

Delayed response alternation: Effects of stimulus presentations during the delay interval on response accuracy of male and female Wistar rats

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The present experiment was designed to investigate the effect of stimulus presentations during the delay interval of an operant delayed spatial response alternation procedure on the response accuracy of male and female Wistar rats. Subjects were exposed to three different delay intervals (5, 10, and 20 sec) during each experimental session. Response accuracy decreased for both males and females as the duration of the delay interval increased. Performance improved over sessions for both sexes. The presentation of stimuli during the delay interval differentially affected the behavior of males and females. Performance of males decreased at all delay intervals when stimuli were presented, whereas no differences in the response accuracy of females were observed.

Studies of memory for recent events using complex maze procedures (Lashley III, Hebb-Williams) have revealed behavioral differences between male and female rats. Males have been shown to behave more efficiently than females (Barrett & Ray, 1970; Davenport, Hagquist, & Rankin, 1970; Dawson, Cheung, & Lau, 1975; Krasnoff & Weston, 1976). Beatty (1979) noted that maze procedures that are most sensitive to behavioral differences between the sexes resemble an open field with a few added partitions. Stewart, Skvarenina, and Pottier (1975) showed that maze performance is inversely related to ambulatory behavior in open-field situations. It has therefore been hypothesized that females make more errors in complex maze procedures because they are more active and they explore more than males, rather than because they are less able to process spatial information. Beatty (1979) suggested that the radial-arm maze procedure (Olton & Samuelson, 1976) may be less susceptible to the interfering effects of sex differences in activity and exploration. Van Haaren, Wouters, and van de Poll (1987a) employed a radial-arm maze procedure to assess behavioral differences between the sexes. Differences between males and females were not observed, thus suggesting that differences in locomotor activity may indeed have been responsible for the observation of sex differences in other complex maze procedures.

Operant delayed spatial response alternation procedures have previously been employed to study memory for recent events in male and female rats (van de Poll, de Bruin, van Dis, & van Oyen, 1978; van Haaren, de Bruin, Heinsbroek, & van de Poll, 1985). Rats were required to alter-

nately press a right and a left lever to obtain food. For accurate performance, the subject had to remember the spatial location of each last response, while the delay interval between response opportunities was experimentally manipulated. Subjects were exposed to the experimental contingencies for a prolonged period of time, to control for the estrus-related variability in the behavior of females. Response accuracy in these experiments (van de Poll et al., 1978; van Haaren et al., 1985) decreased as the delay interval duration was increased in different experimental conditions. Differences between males and females were not observed, either at the no-delay conditions or at the conditions in which the opportunity to respond was delayed for either 1, 5, 7.5, or 15 sec. These authors concluded that it may have been possible that the sequential organization of experimental conditions obscured possible differences between the sexes.

The effects of stimulus presentations during the delay interval on the behavior of rats in procedures designed to study memory for recent events have only been assessed in male subjects. Since behavioral differences between the sexes have now been observed in a number of experimental procedures (van Haaren, Heinsbroek, Louwerse, & van de Poll, 1986; van Haaren, van Hest, & van de Poll, 1987b; van Hest, van Haaren, & van de Poll, 1987a, 1987b), it may well be that the behavior of males and females is differentially affected by the presentation of stimuli during the delay interval of a memory task. The present experiment was designed to research this possibility.

It is not clear whether the presentation of stimuli affects response accuracy to the same extent at all delay intervals. Gordon, Brennan, and Schlesinger (1976) reported that the performance of rats in a T-maze alternation procedure was impaired at all delay intervals ranging from 0 to 40 sec, whereas Grant (1981) reported a decrease in response accuracy at long delay intervals

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(40 sec) only. Three different delay interval durations (5, 10, and 20 sec) were therefore employed in the present experiment. It has previously been observed that response accuracy is higher when different delay intervals are presented within a single session (White & Bunnell-McKenzie, 1985). Subjects were thus exposed to these three different delay interval durations within each experimental session. When all subjects responded reliably in a left-right alternating pattern of responding, stimuli known to affect the response accuracy of subjects in a delayed matching-to-sample procedure (Spetch, 1985) were presented during the different delay intervals.

METHOD

Subjects

The subjects were 8 male and 8 female Wistar rats obtained from Animal House, TNO (Zeist, the Netherlands). They were housed in group cages under a reversed light:dark cycle (lights on from 3:30 p.m. to 3:30 a.m.). The subjects had previously participated in an autoshaping experiment described elsewhere (van Haaren et al., 1987b). Subjects were maintained at approximately 80% of free-feeding body weights. Water was always available in the home cages. The present experiment was started when the subjects were 19 weeks old.

Apparatus

Experiments took place in eight locally constructed Skinner boxes (described in detail by van Haaren et al., 1987b).

Procedure

Preliminary training. All subjects received four sessions of additional training upon completion of the autoshaping procedure (van Haaren et al., 1987b). During these sessions, one of the two response levers was selected at random during each trial and inserted into the experimental chamber. Every second (Sessions 1-2) or fifth (Sessions 3-4) response on the lever produced a food pellet. All subjects reliably pressed both levers upon the completion of these four sessions.

Baseline. At the start of each session, both levers were inserted in the chamber while houselight and stimulus lights were illuminated. A response on either lever started the delay interval, during which both levers were retracted and the stimulus lights were extinguished. After the expiration of the delay interval, both levers were reinserted and the stimulus lights were again illuminated. A pattern of alternating responses was required for reinforcement to be presented. Each response immedi-

ately started the next delay interval. An incorrect response produced a time-out for 4 sec, during which time the levers were retracted from the chamber and both the stimulus lights and the houselight were extinguished. The houselight was again illuminated after the time-out interval had expired. A correct response produced a food pellet (45-mg Bio-Serve food pellet). Subjects were exposed to three different delay intervals within each experimental session: 5, 10, and 20 sec. The order of presentation of the different delay intervals was randomized such that not more than three presentations of the same delay interval could be consecutively presented. Each delay interval was presented 30 times during each session. This baseline procedure was in effect for 35 sessions.

Stimulus presentations during the delay interval. On Sessions 36-45, stimuli were presented on a random-time 20-sec (RT-20) schedule during the delay interval (Condition B). Stimulus presentations consisted of the presentation of a tone (1.25 sec), accompanied either by the illumination of the light in the pellet retrieval unit and the delivery of a food pellet (25% of all stimulus presentations), or by the presentation of a tone (1.25 sec) plus the illumination of the light in the pellet retrieval unit (75% of all stimulus presentations, to ensure that subjects would not gain weight). The baseline procedure during which stimulus presentations were absent was reinstated for the next 10 sessions (Sessions 46-55, Condition A'). All sessions ended after a total of 90 delay intervals had been presented. Sessions were run 5 days a week, Monday through Friday, and always during the subjects' dark period.

RESULTS

Figure 1 shows response accuracy for the different delay interval durations during baseline training (Sessions 1-35). Response accuracy was defined as the number of reinforced responses divided by the total number of responses. The data were analyzed by means of a three-factorial analysis of variance (ANOVA) involving the factors sex, delay interval duration (5, 10, or 20 sec), and blocks of sessions (seven blocks of five sessions each), the latter two being repeated measures. Sex differences in response accuracy were not observed. Males responded somewhat more efficiently than females, but this effect did not reach statistical significance [$F(1,14) = 3.19$, n.s.]. Response accuracy decreased as the duration of the delay interval increased [$F(2,28) = 79.02$, $p < .01$]. Both sexes made more correct responses as training progressed [$F(6,84) = 84.04$, $p < .01$]. The observed

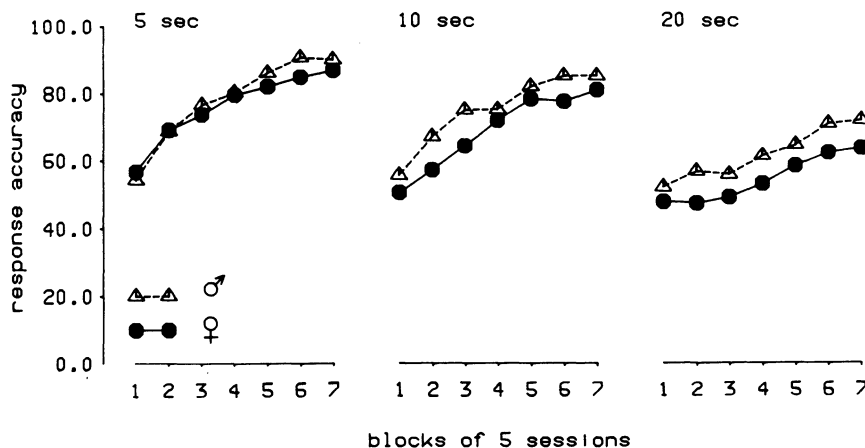


Figure 1. Response accuracy (number of reinforced responses divided by the total number of responses) of male and female Wistar rats in a delayed spatial response alternation procedure with different delay interval durations (5, 10, or 20 sec) in blocks of five sessions.

increase in response accuracy as training progressed was smaller at the longer than at the short delays [$F(12,168) = 6.17, p < .01$].

An ANOVA of the data of the last five sessions (31–35) and the immediately preceding five sessions (26–30) of the baseline condition revealed that all subjects had achieved stable baseline performance at the end of baseline training, since an effect of training was no longer observed [$F(1,14) = 1.36, p > .25$]. The data of Sessions 26–30 and 31–35 were thus pooled to serve as the baseline (Condition A) against which the effect of stimulus presentations during the delay interval could be assessed.

Figure 2 shows the response accuracy for male and female rats when stimuli were presented. A three-factorial ANOVA involving the factors sex, delay interval duration (5, 10, or 20 sec), and condition, the latter two being repeated measures, was used to analyze the data of Sessions 26–35 (baseline, Condition A), Sessions 36–45 (stimuli present, Condition B), and Sessions 46–55 (baseline, Condition A').

Conditions A-B-A'

Response accuracy varied during the different experimental conditions [$F(2,28) = 39.58, p < .01$]. Response accuracy decreased as the delay interval duration was increased [$F(2,28) = 47.57, p < .01$]. A significant delay \times condition interaction effect was observed [$F(4,56) = 12.71, p < .01$].

Conditions A-B

Response accuracy during the baseline condition was compared with the response accuracy when stimuli were presented during the delay interval (Condition B). The effect of delay interval duration was again highly significant [$F(2,28) = 69.31, p < .01$]. Since a delay \times condition interaction effect was not observed [$F(2,28) = 0.42, p > .60$], it may be concluded that stimulus presentations during the delay interval interfered with accurate performance at all delay intervals. Furthermore, the analysis

revealed a significant sex \times condition interaction effect [$F(1,14) = 6.12, p < .03$]: the behavior of males and females was differentially affected by the presentation of stimuli. The effects of stimulus presentations during the delay interval on the behavior of male and female rats were therefore separately analyzed. Stimulus presentations interfered with accurate performance in males [$F(1,7) = 5.47, p < .05$], but not in females [$F(1,7) = 1.06, n.s.$].

Conditions B-A'

An ANOVA comparing the data of Condition B (stimuli present) and Condition A' (reexposure to baseline) showed that the delay interval duration affected response accuracy [$F(2,28) = 33.47, p < .01$]. Response accuracy increased when the stimuli were no longer presented [$F(1,14) = 54.96, p < .01$]. Response accuracy of males and females increased to the same extent, since significant sex \times condition interaction effects were not observed. The significant delay \times condition interaction effect suggested that the increase in response accuracy was delay dependent [$F(2,28) = 19.39, p < .01$].

Conditions A-A'

Comparison of the response accuracy on the sessions prior to (Condition A) and following (Condition A') stimulus presentations revealed a significant main effect of delay interval duration [$F(2,28) = 36.86, p < .01$]. The accuracy of all subjects increased with prolonged training [$F(1,14) = 38.37, p < .01$]. A significant delay \times condition interaction effect was observed, suggesting that accuracy improved mostly at the longer delays [$F(2,28) = 14.46, p < .01$].

DISCUSSION

The results of the present experiment confirm and extend the results of previous experiments that employed an operant delayed spatial response alternation procedure to investigate rats' memory for recent events. A decrease in response accuracy was observed when the duration of the delay interval increased. Since behavior in operant delayed

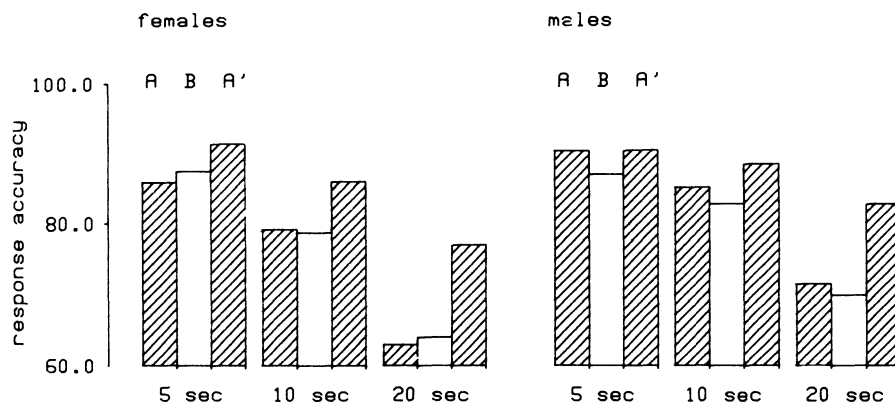


Figure 2. Response accuracy (number of reinforced responses divided by the total number of responses) of female (left part of the figure) and male (right part of the figure) Wistar rats in a delayed spatial response alternation procedure with different delay interval durations (5, 10, or 20 sec) on Sessions 26–35 (baseline, Condition A), Sessions 36–45 (presentation of stimuli during the delay interval, Condition B), and Sessions 46–55 (baseline, Condition A').

response alternation procedures is controlled by stimuli that are no longer physically present at the time of response execution, the results suggest that memory processes are indeed involved. Behavioral differences between the sexes in response accuracy were not observed with the present procedure, either at no-delay conditions (van de Poll et al., 1978) or when longer delay intervals were employed (the results of the present study; van Haaren et al., 1985).

The study of the effects of stimulus presentations during the delay interval of a memory task has been mainly restricted to radial-arm maze procedures and to delayed alternation procedures employing a T-maze. In maze procedures, a rat is usually allowed to make a number of responses in the maze. Next, the rat is exposed to various treatments, which may include removal from the maze, forced choices to an arm of the maze, or presentation of different visual and/or auditory stimuli (Maki, Brokofsky, & Berg, 1979). The rat is then allowed to finish the maze, and the effect of the intervening events on subsequent behavior is assessed. Whereas the radial-arm maze performance of rats has been shown to be remarkably resistant to the effects of stimulus presentations (Maki et al., 1979; Roberts, 1981), the behavior of rats in a T-maze procedure may easily be disrupted (Gordon et al., 1976; Grant, 1981; Miller, Greco, Marlin, & Balaz, 1985). The operant delayed spatial response alternation procedure allows for precise control of the experimental manipulations and the nature of the stimuli. In the present study, response accuracy decreased for males but not for females when stimuli were presented during the delay interval. In addition, it was shown that the presentation of stimuli interfered with accurate performance at all delay intervals.

The results of the present experiments suggest that the behavioral differences between the sexes observed in complex maze procedures do not reflect differences in spatial abilities between males and females, but rather result from differences in activity and exploration that interact with the specific experimental contingencies. It has previously been noted that differences in activity level contribute to behavioral differences between the sexes observed in other experimental procedures. Females are more active and explore more than males (Lester, 1967). Females also make fewer unreinforced responses than do males in procedures that reinforce behavior other than leverpressing (Beatty, 1979; van Hest et al., 1987a), whereas males respond faster than females on continuous reinforcement schedules (van Hest et al., 1987a), on variable interval schedules (Millar, 1975), on random ratio schedules (Heinsbroek, van Haaren, Zantvoord, & van de Poll, 1987), and on schedules that specifically reinforce high rates of responding (van Haaren et al., 1986).

The differential effects of stimulus presentations during the delay interval on response accuracy of males and females in the present experiment may be a function of the fact that presentation of these stimuli elicits behavior that interrupts a previously well-established chain of behavior. Although experimental evidence is not explicitly available, results of other experiments suggest that males are more likely than females to develop behavioral chains, as evidenced, for instance, by the fact that males are slower than females to acquire discrimination reversal (Millar, 1975) or reversal of autoshaping contingencies (van Haaren et al., 1987b). Well-established behavioral chains may be more susceptible to disruption by unexpected experimental events than is behavior that is less stringently organized. Other experiments will have to be designed to explicitly investigate this notion.

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