Flexible coding of temporal information by pigeons: Event durations as remember and forget cues for temporal samples

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The ability of pigeons to use event durations as remember (R) and forget (F) cues for temporal samples was examined. Pigeons were required to indicate whether a houselight sample stimulus was short (2 sec) or long (6 sec) by pecking a red or a green comparison stimulus. After training with a constant 10-sec delay interval, temporal cues (illumination of the center key) were presented 2 sec after the offset of the temporal samples. For one group, a short (2-sec) temporal cue served as the R cue and a long (6-sec) temporal cue served as the F cue. This was reversed for a second group of birds. During training, comparison stimuli were always presented following the temporal R cue, but never following the temporal F cue. Tests for the effectiveness of the temporal R and F cues showed that F cues were equally effective in reducing matching accuracy in both groups of birds. It was concluded that pigeons used the duration of the cue to determine whether or not to rehearse the memory code for the temporal sample.

Pigeons' memory for event duration has typically been assessed by means of a delayed symbolic matching-to-sample procedure. Pigeons have been trained to indicate whether a sample is short (2 sec) or long (8 sec) by pecking a red or green comparison stimulus for reinforcement. This research has demonstrated that when the retention interval between termination of the sample and the onset of the comparison stimuli is increased, a "choose short" response bias is evident (Kraemer, Mazmanian, & Roberts, 1985; Spetch, 1987; Spetch & Rusak, 1989; Spetch & Wilkie, 1982, 1983). That is, pigeons respond to the long sample duration after a long retention interval as if it had been the short duration. Spetch and Wilkie (1982, 1983) proposed that the pigeons' subjective representation of the event duration in working memory becomes systematically shortened during the retention interval. As a result, after a long retention interval, the remembered duration of the long sample is more similar to the actual duration of the short sample. In opposition to this view, some have argued that temporal information is categorically coded along a nontemporal dimension (Kraemer et al., 1985; Parker & Glover, 1987). This could be a prospective categorical code (e.g., peck red or peck green), or a retrospective categorical code (e.g., short or long).

Recently, there has been converging evidence that pigeons remember event durations in an analogical and retrospective fashion. Wilkie and Willson (1990) required pigeons to discriminate 2-, 8-, and 10-sec presentations of light. Choices of red, orange, and green keys were correct after 2, 8, and 10 sec, respectively. Differences in discriminability between the samples and comparison stimuli allowed Wilkie and Willson to examine the pattern of errors as task difficulty increased, and to draw inferences about the nature of coding. Errors were found to be more closely related to difficulty in discriminating sample stimuli than to difficulty in discriminating comparison stimuli. This was consistent with the code for event durations being retrospective.

Support for the hypothesis that this retrospective code is analogical rather than categorical comes from studies of intratrial proactive interference. Both Spetch and Sinha (1989) and Wilkie and Willson (1990, Experiment 3) employed trials in which two samples were presented: a presample and a target sample. The most informative trials were those in which the presample was short and the target sample was long. The categorical model predicts that the presample will decrease accuracy on these trials, because it will proactively interfere with the target sample. The analogical model predicts that the presample will increase accuracy on short-long trials, because of the possibility that the presample and target sample durations summate in working memory. The results in both studies were consistent with the predictions of the analogical model.

Given the evidence that pigeons code temporal information in a retrospective and analogical fashion (Spetch & Sinha, 1989; Wilkie & Willson, 1990), it became interesting to assess how flexible this coding is. A number

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of researchers have acknowledged that animals are capable of processing events either prospectively or retrospectively, depending on the demands of the task (Cohen, Galgan, & Fuerst, 1986; Grant & Spetch, 1991; Honig & Thompson, 1982; Riley, Cook, & Lamb, 1981; Urcuioli & Zentall, 1986). There are several ways in which flexible coding of temporal information could be shown. It might be shown that temporal samples are coded analogically in certain tasks, but categorically in other tasks (Grant & Spetch, 1991). This would be a between-task type of flexibility. On the other hand, within the same task it might be shown that temporal events are coded analogically or categorically depending on their functional significance in the task. This would be a within-task flexibility.

In the present research, we did not investigate the coding of temporal samples themselves, but rather asked whether pigeons are capable of processing event durations in a flexible manner. To answer this question, a directed forgetting procedure was used in which event durations served both as samples and as remember (R) and forget (F) cues. Coding flexibility was defined in terms of how the event durations as samples and cues were treated. If pigeons are inflexible and code all event durations analogically, they may sum the duration of the sample and the cue and respond to the comparison stimuli on the basis of this summed analogical code. On the other hand, if pigeons are flexible and can use event durations in a categorical fashion, they may use the duration of the cue to determine whether the memory code for the temporal sample should be rehearsed.

To assess whether pigeons are capable of selectively maintaining information in working memory, researchers have used postsample cues to signal whether comparison stimuli will be omitted or presented on a particular trial. Following an R cue, comparison stimuli are always presented, whereas following an F cue they are always omitted. By employing a probe-testing procedure in which comparison stimuli are infrequently presented after F cues, it has been shown that F cues control a lower level of matching accuracy than do R cues, which signal presentation of the comparisons (Grant, 1981, 1984, 1986; Kendrick, Rilling, & Stonebraker, 1981; Maki, 1981; Maki & Hegvik, 1980; Maki, Olson, & Rego, 1981; Rilling, Kendrick, & Stonebraker, 1984; Santi & Savich, 1985). Evidence that F cues reduce accuracy more when the retention interval is long (Grant, 1981; Maki & Hegvik, 1980; Maki et al., 1981), and when they are presented early rather than late in the retention interval (Grant, 1981; Stonebraker & Rilling, 1981), supports the hypothesis that maintenance rehearsal is being affected. In almost all of the directed forgetting research, both the samples and the R and F cues have been visual stimuli. Typically, colors have been used as sample stimuli, and line orientations have served as R and F cues. However, Parker and Glover (1987) have obtained a directed forgetting effect in a suc-

cessive delayed matching-to-sample procedure with temporal samples and line orientations as the R and F cues.

In the present research, temporal samples consisted of 2 and 6 sec of houselight illumination, and the comparison stimuli consisted of red and green illumination of the side keys. Pigeons were trained to a high level of accuracy with a constant 10-sec delay interval; then, temporal cues were introduced. Following offset of the temporal sample, there was a 2-sec period of darkness, and then the center key was illuminated with a black dot on a white background for either 2 or 6 sec. Following offset of this temporal cue, the chamber remained dark for the rest of the 10-sec delay interval. For one group of birds, the short temporal cue served as the R cue, and the long temporal cue served as the F cue. This was reversed for a second group of birds. Three different hypotheses concerning the processing of these temporal R and F cues were tested.

According to the first hypothesis, the birds are insensitive to the functional nature of these temporal cues, but they will show reduced matching of the temporal samples because of the amount of delay-interval illumination associated with the temporal cues (see Parker & Glover, 1987). The amount of delay-interval illumination is greatest on F-cue trials in the first group of birds, and on R-cue trials in the second group. Consequently, the delay-interval illumination hypothesis predicts lower accuracy on F-cue trials than on R-cue trials in the first group, but higher accuracy on F-cue trials than on R-cue trials in the second group.

According to the second hypothesis, the temporal cues are processed like samples, in a retrospective and analogical fashion. The birds respond to the sum of the temporal sample and the cue duration even though these events are physically and functionally different. In the first group, the temporal summation hypothesis assumes that the birds learn to choose "short" on a short-sample-short-cue trial, and to choose "long" on a long-sample-short-cue trial. When tested with a long-sample-long-cue trial, the temporal summation hypothesis predicts that the birds would tend to choose "long," which is correct for the sample presented. Consequently, in this group, accuracy should be as high on long-long trials as on long-short trials. In the second group, the temporal summation hypothesis assumes that the birds learn to choose "short" on a short-sample-long-cue trial, and to choose "long" on a long-sample-long-cue trial. The temporal summation hypothesis predicts that when the birds are tested with a short-sample-short-cue trial, they will choose "short," which is correct for the sample presented. Consequently, in this group, accuracy should be as high on short-short trials as on short-long trials, or higher.

According to the third hypothesis, the pigeons do not sum the duration of the sample and the cue, but rather use the duration of the cue to determine whether the memory code for the temporal sample should be rehearsed. In both groups, accuracy should be lower on

F-cue trials than on R-cue trials. This would suggest that pigeons are flexible in their processing of temporal information.

METHOD

Subjects

Eight White Carneaux pigeons, maintained at approximately 80% of their ad-lib weights and housed individually with constant access to grit and water, served as subjects. These birds had extensive prior experience with two-alternative delayed matching tasks involving colors and had also served in one experiment with temporal samples. They had not served in any experiment on the directed forgetting of temporal information.

Apparatus

Four Coulbourn modular operant test cages (Model E10-10), housed individually in isolation cubicles (Model E10-20), were used. Each cubicle was equipped with a ventilation fan and baffled air intake and exhaust system. Each test cage was equipped with three, horizontally aligned, clear plastic keys behind which projectors could display stimuli (a red or green field, or a black dot on a white background) onto a frosted rear projection screen (Coulbourn Model E21-18). Directly below the center key was a 5.7×5 cm opening that provided access to a hopper filled with mixed grain (Coulbourn Model E14-10). A houselight was located 6.5 cm above the center key; it was installed so that the light was directed upward to reflect from the top of the cage (Coulbourn Model E11-01 with bulb SL1819X). All experimental events and response measures were arranged and recorded by a microcomputer system located in an adjacent room.

Procedure

All birds were given 13 sessions of training in a delayed symbolic matching-to-sample task with duration samples. Each trial began with illumination of the houselight as the sample. The sample duration was short (2 sec) or long (6 sec). The sample duration varied randomly between trials, with the constraint that the same duration could not occur on more than four trials in a row. Termination of the sample was followed by presentation of red and green lights on the side keys as choice stimuli. The position of the red and green lights on the side keys was counterbalanced over trials. A response to a side key terminated the choice stimuli. Red was correct after the short sample and green was correct after the long sample. Correct responses were reinforced by a 3-sec access to mixed grain. Following reinforcement, an intertrial interval (ITI) varying randomly between 10 and 30 sec was spent in darkness. A correction procedure was used. Following an incorrect response, a 3-sec blackout occurred, followed immediately by a re-presentation of the same sample duration. The trial was repeated until a correct response occurred. Each session consisted of 120 trials (60 short and 60 long samples). Accuracy for all 8 birds exceeded 85% on each of the last three sessions in this phase of training.

The delay interval was then increased to 10 sec. All birds continued to receive training with a correction procedure until their accuracy exceeded 80% correct at the 10-sec delay. Four birds (Group 1) achieved this after 25 sessions of training. The other 4 birds (Group 2) required 51 sessions in which the delays were gradually increased from 0 to 10 sec.

Once response accuracy exceeded 80%, temporal R and F cues were inserted into the 10-sec delay interval. Following offset of the temporal sample, a 2-sec interstimulus interval spent in darkness preceded the presentation of the R or F cue. The cue consisted of illumination of the center key by a black dot on a white background for either 2 or 6 sec. For the 4 birds in Group 1, the short duration served as the R cue and the long duration as the F cue. This was reversed for the 4 birds in Group 2. Although these two

groups differed in the proficiency with which they performed at the 10-sec delay, interpretation of the results was not compromised. Following offset of the temporal cue, the chamber remained dark for the rest of the 10-sec delay interval. For all birds, red and green comparison stimuli were presented on the side keys at the end of the 10-sec delay interval only if the R cue had been presented. If the F cue had been presented, the comparisons were not presented and the ITI began. Within each session, there were 60 R-cue trials and 60 F-cue trials. During this phase of training, the reinforcer consisted of a 2-sec access to mixed grain. The birds in Group 1 received 20 sessions of directed forgetting training with a correction procedure, and those in Group 2 received 24 sessions. Accuracy on R-cue trials on the last three sessions averaged 80% in Group 1 and 68% in Group 2. The correction procedure was removed for five sessions. Accuracy dropped slightly for both groups. On the last three sessions, it averaged 78% in Group 1 and 61% in Group 2.

Phase 1 tests. The effectiveness of the postsample temporal R and F cues was then tested. Each test session consisted of 120 regular trials, which were the same as those outlined above, plus an additional 24 probe trials. The 24 probe trials in each test session consisted of 12 R-cue and 12 F-cue trials (equally divided among short- and long-sample trials). A single probe trial occurred randomly within each block of 5 regular trials. On probe trials, comparison stimuli were always presented regardless of the nature of the temporal cue presented in the delay interval, and correct responses were reinforced according to the contingencies previously described. A total of 10 test sessions was given.

Phase 2 tests. Baseline levels of accuracy on R-cue trials prior to Phase 1 testing tended to be rather low, despite considerable amounts of training with a correction procedure. Spetch and Rusak (1989) have shown that pigeons' memory for event durations is affected by variations in the ITI, as well as the delay interval. In Phase 1, the ITI varied randomly between 10 and 30 sec within each session, with a mean of 20 sec. In an attempt to improve performance, the ITI was maintained at a constant 20 sec throughout Phase 2. In addition, the temporal cues were removed for several sessions and then reintroduced in order to assess the effects of their presence on matching accuracy. All birds were given 11 sessions of training with temporal samples in which comparison stimuli were only presented following R cues. A correction procedure was used, with an ITI of 20 sec. In all other respects, the sessions were conducted as described for cue training sessions prior to Phase 1 testing. The temporal cues were then removed, and the birds received 10 sessions of training in which the 10-sec delay interval was spent in darkness and comparisons were presented. The correction procedure was still in effect. Finally, the temporal R and F cues were reintroduced for 15 sessions with the correction procedure removed for the last 3 sessions. Testing for the effectiveness of the temporal R and F cues was then conducted for 10 sessions, as in Phase 1.

RESULTS

The mean percent correct correct matching accuracy during Phase 1 testing is shown in Figure 1. The data for the group in which the R cue was short and the F cue was long are shown on the top. The data for the group in which the R cue was long and the F cue was short are shown on the bottom. In both groups, accuracy was higher when the sample was short than it was when the sample was long. Also, accuracy was higher on R-cue trials than it was on F-cue trials. An analysis of variance performed on the test data included groups as a between-subjects factor and type of cue and sample type as within-subjects factors. Only the effect of type of cue [$F(1,6) = 11.40$, $p < .05$] and the interaction of type of cue and sample

Figure 1. Mean percentage of correct responses during testing, as a function of type of sample (short or long), type of cue (R cue or F cue), and group (short R cue and long F cue or long R cue and short F cue) in Phase 1.

type [$F(1,6) = 6.21, p < .05$] were statistically significant. Although accuracy was generally lower on F-cue trials than it was on R-cue trials, F cues lowered accuracy on trials in which the sample was long [$F(1,6) = 57.25, p < .001$], but not on those in which the sample was short [$F(1,6) = 1.11, p > .30$].

Over the initial 11 sessions of Phase 2 training with a correction procedure and a constant 20-sec ITI, accuracy in the group with the short R cues averaged 77%, and in the group with the long R cues it averaged 64%. This difference between the groups was not statistically significant [$F(1,6) = 1.65, p > .24$]. In addition, accuracy did not improve significantly over these sessions [$F(10,60) = 1.71, p > .09$]. The additional training with a constant 20-sec ITI did not improve performance. Accuracy was almost identical to that obtained in the two groups prior to testing in Phase 1—78% and 61%, respectively.

When the temporal cues were removed from the 10-sec delay interval, accuracy increased significantly in both

groups over sessions [$F(9,54) = 4.59, p < .001$]. Accuracy in the first group averaged 86%, and in the second group it averaged 75%. The difference between the groups was not statistically significant [$F(1,6) = 2.18, p > .19$]. Finally, when the cues were reintroduced, accuracy was differentially affected in the two groups. In the group with short R cues, accuracy was maintained at 85%, but in the group with long R cues it dropped to 63%. This difference between the groups was statistically significant [$F(1,6) = 6.85, p < .05$].

The mean percentage of correct matching responses obtained during cue testing sessions in Phase 2 are presented in Figure 2. The data for the group with the short R cues are shown on the top, and those for the group with the long R cues are shown on the bottom. Accuracy was significantly higher on R-cue trials than it was on F-cue trials [$F(1,6) = 21.08, p < .005$], in both groups. Accuracy also tended to be higher on short-sample trials than it was on long-sample trials, but this effect was not significant

Figure 2. Mean percentage of correct responses during testing, as a function of type of sample (short or long), type of cue (R cue or F cue), and group (short R cue and long F cue or long R cue and short F cue) in Phase 2.

[$F(1,6) = 5.12, p = .064$]. No other main effects or interactions were statistically significant.

DISCUSSION

The pattern of results is consistent with the hypothesis that the birds were using the temporal R and F cues to modulate postperceptual processing of the temporal samples. If the birds had been insensitive to the functional nature of the cues, and if they had only been affected by the amount of delay-interval illumination associated with the temporal cues, the pattern of results would have been quite different. The amount of delay-interval illumination was greatest on F-cue trials in the first group, and on R-cue trials in the second group. Consequently, the delay-interval-illumination hypothesis predicts lower accuracy on F-cue trials than on R-cue trials in the first group, but higher accuracy on F-cue trials than on R-cue trials in the second group. Because accuracy in both groups was lower on F-cue trials than on R-cue trials, the delay-interval-illumination hypothesis can be rejected.

The hypothesis that the birds responded to the sum of the temporal sample and the temporal cue can also be rejected. In the first group, the temporal summation hypothesis assumes that the birds learn to choose "short" on a short-sample-short-cue trial, and to choose "long" on a long-sample-short-cue trial. The temporal summation hypothesis predicts that when the birds are tested with a long-sample-long-cue trial, they would tend to choose "long," which is correct for the sample presented. Accuracy should have been as high on long-long trials as on long-short trials, but it was not. Accuracy was lower when the long sample was followed by the long (F) cue than when it was followed by the short (R) cue. In the second group, the temporal summation hypothesis assumes that the birds learn to choose "short" on a short-sample-long-cue trial, and to choose "long" after a long-sample-long-cue trial. The temporal summation hypothesis predicts that when the birds are tested with a short-sample-short-cue trial, they would tend to choose "short," which is correct for the sample presented. Accuracy should have been as high on short-short trials as on short-long trials, or higher. The results showed the opposite. Accuracy was lower when the short sample was followed by the short (F) cue than when it was followed by the long (R) cue.

The present results indicate that pigeons are flexible in their processing of temporal information. They do not learn the required discriminations by summing the duration of the sample and the duration of the temporal cue. Rather, it appears that they use the duration of the cue to determine whether the memory code for the temporal sample should be rehearsed.

Baseline levels of accuracy on R-cue trials did not appear to change significantly as a function of additional training with a constant 20-sec ITI. Removal of the temporal R and F cues was accompanied by an increase in response accuracy in both groups. This suggests that in

addition to their functional significance as signals for comparison presentation, the temporal cues did lower accuracy as a function of the delay-interval illumination that they occasioned. It is well established that delay-interval illumination disrupts memory for visual events (Cook, 1980; D'Amato & O'Neill, 1971; Grant, 1988; Grant & Roberts, 1976; Kendrick & Rilling, 1984; Maki, Moe, & Bierley, 1977; Roberts & Grant, 1978; Salmon & D'Amato, 1981; Tranberg & Rilling, 1980). In addition, Parker and Glover (1987) have shown that it disrupts memory for event durations. The present findings are consistent with those of Parker and Glover. When the cues were removed, accuracy increased an average of 8% in the group with the short R cue, and an average of 14% in the group with the long R cue. When the cues were reintroduced, accuracy declined an average of 1% in the group with the short R cue, and an average of 12% in the group with the long R cue. The tendency for accuracy to be more affected in the group with the long R cue is consistent with the finding that matching of visual samples shows more disruption as the amount of illumination in the delay interval is increased (Roberts & Grant, 1978).

Although the data obtained prior to Phase 2 testing indicated that accuracy was affected by delay-interval illumination occasioned by the temporal cues, the test data replicated those obtained in Phase 1. In both groups, accuracy was lower following F cues than it was following R cues. Over and above the disruptive effects associated with delay-interval illumination, the birds were sensitive to the functional significance of the R and F cues.

One ambiguity in the present findings concerned whether or not F cues had a greater effect on long-sample trials than they had on short-sample trials. Presumably, signaling the bird to forget a short sample should accelerate foreshortening of the memory for that sample. Consequently the bird would be expected to "choose short," which is the correct response on short-sample trials. In Phase 1 tests, this appeared to be the case, because the cuing effect was significant on long-sample trials but not on short-sample trials. In Phase 2 tests, the results were in the expected direction, but the sample $\times$ cue-type interaction was not significant. On short-sample trials, F cues reduced accuracy by an average of 8%, and on long-sample trials, F cues reduced it by an average of 15%. More subjects may be needed for the presence of this possible interaction to be reliably detected.

In summary, the present results clearly demonstrated that pigeons are flexible in their processing of temporal information. The birds did not learn the reinforced discriminations by summing the duration of the sample and the duration of the temporal cue. Rather, it appeared that the duration of the cue determined whether the memory code for the temporal sample was rehearsed. On the basis of previous research (Spetch & Sinha, 1989; Wilkie & Willson, 1990), it is reasonable to assume that the temporal samples in the present research were analogically coded. However, it is also possible that categorical cod-

ing of the temporal R and F cues resulted in the birds' coding the temporal samples categorically as well. Consequently, while some degree of flexibility in the coding of temporal information has been shown in this research, additional research is needed before it can be determined whether this represents between-task or within-task coding flexibility.

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