Anim Cogn (2000) 3 : 1–11

ORIGINAL ARTICLE

Masaki Tomonaga · Tetsuro Matsuzawa

Sequential responding to arabic numerals with wild cards by the chimpanzee (*Pan troglodytes*)

Received: 27 October 1999 / Accepted: 22 November 1999

Abstract One adult female chimpanzee (*Pan troglodytes*) was trained to respond serially to three arabic numerals between 1 and 9, presented on a cathode-ray-tube (CRT) screen. To examine the factors affecting her sequential responding behavior, wild-card items were added to the three-item sequences. When this wild-card item remained until the subject responded to the last numeral (i.e., the terminator condition), her response to the terminator at each point of the sequence was controlled by the ordinal distance between numerals. Thus, the number of responses to the terminator increased as the ordinal distance between numerals increased. When the wild-card item was eliminated by the subject's response (wild-card conditions), the probability of responses to the wild card before the first numeral increased as a function of the serial position of the first numeral. These results were consistent with previous studies of response time and suggest both serial position and symbolic distance effects. It is suggested that the subject might form the integrated 9-item linear representations by training of possible subsets of three-item sequences. Knowledge concerning the ordinal position of each numeral was established through this training.

Key words Sequential responding · Wild cards · Serial position effect · Symbolic distance effect · Chimpanzee (*Pan troglodytes*)

M. Tomonaga (✉) · T. Matsuzawa
Department of Behavioral and Brain Sciences,
Primate Research Institute, Kyoto University,
Inuyama, Aichi 484–8506, Japan
e-mail: tomonaga@pri.kyoto-u.ac.jp, Tel./Fax: +81-568-630549

Supplementary material Fig. S1, an illustration of the experimental subject, Ai, responding to numerals presented on the cathode-ray tube display (photograph by Tetsuro Matsuzawa), is available on the Springer server (http://link.springer.de/journals/10071)

Introduction

Sequential responding or serial learning tasks are frequently used to study transitive inference and linear representations in nonhuman animals (Chen et al. 1997; D'Amato and Colombo 1988, 1989, 1990; Ohshiba 1997; Swartz et al. 1991; Terrace 1987, 1991; Terrace et al. 1995; Tomonaga et al. 1993). In studies of sequential responding, transitive inference, and comparative judgement, certain patterns of results have been reported (Wynne 1998): e.g., the end-anchor effect, serial position effect, symbolic distance effect, and so on. The "end-anchor effect" is where subjects show better performance (higher accuracy and/or faster response times) when the set of items presented contains one or two items at the beginning and end of the whole series. The term "serial position effect" is mainly used in the context of recognition memory, and also in transitive inference studies (Banks 1977; Wynne 1998): subjects show greater accuracy and/or shorter response times when the item's position in the implied series is nearer the beginning of a series than it is the end of a series. For example, imagine that the subjects are trained on a seven-item series, A-B-C-D-E-F-G. When a subset of this series (e.g., B-C-D or D-E-F) is presented in a test situation, subjects show better performance on B-C-D than on D-E-F (D'Amato and Colombo 1988; von Fersen et al. 1991). Since this effect is often intermixed with the end-anchor effect, the actual pattern of results is sometimes not linear in form but U-shaped (Banks 1977). The "symbolic distance effect" refers to better performance when the ordinal distance between items is larger: for example, if subjects show better performance on B-F than on B-C. This effect was observed during serial learning tasks by capuchin monkeys (D'Amato and Colombo 1990), and during transitive inference tasks by pigeons (von Fersen et al. 1991) and rhesus macaques (Washburn and Rumbaugh 1991).

In previous experiments, we trained one adult female chimpanzee to respond to the arabic numerals 1–9 (Tomonaga et al. 1993; Fig. S1). The subject had previously been trained in "numerical" labeling tasks using these numerals

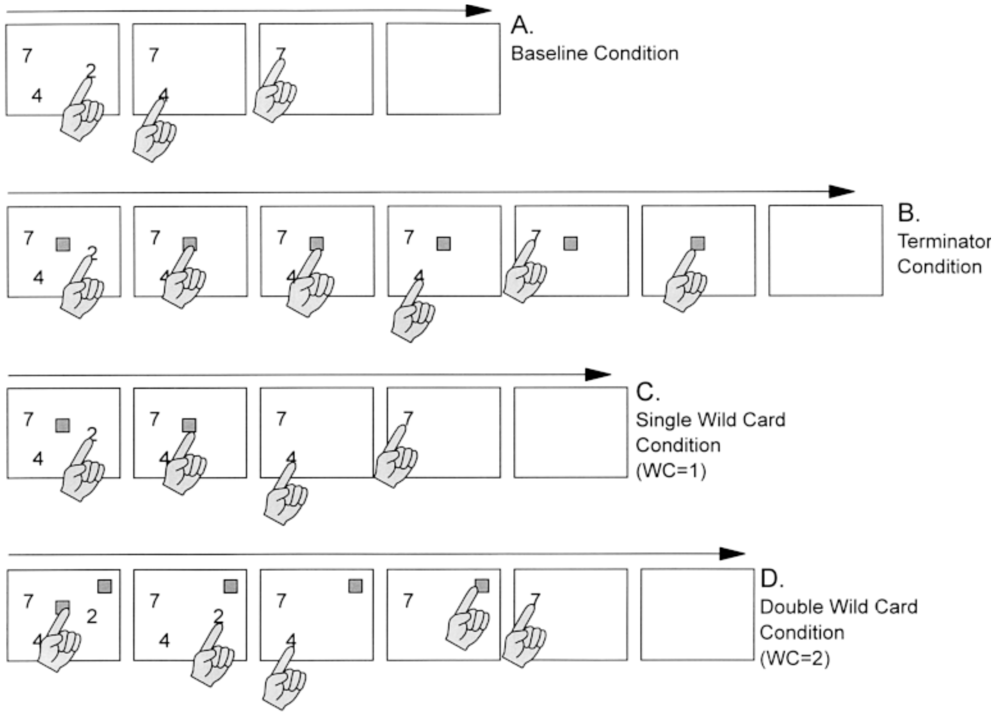


Fig. 1 A–D Schematic diagrams of trials appearing under each type of condition

(Matsuzawa 1985; Murofushi 1997). Although we did not find a transfer from cardinality of numerals to ordinality, the analyses of response time data for all 84 three-item sequences revealed three major characteristics of sequential responding behavior. First, the response time to the first item was much longer than that to the second and third ones. These results indicated that the subject judged the whole order of presented numerals before making the first response (Ohshiba 1997; Swartz et al. 1991). Second, her initial response time increased significantly as the serial position of the first item became further separated from the beginning of the whole series of numerals. This was considered to reflect a serial position effect as noted above. Third, if the sequence had a larger ordinal gap between the first and second items, her initial response time was shorter than when a smaller gap was presented. This effect was interpreted as the symbolic distance effect.

To investigate her knowledge about the serial order of numerals further, we introduced a "wild-card" procedure in the present experiment. D'Amato and Colombo (1989) investigated the capuchin monkeys' knowledge of ordinal positions of stimuli by substituting one of the items in a five-item sequence (for example, A-B-C-D-E) with a wild-card item (A-B-*X*-D-E). Terrace et al. (1995) also tested pigeons with the same procedure. The monkeys showed a significantly better thanchance performance in these wild-card sequences, but the pigeons responded randomly. To solve these wild-card sequences successfully, the subjects need to know the ordinal positions of each item. Thus, monkeys might establish some knowledge regarding the ordinal position of items in the whole sequence, whereas pigeons do not.

Our procedure differs from that of D'Amato and Terrace because we trained all subsets of three-item sequences from the whole series 1–9. It was, therefore, not possible to *substitute* an item with a wild card. Instead, we *added* a wild-card item to the three-item sequences: for example, the subject was presented with the numerals 2, 4, 7, and one or two wild-card items (Fig. 1). This procedure was originally introduced as pretraining, to extend the length of presented sequences from three to four items in order to form a longer response chain.

In the initial condition (terminator condition), the response to the wild-card item had no effect until all the numerals had first been responded to (Fig. 1B). The subject was required to respond to this item at the end of a trial to get the reward. Thus, the new item functioned as a "terminator" of the trial. The subject did not need to respond to this item during the sequential responses to the numerals. Nevertheless, she often responded to this item in between responses to the numerals. Under the second and third conditions (wild-card conditions), the wild-card item(s) disappeared at the subject's response (Fig. 1C, D). The subject was allowed to respond to the wild card(s) at any point during the sequence. Each trial ended when the subject had selected all items including the wild-card item(s). As described later, the subject showed a consistent trend in responses to the wild-card items under each condition.

The main purpose of this study was to examine the factors controlling responses to wild-card items under these experimental conditions. In particular, we explored the relationship between patterns of responses to the wild-card items and the two standard effects in sequential responding behavior: the serial position and symbolic distance effects.

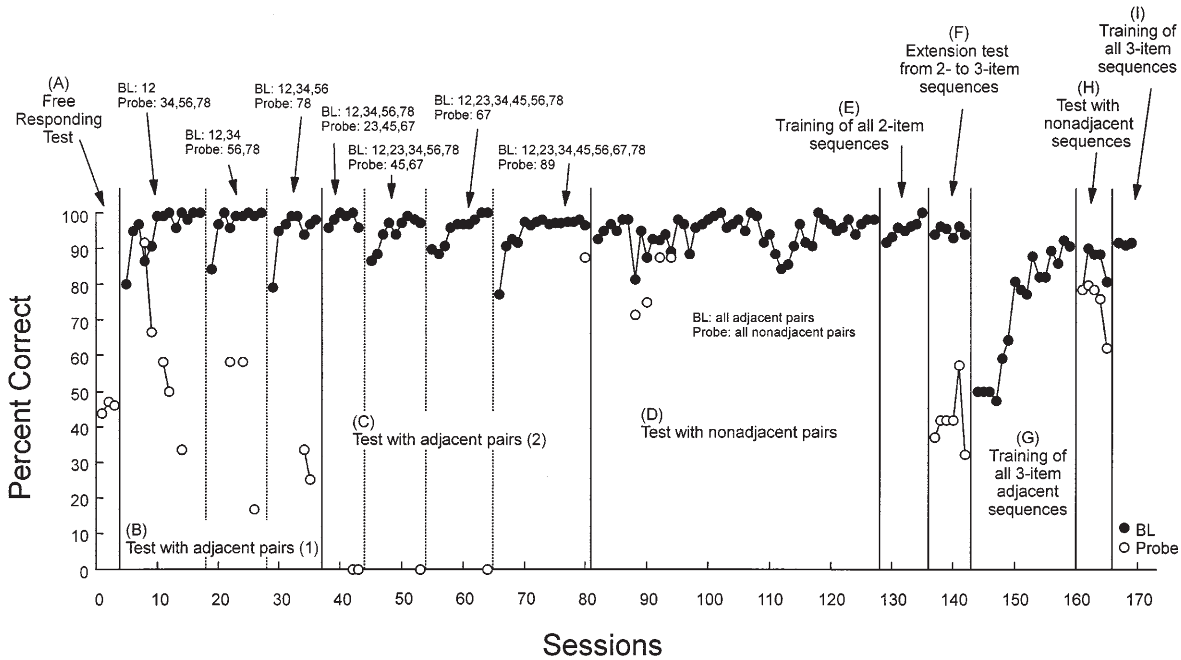


Fig. 2 Mean percentage of correct trials for baseline (*solid circles*) and probe (*open circles*) trials during training of two- and three-item sequences prior to the present experiment

Methods

Subject

One adult female chimpanzee (*Pan troglodytes*), Ai, served as the subject of this experiment. She was approximately 14 years old at the start of this experiment. She lived in an outdoor enclosure with five other adult chimpanzees and maintained her free-feeding body weight during the experiment. She had been trained in various perceptual and cognitive tasks, such as numerical labeling with arabic numerals (Matsuzawa 1985; Matsuzawa et al. 1986). Sequential responding with these numerals was subsequently introduced before the start of this experiment (Tomonaga et al. 1993).

The care and use of the chimpanzee followed the *Guide for the Care and Use of Laboratory Primates* of the Primate Research Institute, Kyoto University, Japan.

Apparatus

Ai was tested in an experimental room (2.7 m wide × 2.1 m high × 1.5 m deep) adjacent to the outdoor enclosure. A 14-inch (35-cm) cathode-ray tube (CRT) display with an optical touch panel (Carol Touch, UL-94V-0) was installed in the room. A 2 cm × 2 cm key was installed below and to the left of this CRT. This key was used for trial initiation. A response was defined as a touch on the CRT. The experiment was controlled by a personal computer (NEC, PC-98XA). Response time was measured with a timer board [CONTEC, TIR-6-(98)] installed in the computer. A food tray was installed 5 cm below the CRT and a universal feeder delivered small pieces of food (e.g., apples, pineapples, peanuts, almonds, raisins) into the food tray (see Fig. S1).

White arabic numerals (1–9) were used as stimuli. The wildcard item was a white square. Individual stimuli were 4.5 cm × 4.5 cm in size.

Procedure

Sequential responding task

A sequential responding task was used in the present experiment. Figure 1 represents the general procedure. A trial proceeded as follows. After a 3-s intertrial interval (ITI), a 1-s beep was sounded. When the subject pressed the trial-initiation key three times, the stimulus items were presented on the CRT. The subject was required to touch these items in the appropriate order. When the subject touched an item correctly, a 0.1-s click sound was presented as response feedback, and that item disappeared. If the subject responded to all items in the correct order, a 1-s chime sounded followed by a food reward. If the subject made an error, all remaining items disappeared and a 0.5-s buzzer sounded. When she made an error, the same trial reappeared as a correction trial until she accomplished a correct sequence. These correction trials used the same stimulus items as the original trial, but the items were presented at different locations from those used in the original trial.

In the present experiment, the items disappeared one by one as the subject responded. Our procedure is, therefore, not the simultaneous chaining procedure (cf. D’Amato and Colombo 1988; Terrace 1987), in which all items remain on the display until the subject has completed the sequential responses.

Acquisition of two- and three-item sequential-responding behavior

Before describing the present experiment, previous experiments with Ai are briefly summarized here (see Tomonaga et al. 1993 for details). Figure 2 shows the percentage of correct trials for baseline (differentially reinforced) and probe (nondifferentially reinforced) trials during sessions leading up to the present experiment.

After the shaping of sequential responding behavior, Ai was initially given three free-responding test sessions, where one of four pairs of adjacent arabic numerals (1-2, 3-4, 5-6, and 7-8) was presented at each trial (Fig. 2, A). Ai was required to touch these numerals sequentially. Any order of responses was nondifferentially reinforced. Ai had been trained on numerical labeling tasks using arabic numerals (Matsuzawa 1985; Matsuzawa et al. 1986, 1991; Murofushi 1997). If she had acquired some knowledge of ordinal properties among numerals during the numerical labeling training, she might have responded to these pairs in a consistent order (“upward” or “downward”). She showed, however, no consistent patterns and selected items randomly. In the next phase, she was trained with each pair of adjacent numerals successively with differential reinforcement. Thus, she was required to select the smaller numeral first (Fig. 2, B). After her performance had reached 90% correct responses for each pair, the remaining untrained pairs of adjacent numerals were tested under nondifferential reinforcement. She was trained in the order 1-2, 3-4, 5-6, and then 7-8. At no point during the differential reinforcement training of pairs of adjacent numerals did she show evidence of transfer of sequential responding from “small” to “large” numerals to the other untrained pairs. After this series of transfer tests, she was explicitly trained on other adjacent pairs (2-3, 4-5, and 6-7), successively, as in the previous phase (Fig. 2, C). She showed a reverse response pattern (i.e., “large” to “small”), based on the previous training of each numeral (e.g., 2 was always responded to second and 3 first in the previous phase). Only on the 8-9 pair did she score well, 87.5%. In the next phase, she was trained on all possible combinations of adjacent pairs and transfer to the pairs of nonadjacent numerals was tested (Fig. 2, D). Unlike previous phases, she showed a total of 80.4% of correct responses in the probe pairs of nonadjacent numerals. Following the overtraining of adjacent two-item sequences, she was trained on all possible two-item sequences until her performance exceeded 90% correct (Fig. 2, E).

Once discrimination met the criterion, the length of sequence was extended from two items to three. These three-item sequences were initially tested under nondifferential reinforcement contingencies (Fig. 2, F). Ai showed significantly above-chance performance on the three-item probe sequences (45.3% correct in total). She showed even better performance on the nonadjacent three-item probe sequence (70% correct in total) after the explicit training of sequences of three adjacent items (Fig. 2, G). Following the completion of these test series on sequence extension, she was differentially trained using all 84 three-item sequences.

Baseline three-item sequence training

One month after the sequential-responding experiments described above, Ai started the present experiment from the baseline three-item sequence training. In this phase, no wild-card items were presented (Fig. 1A). Each session consisted of 168 trials in which each of the 84 possible three-item sequences appeared twice. This training consisted of nine sessions.

Terminator condition

Immediately after the baseline training, Ai was shifted to the first experimental condition. As noted in the introduction, one white square was added to the three-item sequence under this condition (see Fig. 1B). The subject was allowed to touch this stimulus at any point during the sequence. However, touching this stimulus had no effect until all the other numerals had disappeared, so touching the white square functioned as a trial-termination response. Each response to the “terminator” stimulus produced a 0.1-s click sound. As noted before, this procedure was initially intended to shape sequential responses to more than three items. The number of responses to the terminator stimulus at each point of the sequence was recorded in each trial. Each session consisted of 168 trials as in the baseline condition. The subject was given 12 sessions. After this condition, she was given three additional baseline sessions.

Wild card conditions

Next, Ai was shifted to the second experimental phase. In this phase, three types of conditions were randomly alternated across sessions. The first condition was baseline (Fig. 1A). The second condition was a single wild-card condition (WC = 1, Fig. 1C), and the third condition was a double wild-card condition (WC = 2, Fig. 1D). In the latter two conditions, one or two wild-card items appeared in addition to the numerals. The subject was allowed to touch the wild card at any point during the sequence. Under these wild-card conditions, the wild card disappeared when the subject touched it, unlike the terminator condition. At what point the subject touched the wild card(s) was recorded in each trial. As for the previous conditions, each session consisted of 168 trials. Ai was given five sessions of baseline and ten sessions of each wild-card condition.

Four-item sequence training

After the wild-card conditions, Ai was tested to transfer to four-item sequences, and then trained on four-item sequences of adjacent numerals over 29 sessions, followed by a 6-session training in which all 126 four-item sequences appeared in each session (Tomonaga et al. 1993). Response time data for the six sessions of all four-item sequences were used as control data for response time analyses in the present experiment. She showed 88.6% correct in total during these six sessions.

Results

Accuracy

Ai scored 91.2% and 94.4% of correct responses during the first and second baseline three-item sequence training, whereas accuracy was 86.1% under the terminator condition. A randomization test based on 10,000 permutations (Edgington 1987) revealed a significant difference be-

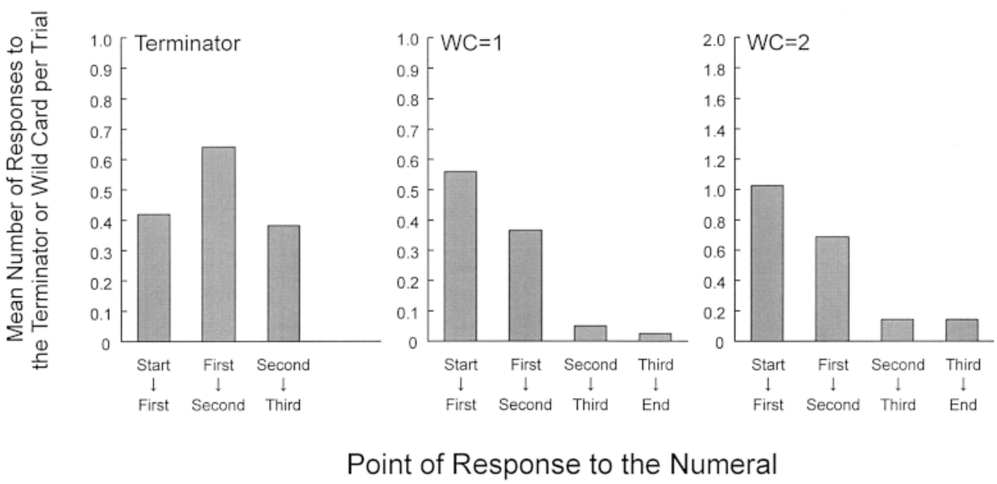


Fig. 3 Mean number of responses to the terminator and wild card(s) per trial at each point of the sequence under each condition

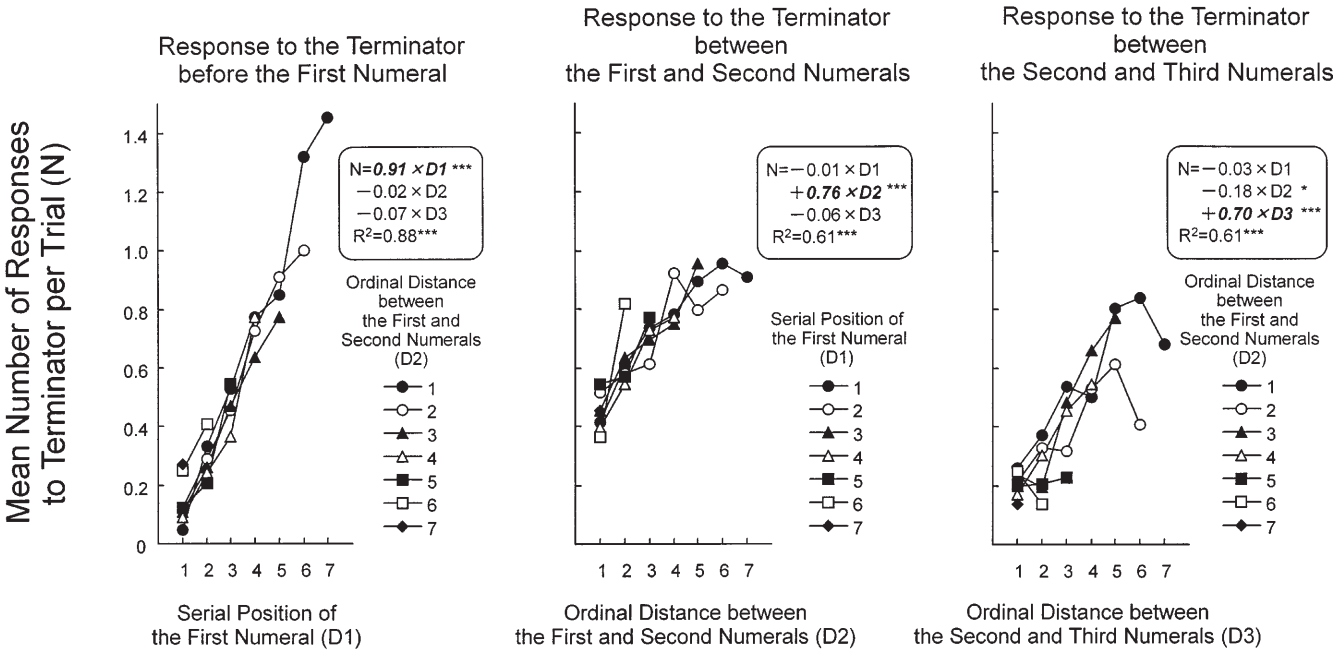


Fig. 4 Mean number of responses to the terminator per trial at each point of response under the terminator condition. *Horizontal axes* represent the most important independent variables as determined by separate multiple regression analyses. Results of multiple regression analyses are shown in *boxes*

tween the baseline and terminator conditions ($P < 0.001$). During the second phase (wild-card conditions), Ai scored 95.1%, 90.6%, and 85.5% for baseline, WC = 1, and WC = 2 conditions, respectively. Multiple-comparison randomization tests based on 10,000 permutations demonstrated clearly that accuracy was higher during baseline than under the two wild-card conditions (Ps < 0.005). Additionally, accuracy achieved during the WC = 1 condition was higher than that of WC = 2 ($P < 0.001$).

Responses to the terminator and wild cards

Terminator condition

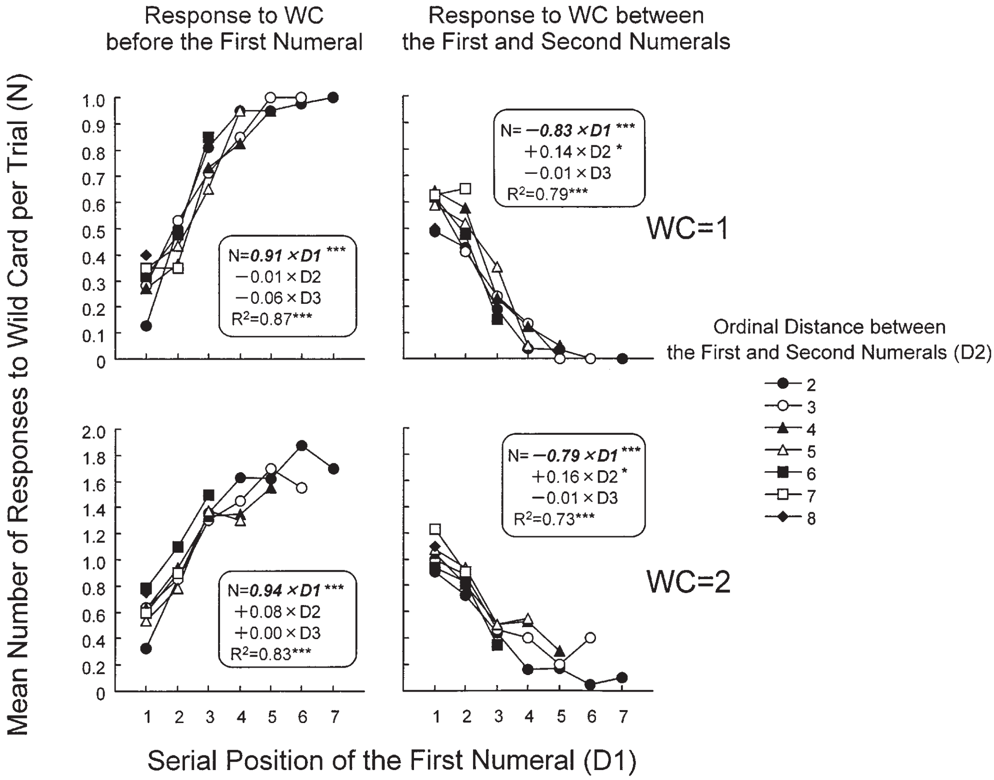
The left panel of Fig. 3 presents the mean number of responses per trial to the terminator stimulus at each point of sequential response to the numeral under the terminator condition. As the subject was allowed to respond to the terminator at any time under this condition, the maximum number of responses to the terminator stimulus at each point was unlimited. Although the mean number of responses to the terminator did not show any increasing or decreasing trend as a function of the point of response to the numeral, the number of responses between the first and second numerals was larger than that at other response points.

Multiple regression analyses revealed that the number of responses to the terminator was not controlled simply by the response points, but also by the combinations of numerals in each sequence. The independent variables of these analyses were the same as those in the response time analysis of previous experiments (Tomonaga et al. 1993), i.e., the serial position of the first numeral (designated as D1), the ordinal distance between the first and second numerals (D2), and the ordinal distance between the second and third numerals (D3). These analyses were conducted separately from the number of responses (dependent variables) at each point of the sequential responses.

Figure 4 shows the mean number of responses per trial to the terminator at each point during the sequential responses as a function of the independent variables in the terminator condition. Standardized multiple regression equations and multiple correlation coefficients (R^2) are also shown in the boxes. The horizontal axis in each panel represents the most dominant independent variable. Each symbol denotes one of the other independent variables. Each point of the graph represents the mean value averaged across the remaining variable. For example, the filled circle at 1 of D1 in the left panel represents the mean number of responses to the terminator before responding to 1 averaged across data from the three-item sequences 1-2-3, 1-2-4, 1-2-5,…,1-2-9.

As shown in these figures, the mean number of responses to the terminator at each response point was controlled mainly by the ordinal distance between the numerals at that response point. The serial position of the first numeral (D1) was analogous to the ordinal distance between the zero point and the first numeral. Interestingly, the number of responses to the terminator stimulus before the response to the first numeral increased with its serial position. Furthermore, the numbers of responses to the terminator between the first and second, and between the second and third numerals also increased as a function of ordinal distance between these numerals.

Fig. 5 Mean number of responses to the wild card per trial at each point of response under the terminator condition. *Horizontal axes* represent the most important independent variables as determined by separate multiple regression analyses. Results of multiple regression analyses are shown in *boxes*



Wild card conditions

The center and right panels of Fig. 3 present the mean number of responses per trial to the wild-card item(s) at each point of sequential response to the numeral under the wild-card conditions. The subject could respond to the wild card(s) only once under wild-card conditions. Thus, the maximum number of responses to the wild card(s) at each point was one for WC = 1 condition, and two for WC = 2 condition, respectively. In contrast to the terminator condition, the subject responded to the wild card most frequently before the first numeral or between the first and second numerals. The number of responses to the wild card between the second and third numerals and after the third numerals was quite small (0.07 for WC = 1, and 0.29 for WC = 2).

Figure 5 shows the mean number of responses per trial to the wild-card item(s) at each point of response under the wild-card conditions. The horizontal axes show the serial position of the first numeral (D1). Each symbol represents the ordinal distance between the first and second numerals (D2). Each point is the mean value averaged across the ordinal distance between the second and third numerals (D3). The upper panels show the results for the WC = 1 condition, and the lower panels those for the WC = 2 condition. The lefthand panels show the number of responses to the wild card before the response to the first numeral, and the righthand panels show that between the first and second numerals. As for the terminator condition, we conducted multiple regression analyses but excluded data of later response points from these analyses because their proportions were quite low, as is evident from Fig. 3. The boxes in Fig. 5 show the standardized multiple regression equations and multiple correlation coefficients, which were all significantly different from 0 [$Fs(3,80) > 72.70$, $Ps < 0.001$].

These results seem to differ from those of the terminator condition. The number of responses to wild-card items was primarily affected by the serial position of the first numeral. That is, the subject responded to the wild card(s) before the first numeral more often when its serial position was further separated from the beginning of the whole series. Conversely, the number of responses to the wild card(s) between the first and second numerals decreased when the serial position of the first numeral was further separated from the beginning. The number of responses to the wild-card item(s) between the first and second numerals was also affected by the ordinal distance between them (D2), but this effect was quite small.

Response time

To verify the occurrence of serial position and symbolic distance effects in response times, as seen in previous experiments (see Introduction), the initial response time data from the second and third baseline training of three-item sequences, and the subsequent training of the four-item sequences were analyzed in the same manner as that in Tomonaga et al. (1993).

Based on the mean initial response times (RT) for all 84 three-item sequences, we conducted multiple regres-

Table 1 The results of multiple regression analyses of response time data

	R^2	Intercept	Partial correlation coefficients				df^a
			D1	D2	D3	D4	
3-Item sequence (Tomonaga et al. 1993)	0.602***	0.799	0.031***	–0.030***	–0.024***		80
3-Item sequence (this experiment)	0.588***	0.757	0.040***	–0.024***	–0.026***		80
3-item sequence, excluding end-anchor effect (this experiment)	0.565***	0.816	0.025*	–0.039*	–0.025*		31
Wnnn (WC = 1), including all sequences	0.163**	0.796	–0.010*	–0.019***	-0.009^{ns}		79
Wnnn (WC = 1) excluding sequences starting with 1	0.220**	0.819	–0.018**	–0.016**	-0.008^{ns}		52
nWnn (WC = 1)	0.327***	0.809	0.018*	–0.030***	–0.016*		71
4-Item sequence	0.224***	0.724	0.038***	–0.023*	-0.007^{ns}	0.007^{ns}	121

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$
[a] Degrees of freedom for *t*-tests of partial correlation coefficients

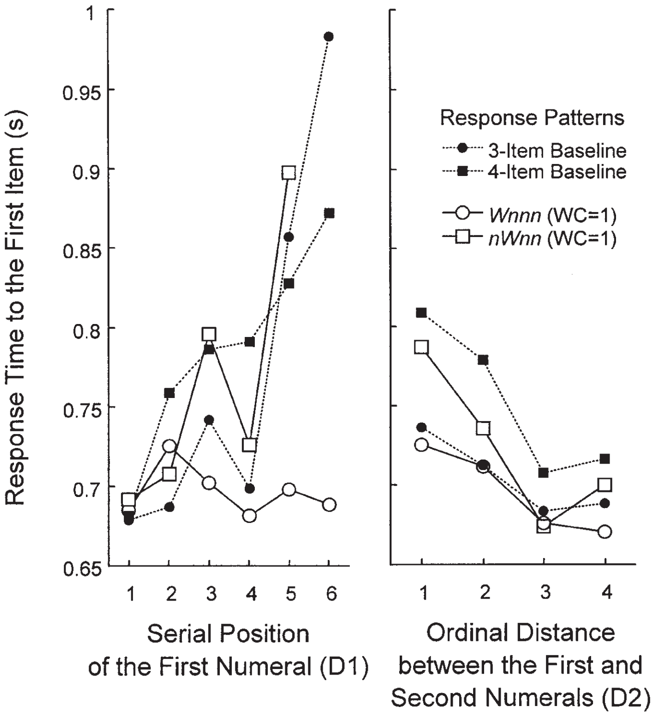


Fig. 6 Mean response times to the first item in the 3-item and 4-item baseline training sessions and for the two types of response patterns under the WC = 1 condition as a function of the serial position of the first numeral and ordinal distance between the first and second numerals (*Wnnn* WC = 1 trials in which the subject responded the wild card before the first numeral, *nWnn* WC = 1 trials in which the subject responded to the wild card immediately after the first numeral)

sion analyses (Table 1). Independent variables were the same as those in previous experiments, i.e., the serial position of the first item (D1), the ordinal distance between the first and second items (D2), and the ordinal distance between the second and third items (D3). The table shows the multiple regression coefficients (R^2) and partial correlation coefficients for each independent variable. Analysis of variance was used to test whether the multiple regression coefficients were significantly above 0, and *t*-tests were conducted to see whether each partial correlation coefficient was significantly different from 0. The resultant multiple regression equation was comparable to that of previous experiments (Tomonaga et al. 1993, see also Table 1). The partial regression coefficient for D1 was greater than 0, indicating the serial position effect, and those for D2 and D3 were less than 0, indicating the symbolic distance effect. For the four-item sequences, only the partial correlation coefficients of D1 and D2 were significant (Table 1). To corroborate these analyses, Fig. 6 represents the initial response time data from the three- (filled circle) and four-item (filled square) sequences as a function of the serial position of the first item (D1, left panel) and the ordinal distance between the first and second items (D2, right panel). In sum, the subject's initial response times were longer when the serial position of the first item (D1) was further from the beginning of the whole sequence, and shorter when the ordinal distance between the first and second items (D2) or between the second and third items (D3) was larger.

As noted in the Introduction, the serial position effect is sometimes intermixed with the end-anchor effect (Banks 1977; Wynne 1998). To remove this influence, we additionally analyzed the data from the 35 three-item sequences in which the first (1) and/or the last (9) items of the whole series were not included. The results in Table 1 show essentially the same patterns as the previous analyses.

Figure 7 shows the mean response times as a function of response patterns during the wild-card conditions (WC = 1 and WC = 2). Note that the second, third, fourth, and fifth response times represent the interval between responses. For comparisons, data from the three- and four-item baseline sequences are also shown. The subject displayed the longest response time in her initial response and little difference among the rest of the response times in the three- and four-item baseline sequences.

In wild-card trials, the subject showed the same patterns of response times when she did not respond to the wild card at the end of the sequence. When she selected the wild item last, however, response times were as long as the initial response times. Figure 7 also shows the proportion of each response pattern in parentheses. The proportion of response patterns in which the subject responded to the wild card last was lower than the other patterns (2.4% in WC = 1, and 14.4% in WC = 2).

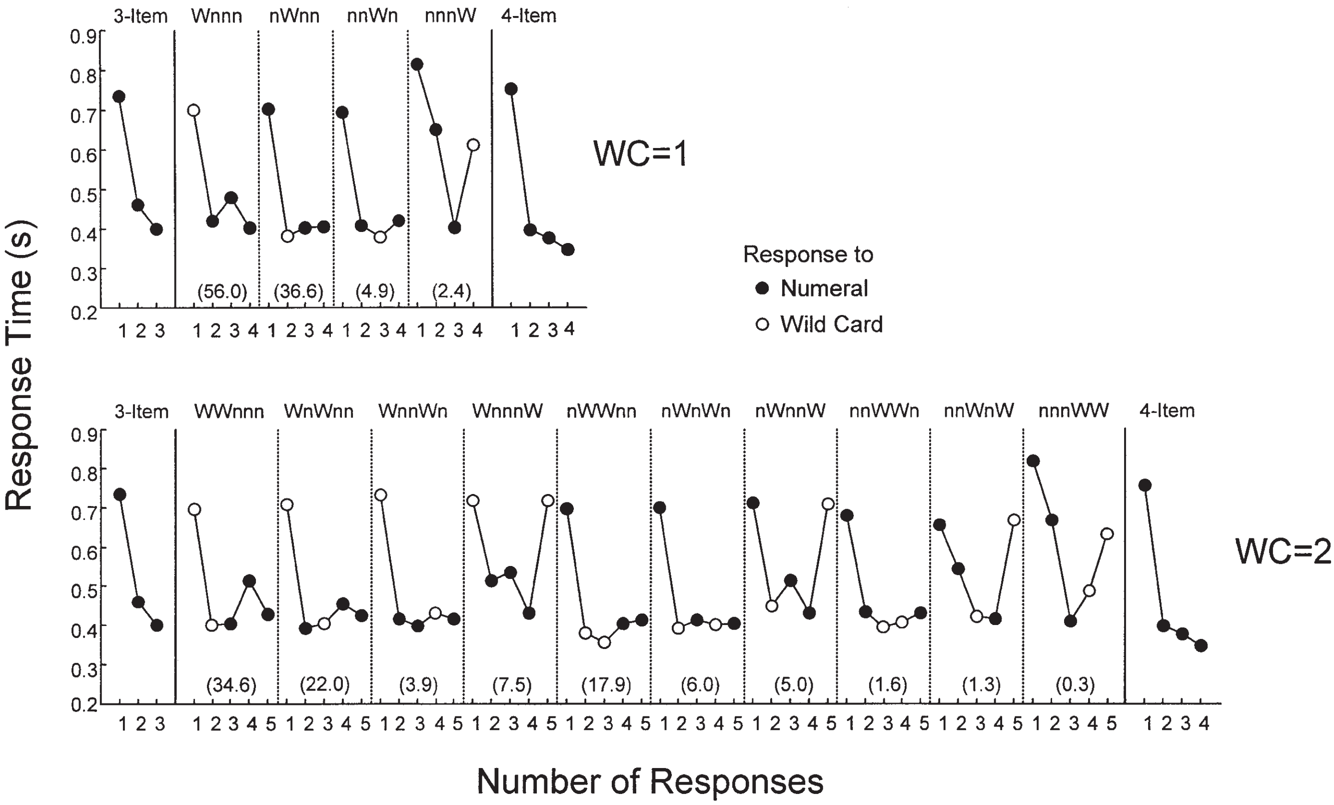


Fig. 7 Mean response times at each point of the sequential responses under the WC = 1 and WC = 2 conditions as a function of response patterns. Each panel also shows the results from the 3- and 4-item baseline training. The rate of each response pattern as a proportion of the total is shown in *parenthesis* above the *horizontal axis*. Note that response times for the second, third, fourth, and fifth responses represent the interval between responses

To examine the relationship between response time data and patterns of responses to the wild cards, we conducted the same analyses on response time data for the WC = 1 condition. Figure 6 also shows the initial response time for the two types of response patterns under the WC = 1 condition. The first response pattern is that in which the subject selected the wild card first (denoted *Wnnn*). The second is the pattern in which the subject selected the wild card right after the first numeral (denoted *nWnn*). We also conducted multiple regression analyses on the response time data of these response patterns (Table 1). From the lefthand panel of Fig. 6, the difference between the *Wnnn* pattern and other sequences is very clear. For the response pattern *Wnnn*, the initial response time decreased as a function of the serial position of the first numeral especially when that serial position was 2 or above. In addition, we conducted the multiple regression analysis on data from the *Wnnn* pattern, excluding data from those sequences that started with the numeral 1 (Table 1). The results indicate a larger negative value for the partial correlation coefficient of D1. In contrast, response time increased as a function of the serial position of the first numeral in the response pattern *nWnn*, which resembled the baseline conditions (Fig. 6). Multiple regression equations confirmed these results.

The righthand panel of Fig. 6 clearly shows the symbolic distance effect for the response patterns *Wnnn* and *nWnn*. That is, initial response time decreased as a function of the ordinal distance between the first and second numerals (see also Table 1). Under wild-card conditions, the symbolic distance between the numeral might not affect responses to the wild card but might affect instead the initial response time.

Discussion

This experiment replicated previous findings on response times in sequential responding by the same chimpanzee. Both the serial position and symbolic distance effects were observed in the subject's initial response times to three-item baseline sequences. Furthermore, the subject's initial response times were much longer than the second and third response times (Fig. 7). Had the subject responded to the item in a step-by-step manner at each point of response, all graphs would have been negatively accelerated and linear in form. The results suggested that the subject identified the items being presented, judged the pertinent response order, and planned the appropriate motor patterns of sequential responses before making the initial response (D'Amato and Colombo 1988; Ohshiba 1997; Swartz et al. 1991). This possibility was further confirmed by a subsequent study with the same subject (Biro and Matsuzawa 1999). Though much shorter than the first decrease in response time, there were slight decreases in the second, third, and fourth response times (Fig. 7). This possibly reflects the procedure employed in the present experiment, whereby items were eliminated by the subject's response, unlike simultaneous chaining in which items remain on the screen until the end of the trial. It is known that the presence of distractors increases manual response times both in humans (Tipper et al. 1992) and chimpanzees (M. Tomonaga, unpublished work). This distractor effect might affect the subject's motor performance in sequential responding, so that a decrease in the number of numerals during the course of sequential responding might accelerate the subject's responses.

Under wild-card conditions, when the subject selected the wild card last, she took as long to respond to it as for the initial response. As shown in the results, however, the proportion of these response patterns was relatively low (less than 15% averaged across wild-card conditions). In previous experiments (Tomonaga et al. 1993), the subject occasionally stopped her sequential response before selecting the last item when the three-item probe sequences were presented during the sequence-extension tests conducted after training for the two-item sequences (10.5% in total of probe sequence trials). This behavior suggested that the subject had misjudged the response order of whole items on the basis of two of the three numerals. This proportion is comparable to the proportion of response patterns in the present experiment in which the subject selected the wild-card item last. Taken together, in these trials, the subject might have ignored the wild card and planned the response order only on the basis of the remaining numerals.

The subject's response time to the first numeral was shorter when its serial position was closer to the beginning of the whole numeral series. This is often referred to as the serial position effect (Wynne 1998). Furthermore, the response time to the first item was shorter when the ordinal distances between the first and second, and between the second and third numerals were longer. This was considered as evidence for the symbolic distance effect. The fact that the symbolic distance between the subsequent numerals affected the initial response times further supported the possibility that the subject judged the response order of numerals before emitting the first response.

Responses to the wild-card item(s) under the two different conditions were also governed by the serial position of the first numeral. However, the symbolic distance between numerals was also effective in the terminator condition. When the novel item was presented as the terminator (i.e., did not disappear until she had selected all numerals), the number of responses to the terminator before the first numeral increased as a function of its serial position, and those after the first numeral increased as a function of ordinal distance between the subsequent numerals. The response to the terminator was reinforced only when the subject responded to it at the end of sequence. A response to the terminator at the other response point should therefore have been eliminated by this reinforcement contingency. The present results could not be explained by simple reinforcement.

Under those wild-card conditions for which the wild card(s) disappeared at the subject's response, her response to wild-card items before the first item increased as a function of the serial position of the first item, whereas her response to it between the first and second numerals decreased as a function of the serial position of the first item. This negative relationship between the numbers of responses to wild cards before and after the response to the first numeral was not surprising. Under wild-card conditions, the subject was allowed to respond to each wild card only once. So, if the number of responses to the wild card increased at one response point, then the number could only decrease at the other response point. The relationship between the number of responses to wild-card items and the ordinal distance between numerals was very weak. Similar difference in the degree of effects of the serial position and the symbolic distance was also observed in capuchin monkeys (D'Amato and Colombo 1988, 1990) during tests with subsets of the whole series.

Why was the response to wild cards affected by the serial position of the first numeral? One plausible explanation is as follows. Since the chimpanzee had learned the ordinal position of each item, she might use the wild cards for behaviorally filling in the gap before the first numeral, especially when the first numeral was not 1. Of course, this is quite speculative and we should consider other possibilities. Nevertheless, the analyses of response times under the wild-card condition (WC = 1) support this view. Imagine that the subject used the wild card as a missing numeral. If she judged the whole order of items including the wild card before executing her sequential responses, the initial response times would show different patterns when the subject selected the wild-card item first and when she did not. On the other hand, if the subject did exclude the wild card when she judged the whole order of the numerals, and incidentally selected the wild card as a result of reinforcement history or other controlling factors, the initial response times would be under the control of the serial position of the first numeral and the ordinal distance between numerals, irrespective of the response point of the wild card. Figure 6, however, indicates that the former explanation is more likely. For the response pattern *Wnnn*, the initial response time decreased across the serial position of the first numeral, whereas the response time increased for the pattern *nWnn*. If the wild card functioned as a constant missing numeral before the first numeral, the initial response time might be affected by the ordinal distance between the wild card (missing numeral) and the first numeral. This distance might cause the symbolic distance effect. The observed decreasing pattern of initial response time (when the first numeral was larger than 1) strongly supports this possibility. Interestingly, when the first numeral was the smallest numeral (1), her initial response time was faster than when it was 2. When the first numeral was 1, there was no missing numeral before the first numeral. Some other factors might plausibly affect her initial response time in this case.

On the other hand, the initial response time decreased as a function of the ordinal distance between the first and second numerals under every condition. If the subject utilized the wild card as a missing numeral between the first and second numerals on the screen, the initial response time might not have shown the decreasing patterns as in the baseline condition. The fact that the symbolic distance effect on response time remained, irrespective of the response to the wild card, is related to the fact that the mean number of responses to the wild card was not affected by the symbolic distance between the first and second numerals. Under the wild-card condition, the symbolic distance between numerals may not affect responses to the wild card but, rather, to the initial response time.

Under the terminator condition, the response to the terminator was affected by both the serial position of the first numeral and the symbolic distance between numerals. These results should be interpreted in a different way from the results of the wild-card conditions. A terminator that remained irrespective of the subject's response might affect her processing of sequences. If the subject judged the response order of items including the terminator before response execution, a terminator that remained might require the subject to change her plan of sequential responses. Thus, if the subject re-planned the order of the sequential responses on the basis of the items remaining on the display, the terminator might be used again as a missing numeral before the smallest numeral on display. So, the response to the terminator might be repeatedly affected by the serial position of this smallest numeral. Incidental serial judgement at each point of response, however, does not explain the present results. Imagine that the subject responded to the terminator first and then responded to the smallest numeral when given the sequence 7-8-9. If the serial judgement account was in effect, the subject should have re-planned the order before making the next response in the presence of 8, 9, and the terminator. The subject's judgement might have been affected by the serial position of the smallest numeral (that is, 8), so that, the subject might respond to the terminator before responding to 8 as a result of the serial position effect. As in Fig. 4, this was not the case.

Another way to account for the results of the terminator condition is that the subject judged the order of sequential responses to items on the basis of knowledge of the property of repeated availability of the terminator stimulus that remained at the end of sequential responses. She might then plan her response order by considering the repeated use of the terminator to fill the gap between numerals. This possibility could be examined by analyzing her initial response times during the terminator condition. Unfortunately, we did not collect the response time data under this condition and need to further test the possibility of flexible use of novel items under different contingencies.

Recently, transitive inference has been intensively investigated in nonhuman animals using concurrent discrimination procedures (Boysen et al. 1993; Davis 1992; Gillan 1981; McGonigle and Chalmers 1992; Treichler and Van Tilburg 1996, in press; von Fersen et al. 1991; Wynne 1995; T. Tanaka and M. Sato, unpublished work). In many of studies, researchers reported positive evidence for transitive inference (for example, train A+B-, B+C-, C+D-, D+E-, and then test BD), serial position effect (better for B+C- than C+D-), and symbolic distance effect (better for B+D- than B+C- or C+D-). These results can be explained by both cognitive and associative (or reinforcement theory) accounts. Wynne (1995) suggested that the reinforcement accounts based on e.g., the Rescorla-Wagner model could readily explain the serial position and symbolic distance effects. The present results of sequential responding might be also explained in terms of these types of associative accounts. It is still unclear, however, whether the associative account is effective in serial learning tasks such as the present experiment. At the very least, analyses of response-time data from previous and the present experiments suggest that the chimpanzee performed this task in a rather different way to pigeons. Chimpanzees and capuchin monkeys (D'Amato and Colombo 1988) assess the order of all items before making the initial response. These findings add support for cognitive accounts for the chimpanzee's sequential responding behavior.

Acknowledgements The authors wish to thank Drs. Kazuo Fujita, Shoji Itakura, and the staff of the Department of Behavioral and Brain Sciences, Primate Research Institute, Kyoto University. Special thanks are due to Mr. Sumiharu Nagumo for his technical assistance. The members of the Laboratory Primate Center cared for the chimpanzee. Ms. Vanessa Hayes critically read an early version of English manuscript. This research was financially supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science, Sports, and Culture, Japan (grant 05206113).

References

Banks WP (1977) Encoding and processing of symbolic information in comparative judgements. Psychol Learn Motiv 11:101–159

Biro D, Matsuzawa T (1999) Numerical ordering in a chimpanzee (*Pan troglodytes*): planning, executing, and monitoring. J Comp Psychol 113:178–185

Boysen ST, Berntson GG, Shreyer TA, Quigley KS (1993) Processing of ordinality and transitivity by chimpanzees (*Pan troglodytes*). J Comp Psychol 107:208–215

Chen S, Swartz KB, Terrace HS (1997) Knowledge of the ordinal position of list items in rhesus monkeys. Psychol Sci 8:80–86

D'Amato MR, Colombo M (1988) Representation of serial order in monkeys (*Cebus apella*). J Exp Psychol Anim Behav Proc 14:131–139

D'Amato MR, Colombo M (1989) Serial learning with wild-card items by monkeys (*Cebus apella*): Implications for knowledge of ordinal position. J Comp Psychol 103:252–261

D'Amato MR, Colombo M (1990) The symbolic distance effect in monkeys (*Cebus apella*). Anim Learn Behav 18:133–140

Davis H (1992) Transitive inference in rats (*Rattus norvegicus*). J Comp Psychol 106:342–349

Edgington ES (1987) Randomization tests, 2nd edn. Marcel Dekker, New York

Fersen L von, Wynne CD, Delius JD, Staddon JE. (1991) Transitive inference formation in pigeons. J Exp Psychol Anim Behav Process 17:334–341

Gillan DJ (1981) Reasoning in the chimpanzee. II. Transitive inference. J Exp Psychol Anim Behav Proc 7:150–164

Matsuzawa T (1985) Use of numbers by a chimpanzee. Nature 315:57–59

Matsuzawa T, Asano T, Kubota K, Murofushi K (1986) Acquisition and generalization of numerical labeling by a chimpanzee. In: Taub DM, King FA (eds) Current perspectives in primate social dynamics. Van Nostrand Reinhold, New York, pp 416–430

Matsuzawa T, Itakura S, Tomonaga M (1991) Use of numbers by a chimpanzee: a further study. In: Ehara A, Kimura T, Takenaka O, Iwamoto M (eds) Primatology today. Elsevier, Amsterdam, pp 317–320

McGonigle B, Chalmers M (1992) Monkeys are rational! Q J Exp Psychol B 45:189–228

Murofushi K (1997) Numerical matching behavior by a chimpanzee (*Pan troglodytes*): subitizing and analogue magnitude estimation. Jpn Psychol Res 39:140–153

Ohshiba N (1997) Memorizations of serial items by Japanese monkeys, a chimpanzee, and humans. Jpn Psychol Res 39:236–252

Swartz KB, Chen S, Terrace HS (1991) Serial learning by rhesus monkeys. I. Acquisition and retention of multiple four-item lists. J Exp Psychol Anim Behav Proc 17:396–410

Terrace HS (1987) Chunking by a pigeon in a serial learning task. Nature 325:149–151

Terrace HS (1991) Chunking during serial learning by a pigeon. I. Basic evidence. J Exp Psychol Anim Behav Proc 17:81–93

Terrace HS, Chen S, Newman AB (1995) Serial learning with a wild card by pigeons (*Columba livia*): effect of list length. J Comp Psychol 109:162–172

Tipper SP, Lortie C, Baylis GC (1992) Selective reaching: evidence for action-centered attention. J Exp Psychol Hum Percept Perform 18:891–905

Tomonaga M, Matsuzawa T, Itakura S (1993) Teaching ordinals to a cardinal trained chimpanzee (in Japanese with English summary). Primate Res 9:67–77

Treichler FR, Van Tilburg D (1996) Concurrent conditional discrimination tests of transitive inference by macaque monkeys: list linking. J Exp Psychol Anim Behav Proc 22:105–117

Treichler FR, Van Tilburg D (1999). Training requirements and retention characteristics of serial list organization by macaque monkeys. Anim Cogn 2:235-244

Washburn DA, Rumbaugh DM (1991) Ordinal judgments of numerical symbols by macaques (*Macaca mulatta*). Psychol Sci 2:190–193

Wynne CDL (1995) Reinforcement accounts for transitive inference performance. Anim Learn Behav 23:207–217

Wynne CDL (1998) A minimal model of transitive inference. In: Wynne CDL, Staddon JER (eds) Models of action: mechanisms for adaptive behavior. Erlbaum, Mahwah, pp 269–307