space are both relevant. One of the advantages of studying time-place learning is that the properties of one system (e.g., temporal processing) may be examined during simultaneous processing of information in the other system (e.g., spatial processing).

In initial work on time-place learning, food was available at fixed times of day and at fixed locations. To obtain food, it was necessary to go to the correct location at the

appropriate time of day. Of course, when food is available at only one location, it is possible to inspect all possible locations to identify which location is currently providing food. Therefore, to document time-place learning, it is necessary to demonstrate that animals anticipate the availability of food before any food is presented. Anticipation of food availability has been documented in garden warblers (Biebach, Falk, & Krebs, 1991; Biebach, Gordijn, & Krebs, 1989; Biebach, Krebs, & Falk, 1994; Krebs & Biebach, 1989), pigeons (Saksida & Wilkie, 1994), and rats (Mistlberger, de Groot, Bossert, & Marchant, 1996; Widman, Gordon, & Timberlake, 2000).

A variety of tests suggest that time-place learning is based on the association of a time of day (i.e., the phase of a circadian oscillator with a period near 24 h) and a spatial location (Biebach et al., 1991; Mistlberger et al., 1996; Saksida & Wilkie, 1994). However, using time of day is not the only mechanism that produces high accuracy in a time-place learning task. Carr and Wilkie (1997) suggested that animals may use an ordinal timer in a daily time-place learning task. When shorter intervals (4–8 min) were examined, animals used an interval timer (Carr, Tan, Thorpe, & Wilkie, 2001; Carr & Wilkie, 1998). In addition, the amount of effort required to get to the location (Widman et al., 2000) and the type of response (Means, Arolfo, Ginn, Pence, & Watson, 2000) influence the strategy that animals use.

In Carr and Wilkie's (1998) interval time-place task, food was available sequentially at one of four locations. The amount of time during which food was available was the same at each location for a given animal, and this amount was varied across groups. For example, for one group of rats, food was available contingent on leverpressing for 4, 4, 4, and 4 min at Locations 1, 2, 3, and 4, respectively. For other

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groups of rats, the intervals were 6–6–6–6 and 8–8–8–8 min. In this experiment, the rats devoted most of their responses to the temporally correct location. In addition, the rats began to inspect the next location before the active location changed. The variability of the response distributions suggests that the rats were timing the interval associated with each location. Indeed, the shapes of the response distributions were orderly and adhered to the scalar property: The widths of the distributions were proportional to the interval being timed by the different groups of rats. Proportional timing is considered a hallmark of short-interval timing (Gibbon, 1977, 1991).

The rats in Carr and Wilkie's (1998) experiment timed the interval associated with each location. However, for a given rat, the interval was the same for each location. Therefore, each rat timed a single interval duration. In addition, because each location was active during only one segment of the daily session, revisiting a location that had already provided food was not required. Consequently, the number of relevant spatial locations decreased throughout the session. This work demonstrates that rats produce excellent temporal distributions in an interval time–place learning task when a single interval is being timed. However, it is unclear whether temporal and spatial discriminations will be observed when the task demands are increased. The present experiment was designed to address this question by examining discrimination of multiple intervals while retaining the spatial demands throughout the task.

A fixed interval (FI) was in effect at a given location; the first response at the to-be-rewarded location after the fixed interval elapsed produced food. After food was obtained at the active location, the next reward was available at the next location in a clockwise direction, using four locations in a relatively large box. The sequence of spatial and temporal combinations was the following: Location A, 60 sec; Location B, 30 sec; Location C, 30 sec; and Location D, 60 sec. After the fourth location was reached, the sequence was repeated, with several repetitions of the sequence each session. To reduce the frequency of inspecting inactive locations, differential reinforcement for a low rate of inspecting inactive locations was manipulated across groups of rats. This manipulation was based on Cheng's (1992a) observation that penalizing early responses sharpens temporal distributions. In the penalty group, the number of pellets delivered at the active location was contingent on the number of responses at the inactive locations; the magnitude of rewards ranged from one to eight pellets, contingent on many or few responses, respectively, at inactive locations. In the no-penalty group, the reward magnitude was always one pellet.

This task has the following properties: Each location is paired with an interval (30 or 60 sec), the entire interval is available for anticipatory responses (as in a standard FI procedure), and throughout the session, short and long intervals are tested and revisits to each location are required. Errors may occur in the spatial domain (approaching an inactive location), in the temporal domain (responding at the inappropriate time), or in both. The purpose of the experiment was to examine the properties of timing (i.e., the

scalar property) during simultaneous temporal and spatial processing.

METHOD

Subjects

Thirteen male Sprague-Dawley rats (*Rattus norvegicus*; derived from the Charles River CD strain) were individually housed in a colony, with lights on at 800 and off at 2000. The rats were on a restricted diet of approximately 15–20 g. Water was available at all times in the colony.

Apparatus

Testing was conducted in an open-field box (43.2 × 43.2 cm PVC base) with clear acrylic walls (30.5 cm in height) and an open top (MED Associates, ENV-515, Georgia, VT). A food trough (MED Associates, ENV-200R2M) was horizontally centered on each wall, 7 cm above the floor. A photobeam (MED Associates, ENV-254), placed 1 cm inside the food trough (1 cm from the trough bottom), detected head entries into the food trough. A response was registered at the time that the photobeam was interrupted. The photobeam interruption had to end before the next response was registered. Additional photobeams (MED Associates, ENV-258) were placed outside the box, but these were not used in the present experiment. A pellet dispenser (MED Associates, ENV-2031R) was positioned behind each food trough. The open field was placed on a table (74 cm above the floor) in a 3.43 × 2.11 m room. Visual stimuli in the room (desk, computer, doors, metal rack, boxes, etc.) were in fixed locations in the room. In a nearby room, a 486 66-MHz computer running MED-PC for Windows (1997; Version 1.10) controlled experimental events and recorded the time at which each event occurred with 10-msec accuracy.

Procedure

Pretraining consisted of three sessions in which a 45-mg food pellet (P. J. Noyes Co., Improved Formula A/I; Lancaster, NH) was delivered contingent on the rat's interrupting the photobeam inside the food trough, using a 1-sec FI schedule. A maximum of 10 pellets were delivered to each location. Each pretraining session ended when 40 pellets were dispensed or 30 min had elapsed.

During training sessions, the delivery of food was contingent on a response at an active location. The consequence of responses at inactive locations was manipulated across independent groups of rats. In the penalty group ($n = 6$), the number of pellets delivered at the active location was contingent on the number of responses at the inactive locations. The magnitude of rewards ranged from one to eight pellets, contingent on many or few responses, respectively, at inactive locations. In the no-penalty group ($n = 7$), the reward magnitude was always one pellet.

No-penalty group. Training sessions were conducted with individual rats tested in a fixed sequence at 800–1330 and 1500–1700, 5 days per week. The session was started approximately 15 sec after a rat was placed in the box. A food pellet was delivered at an active location, contingent on the first response after the FI elapsed; a new interval did not begin until the food pellet was earned at the current active location (i.e., there was no limited hold on food availability at the active location). The active location (A, B, C, or D) changed in a clockwise direction by one location in the sequence after the reward was delivered. The FIs in effect at Locations A and D were 60 sec. The FIs in effect at locations B and C were 30 sec. The FI for a given location began immediately after food was delivered at the previous location in the sequence, which was 0.11 sec after the to-be-rewarded response on the previous trial. Training consisted of sixty 40-min sessions. Approximately 44–50 pellets were obtained in each session.

Penalty group. The procedure was the same as that described for the no-penalty group, except where otherwise indicated. The number of pellets delivered for the first response after the FI was contin-

Table 1
Reward Magnitude Contingencies in the Penalty Condition

Number of Pellets	Number of Responses at Incorrect Locations	
	FI 30	FI 60
8	0–3	0–6
4	4–8	7–16
2	9–13	17–26
1	>13	>26

gent on the number of responses at inactive locations on the current trial (see Table 1). In order to avoid penalizing photobeam interruptions that occurred while a pellet from the previous trial was consumed, incorrect responses during the initial 2 sec of each trial did not affect the reward magnitude. The interval on a new trial began immediately after the to-be-rewarded response on the previous trial. Rewards were delivered at a rate of one pellet per 0.51 sec.

The first active location in the session was randomly assigned to the rats prior to the start of the experiment, and this location was the first reinforced location of each session. The active locations changed in a clockwise direction from this initial location. Each session's duration was 35 min. Training of the penalty group was conducted 2 months after the training of the no-penalty group was completed.

Data Analysis

The first 10 trials were omitted from all analyses. The analysis of response distributions was conducted on the last 20 sessions.

RESULTS AND DISCUSSION

Acquisition of the time–place contingency was examined by calculating the percentage of food site inspections that were directed toward the active location during the last 20% of each trial. Figure 1 plots percent correct as a function of sessions averaged across each correct location. At the start of the experiment, percent correct was near the

chance level of 25%. Percent correct reached approximately 70% by the end of the experiment.

Figures 2 and 3 plot the rates of approaching the active location (filled symbols) and the inactive locations (unfilled symbols) on each active location trial type (panels A–D) for the no-penalty and the penalty groups, respectively. Several patterns are apparent in Figures 2 and 3. First, the rate of food site inspection increased throughout the FI at each active location. This suggests that the rats timed the FI associated with each active location. Second, a small peak appears near the start of each trial at the location that precedes each active location, which is presumably the result of photobeam interruptions that occurred while the food was consumed at the just-rewarded location. And third, response rates were above zero at inactive locations. These prominent response rates suggest that the rats made spatial errors—approached locations that were not correct for a current trial.

The patterns in Figure 3 are similar to those observed in Figure 2, except in the following respects. Response rates at incorrect locations were lower in the penalty group, with the exception of more pronounced perseveration at the previously rewarded location in the penalty condition during the initial 10–20 sec of the trials. It is possible that perseveration at the just-rewarded location was prolonged because more time was required to consume larger reward magnitudes. For example, when the reward magnitude was eight pellets, the food dispenser dropped the final pellet more than 4 sec into the next trial, at which point additional photobeam interruptions would occur while several pellets that may have remained in the food trough were consumed. To quantify the effect of the penalty on visiting inactive locations, the maximum rate at inactive locations was calculated; to curtail the influence of perseveration at

Figure 1. Percent correct during the last 20% of the trials, plotted as a function of blocks of five sessions. Error bars represent ± 1 SE.

Figure 2. Number of photobeam interruptions per sec and as a function of time at each active (filled symbols) and inactive (unfilled symbols) location on four trial types (panels A–D) in the no-penalty group.

the just-rewarded location, that location was omitted from this calculation. Although the penalty contingency did not eliminate visits to inactive locations, the mean maximum rates were lower in the penalty group ($M = 0.30$, $SE = 0.04$) than in the no-penalty group ($M = 0.43$, $SE = 0.04$) on 60-sec trials [$t(11) = 2.07$, $p < .05$]. Mean maximum rates were lower on 30-sec trials in the penalty group

($M = 0.13$, $SE = 0.02$) than in the no-penalty group ($M = 0.16$, $SE = 0.04$), but this difference was not reliable [$t(11) = -1.48$, $p > .05$].

Temporal Control

The temporal control over spatial errors was examined by plotting response rates as a function of time at incorrect lo-

Figure 3. Number of photobeam interruptions per sec as a function of time at each active (filled symbols) and inactive (unfilled symbols) location on four trial types (panels A–D) in the penalty group.

cations on 60-sec trials (i.e., Locations B and C on trials when Locations A and D were active). Because photobeam interruptions occurred during food consumption at the just-rewarded location, the responses at Location C during trials on which Location D was active were omit-

ted from this analysis. Figure 4 plots response rates expressed as a proportion of the maximum rate as a function of time on these 60-sec trials for the no-penalty and the penalty groups. In the no-penalty condition, the peak response rate occurs near 30 sec. In the penalty condition, re-

Figure 4. Proportional response rate (number of photobeam interruptions expressed as a proportion of the maximum rate) at inactive locations plotted as a function of time in 5-sec blocks on 60-sec trials. Response rate increases to a peak or a plateau near 30 sec, which is the interval associated with these locations. Error bars represent $\pm 1 SE$.

sponse rate increased as a function of time during the first half of the 60-sec interval, at which point response rate was relatively constant at its maximum level. Despite the penalty applied to responding at inactive locations, the rate of inspecting inactive locations increased as a function of time. The increase in inspection rates at inactive locations in the penalty condition was similar to the increase that reached a peak near 30 sec in the no-penalty condition. This suggests that the inspections of inactive locations in the penalty condition were in anticipation of the 30-sec intervals that were sometimes rewarded at these inactive locations.

To quantify the peak for the no-penalty group, the time at which the proportional response rate crossed 70% was determined for each rat. The peak time was defined as the midpoint of the first and second transitions. The mean peak occurred at 35.8 sec ($SE = 1.1$) in the no-penalty group. Although the increase in response rate occurred slightly earlier in the penalty group than in the no-penalty group, the mean time of transition across the 70% response rate was not reliably different in the penalty ($M = 18.71$, $SE = 2.91$) and the no-penalty ($M = 23.45$, $SE = 1.29$) groups [$t(11) = 1.57$, $p > .05$]. To characterize the difference in response rates at the end of the 60-sec interval, the slope of the response distribution during the last half of the trial was calculated for each rat. The mean slope in the penalty group ($M = -0.0022$, $SE = 0.0017$) was not reliably different from zero [$t(5) = -1.32$, $p > .05$]. In contrast, the mean slope in the no-penalty group ($M = -0.0131$, $SE = 0.0045$) was reliably different from zero [$t(6) = -2.92$, $p < .05$]. In addition, these slopes were marginally different from each other [$t(11) = 2.13$, $p = .056$], and at the end of the trial, the proportional response rate in the

penalty group was higher than that in the no-penalty group [$t(11) = 2.90$, $p < .05$].

On 60-sec trials, response rates before 30 sec increased at inactive locations associated with 30 sec. These food site inspections were made at the spatially incorrect locations for the current trial. In addition, these inspections were made at the temporally incorrect time for the current trial. However, the temporal and the spatial errors were in agreement: The rats searched at the correct time and place combination that occurred on other trials. This suggests that on a given trial, the rats were (1) timing the short interval and approaching the locations associated with the short interval and (2) timing the long interval and approaching the location associated with the long interval.

The properties of temporal processing at active locations were examined by evaluating the scalar property. The FI30 response distribution was determined by averaging response rate at the active locations on 30-sec trials for each rat, which were then expressed as a proportion of the maximum response rate. The FI60 response distribution was determined by averaging response rate at the active locations on 60-sec trials for each rat, which were then expressed as a proportion of maximum response rate. Figure 5 plots proportional response rates for FI30 and FI60 as a function of relative time for the no-penalty and the penalty groups (top and bottom panels, respectively). Relative time was defined as elapsed time in the trial divided by the rewarded interval. The FI30 and FI60 distributions fail to superimpose in relative time. There is a large displacement between the FI30 and the FI60 distributions for both groups, with better proportional precision for FI60 than for FI30. To quantify the failure of superposition, each distribution was subjected to a 7-point running mean

Figure 5. Proportional response rate (number of photobeam interruptions expressed as a proportion of the maximum rate) at active locations plotted as a function of relative time (time expressed as a proportion of the fixed interval in 5-sec blocks) for the no-penalty (top panel) and the penalty (bottom panel) groups. Food site inspections do not superimpose in relative time. Error bars represent ± 1 SE.

smooth, and the transition across the proportional response rate of 70% was calculated for each rat on FI30 and FI60 trials. For the no-penalty group, the mean transitions occurred at relative times of 0.58 ($SE = 0.03$) and 0.76 ($SE = 0.03$) for FI30 and FI60 distributions, respectively. For the penalty group, the mean transitions occurred at relative times of 0.43 ($SE = 0.06$) and 0.64 ($SE = 0.02$) for FI30 and FI60 distributions, respectively. The transition occurred reliably earlier for the FI30 distribution than for the FI60 distribution in the no-penalty [$t(6) = 3.68$] and the penalty [$t(5) = 2.63$] groups (p 's $< .05$).

To evaluate the impact of the different reward contingencies, proportional response rates were averaged across FI30 and FI60 active locations as a function of relative time for each group. Response rate increased more rapidly as a function of time in the penalty group than in the no-penalty group at active locations. This observation was confirmed by comparing mean transitions across 70% for the no-penalty ($M = 0.67$, $SE = 0.02$) and the penalty ($M = 0.53$, $SE = 0.02$) groups, which differed reliably [$t(11) = 4.84$,

$p < .001$]. The penalty contingency, which was applied to responses at inactive locations, produced a more rapid increase in responding at the active locations.

Response Interference Hypothesis

A likely explanation for the observed failure of superposition is response interference: A visit to an inactive location necessarily prevents or postpones a visit to the active location. If the response interference hypothesis explains the failure of superposition, the data should superimpose on trials in which few or no responses occur at inactive locations. The data were partitioned into subsets representing low response interference (trials with five or fewer photobeam interruptions at incorrect locations) and high response interference (the remaining trials). Because this analysis was conducted on subsets of the data, the data were averaged across rats from both groups. The mean response rate functions appear in Figure 6. The top panel shows all the data for each active location; the middle and bottom panels show the data from the low- and high-interference

Figure 6. Proportional response rate (number of photobeam interruptions expressed as a proportion of the maximum rate) at active locations, plotted as a function of relative time (time expressed as a proportion of the fixed interval) in 5-sec blocks. All the trials (top panel) were partitioned into two subsets, with five or fewer photobeam interruptions at incorrect locations in one (bottom panel) and all the remaining trials in the other (middle panel). The data were averaged across rats from the no-penalty and the penalty groups. Error bars represent ± 1 SE.

subsets, which represent 54% and 46% of the trials, respectively. To quantify the separation between the curves plotted in Figure 6, the time at which response rates crossed 70% was calculated for each condition. These transition times from each subset were subjected to a repeated measures analysis of variance. A significant effect of transition times was observed in each subset [data from all the trials (Figure 6, top panel), $F(3,36) = 9.07, p < .001$; high response interference (middle panel), $F(3,36) = 9.91, p < .001$, low response interference (bottom panel), $F(3,36) = 6.82, p < .001$]. Planned contrasts on the differences between FI30 and FI60 trial types revealed significant differences in each subset. When all the trials were included (Figure 6, top panel), Locations B and D differed, as did Locations C and D [$F(1,36) > 11.36, ps < .01$]. In the high response interference subset (Figure 6, middle panel), Locations A and B differed, as did Locations B and D. In the low response interference subset (Figure 6, bottom panel), all pairwise comparisons of FI30 and

FI60 trial types (i.e., A vs. B, A vs. C, B vs. D, and C vs. D) differed significantly [$F(1,36) > 4.78, ps < .05$].

To compare the magnitude of separation between the FI30 and the FI60 curves, we calculated the absolute difference between each FI60 condition and the average of the FI30 conditions. This measure was reliably different from zero in each subset [$t(12) > 5.68, ps < .05$]. This measure was used to compare the magnitude of the transition effect in high- and low-interference conditions. The magnitude of the transition difference was larger in the high-interference subset (Figure 6, middle panel) than in the low-interference condition [Figure 6, bottom panel; $t(12) = 3.38, p < .01$]. Taken together, these analyses provide support for the response interference hypothesis: The gap between FI30 and FI60 conditions decreased as response competition at incorrect locations increased. The existence of significant gaps between the FI30 and the FI60 functions in the low-interference subset suggests the involvement of an additional process that remains to be identified.

Because it is unusual to observe violations of superposition, we examined several alternative measures of temporal performance. In the remaining analyses, we will examine a discriminative index, individual trials, and transition probabilities. These analyses provide converging lines of evidence that the timing is not scalar.

Discriminative Index

Our next measure of temporal performance included responses at inactive as well as active locations. A discriminative index was calculated as the proportion of responses allocated to the active location (i.e., the number of responses at the active location divided by the sum of responses at all locations). The discriminative index has a value of zero when no responses are allocated to the active location, a value of one when all responses are allocated to the active location, and a value of .25 when responses are allocated equally across the four locations. Figure 7 plots the discriminative index as a function of relative time for FI30 and FI60. The allocation of responses to the active location increased as a function of relative time more rapidly in FI30 than in FI60, although the magnitude of the differences between FI30 and FI60 was smaller in the penalty group. This relatively rapid increase in response allocation to the active location on FI30 trials is consistent with the failure of superposition documented in Figure 5, in which responses at the active location increased more rapidly in FI30 than in FI60.

Analysis of Individual Trials

Each individual trial was analyzed to identify the times at which the rats switched from one location to another. A

start was defined as the first photobeam interruption that occurred at a location different from that of the previous photobeam interruption. The first photobeam interruption on each trial was also considered a start time. Because there were no constraints on the number of switches between locations, multiple starts could occur at the same location. Frequency distributions were obtained for each location on each trial. These distributions were normalized for each rat by dividing each frequency by the maximum frequency for that location. Next, the normalized distributions were averaged across rats, and the average distribution was normalized in the same fashion. This measure, referred to as *relative frequency*, was applied in order to equate the different heights of FI30 and FI60 distributions.

Figure 8 plots the frequency distributions of start times that occurred at active locations on FI30 and FI60 trials. The rats started to inspect the active location earlier on FI30 than on FI60 trials (top panels). However, when the distributions are examined in relative time, they fail to superimpose (bottom panels). The peak of each distribution was estimated by the modal time for each rat. Peaks on FI30 trials ($M = 0.32, SE = 0.07$) occurred earlier than on FI60 trials ($M = 0.79, SE = 0.06$) in relative time [$t(12) = 5.62, p < .001$]. This observation is consistent with the failure of superposition observed in response rate (Figure 5) and discriminative index (Figure 7) functions.

Transition Probabilities

To examine the sequence of visits, the probability of a transition was calculated as a function of time for each location on each trial. Figure 9 plots these transition probabilities for the no-penalty and the penalty groups (left and

Figure 7. Discriminative index (number of photobeam interruptions at the active locations expressed as a proportion of total photobeam interruptions) on 30-sec (unfilled symbols) and 60-sec (filled symbols) trials, plotted as a function of relative time (time expressed as a proportion of the fixed interval) in the no-penalty (circles) and the penalty (squares) groups.

Figure 8. Frequency distributions of the times at which the rats started to visit FI30 (unfilled symbols) and FI60 (filled symbols) locations for the no-penalty (left panels) and the penalty (right panels) groups. The data are plotted with respect to time (top panels) and relative time (bottom panels). Switch times do not superimpose. See the text for details.

right panels, respectively). In general, at the start of each trial, the rats were at the location that was active from the previous trial. Photobeam interruptions are expected at these recently active locations because consuming the pellets will break the photobeam. Later in the trial, the probability of a start at the active location increased. The probability of a start also increased at inactive locations. By the end of the trial, the highest probability occurred at the active location in all cases. On FI60 trials, the probability of visiting a 30-sec inactive location increased prior to 30 sec. Visits to a 30-sec inactive location prior to 30 sec is consistent with the response rate functions (Figure 4), which suggest that the rats anticipated the 30-sec interval associated with the inactive 30-sec locations. In only one trial type (Active Location A, panel A) did the rats appear to patrol the locations, on average, in a sequential order.

Nonscalar Timing

The data presented thus far show that the 30- and the 60-sec intervals do not superimpose when plotted in relative time. This suggests that timing was not strictly proportional. However, it does not address whether the rats' timing behavior is better characterized as proportional than as absolute. To address this question, we examined the relation between the variability and the central tendency of start time distributions. Fetterman and Killeen (1995) manipulated the duration of short, medium, and long intervals that were associated with three locations and varied the magnitudes of these intervals across conditions. They observed an overall increase in the standard deviation of switch times as a function of the mean switch time between

locations. However, they also documented discontinuities; timing of the second switch was more accurate than timing of the first switch for a given mean switch time. Although our procedure used only two target intervals, the rats switched locations at various different times, which makes it possible to examine a range of switch-time means and variances. For each rat, we determined the mean and the standard deviation of the distribution of start times at each location on each trial type (i.e., four locations per active location trial type per rat).

Figure 10 plots the standard deviation of start times as a function of the mean start time. Each point in the figure describes a distribution of start times. For each active location trial type, there are four distributions, one for each location visited during that trial type; therefore, there are four data points associated with each active location in the figure. The data are combined across rats from both groups, because this analysis was conducted on relatively small subsets of data (i.e., each location on each trial type). Proportional timing requires that the standard deviation increase by a multiplicative constant as a function of the mean start time, with an intercept of zero. Note that the data increase linearly for the FI30 data (unfilled symbols in Figure 10), but not for the FI60 data (filled symbols). Linear regression was conducted on the eight standard deviation and mean paired values for each rat separately for the FI30 and the FI60 conditions. The FI30 condition was characterized by a positive slope [$M = 0.37$, $SE = 0.07$; $t(12) = 5.08$, $p < .001$] and a nonzero intercept [$M = 11.96$, $SE = 1.67$; $t(12) = 7.16$, $p < .001$]. In contrast, the slope in the FI60 condition ($M = -0.04$, $SE = 0.09$) was not re-

Figure 9. The probability of a transition (i.e., a start at a new location) is plotted as a function of time in 5-sec blocks at each active (filled symbols) and inactive (unfilled symbols) location on four trial types (panels A–D and E–H for the no-penalty and the penalty groups, respectively).

liably different from zero [$t(12) < 1$, $p > .05$]. The same conclusions were reached when the regression analyses were conducted separately on sets of four paired scores corresponding to each active location trial type (slopes for

FI30 Locations B and C, $t_s > 3.68$, $p_s < .01$; slopes for FI60 Locations A and D, $t_s < 1.10$, $p_s > .05$).

Constant variability as a function of increasing mean times is a strong violation of the scalar property. One potential

Figure 10. The standard deviation (SD) of start time distributions is plotted as a function of the mean of the start time distributions. The data from each of the four locations is plotted separately for each active location trial type. The data were averaged across rats from the no-penalty and the penalty groups. The SDs increase as a function of time from 30-sec trials (unfilled symbols), but not from 60-sec trials (filled symbols). Error bars represent ± 1 SE.

explanation of this nonscalar timing is that the rats may have visited each location for a relatively constant amount of time on 60-sec trials; for example, this pattern could occur if the rats had incomplete sequential information about which location or interval was in effect on the current trial. To address this question, we calculated the dwell time for each start time. This was done by defining an end time as the last response that occurred at a location (i.e., these end responses immediately preceded the next start time on the trial); the last response of the trial was also included as an end time. The dwell time was defined as the end time minus the start time. Mean dwell times varied across Locations A–D on Active Location A and D trials [$F(3,36) = 7.54$ and $F(3,36) = 12.12$, respectively, $ps < .001$]. In addition, the dwell time was longer on FI30 trials ($M = 9.84$, $SE = 0.78$) than on FI60 trials [$M = 6.72$, $SE = 0.84$; $t(12) = -3.12$, $p < .001$]. Therefore, dwelling at each location for a relatively constant amount of time does not appear to be an adequate explanation for the nonscalar timing on FI60 trials documented in Figure 10. This raises the possibility that the rats timed the intervals on the 60-sec trials in absolute time (Kristofferson, 1984).

Conclusions

The purpose of this research was to examine timing in a situation in which rats were required to simultaneously process temporal and spatial information. In experiments in which multiple intervals are discriminated (e.g., Roberts, 1981) or processed concurrently (e.g., Cheng, Westwood, & Crystal, 1993; Leak & Gibbon, 1995; Meck & Church, 1984), the properties of timing are similar to those in which a single interval is timed (although for an exception, see Fetterman & Killeen, 1995). In general, the preci-

sion of temporal discrimination is proportional to the magnitude of each interval being timed. The present work sought to test the generality of the scalar property when time and space were relevant.

In the experiment, food was available at a location that changed sequentially across successive trials. Each location was associated with one of two FIs. The rate of inspecting the active locations increased as the time of food availability approached. In addition to timing the interval associated with an active location on each trial, the temporal features of the rats' behavior at inactive locations corresponded to the intervals associated with these inactive locations (see Figure 4). This pattern of inspections would increase the likelihood that a rat would obtain food (1) after 30 sec at a 30-sec location, if it was available at that time, and (2) after 60 sec at a 60-sec location, if it was available at that time. This strategy would be especially useful if no information was available to the rat about which location was active on a given trial (i.e., incomplete sequential processing). Although the rats appeared to use a strategy in which they checked inactive locations at the times associated with these locations, the highest rate of inspections always occurred at the active location on each trial type. Although the procedure was designed to require temporal and spatial processing at each active location on each trial, the data suggest that the rats processed both the temporal and the spatial features associated with multiple locations on each trial type.

Under conditions of simultaneous temporal and spatial processing, anticipation of the active locations associated with 30- and 60-sec intervals was examined. The response distributions did not superimpose in relative time. This violation of the scalar property was large (approximately 20%),

unlike some previous reports of nonscalar timing (Crystal, 1999, 2001a, 2001b; Crystal, Church, & Broadbent, 1997).

In conclusion, the present work suggests that tracking temporal and spatial criteria produced a violation of the scalar property. Although there is extensive evidence to support theories of timing that predict the scalar property, the majority of that evidence comes from relatively similar tasks. For example, the evidence typically comes from a small testing environment in which response cost is low. When a spatial component has been included in this work (e.g., Fetterman & Killeen, 1995; Matell & Meck, 1999), the relevant spatial locations are relatively close to each other. In contrast, the temporal processes that govern foraging may be studied better under conditions that have higher response costs (Widman et al., 2000).

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