Individual Response Strategies in List Learning by Orangutans[*]

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ABSTRACT

Two orangutans learned eight lists of items in a recognition memory procedure that allowed the list items to be reported in any order. In a previous study using this same procedure, the orangutans developed a spatial response strategy that was applied to acquisition of novel lists. The purpose of the present study was to determine whether serial order information would supersede the already established response pattern. One subject maintained the established response strategy while the other showed a gradual weakening of that pattern that appeared as lists were acquired. Neither subject demonstrated a serial position effect although serial order information may have affected the shift in response strategy. The obtained individual differences are striking in light of previous studies that have shown quantitative differences but no qualitative differences in serial learning by monkeys and orangutans.
Keywords: Response strategies, list learning.

RESUMEN

Estrategias de respuesta individual en el aprendizaje de listas por orangutanes. Dos orangutanes aprendieron ocho listas de elementos en un procedimiento de memoria de reconocimiento que permitió que los elementos de la lista fueran informados en cualquier orden. En un estudio anterior usando el mismo procedimiento, los orangutanes desarrollaron una estrategia de respuesta espacial que se aplicó posteriormente a la adquisición de nuevas listas. El propósito del presente estudio es determinar si la información del orden serial reemplazaría el patrón de respuesta ya establecido. Un sujeto mantuvo la estrategia de respuesta ya establecida mientras que el otro demostró un debilitamiento gradual de dicho patrón, debilitamiento que fue apareciendo a medida que las listas fueron adquiriéndose. Ninguno de los dos sujetos demostró un efecto de la posición serial aunque la información del orden serial pudo haber afectado al cambio en la estrategia de respuesta. Las diferencias individuales obtenidas son llamativas a la luz de los estudios anteriores que demostraron diferencias cuantitativas pero no cualitativas en el aprendizaje serial en monos y orangutanes.
Palabras clave: estrategias de respuesta, aprendizaje de listas.

Comparative analyses of basic psychological processes such as memory can inform theoretical understanding of the process while also exploring cognitive characteristics of the species under study. Similarities obtained across species suggest general theoretical principles of memory that can be tested further in other species, or in the same organisms in other experimental settings. Conversely, differences obtained across species suggest qualifications of hypothesized general principles which may best be interpreted in the context of the ecology of individual species. There are important considerations in designing experimental tasks to apply in a cross-species analysis of basic psychological processes. Inherent behavioral or perceptual differences across species may prohibit using the same procedure with each subject species. The tasks must be conceptually analogous but designed to facilitate performance in individuals of each species and to allow clear interpretation of data obtained from each modification of the task (Shumaker & Swartz, 2002).

Within the Order *Primate*, humans, bonobos, chimpanzees, gorillas and orangutans are classified in the same family, *Hominidae*, the great apes (Groves, 2001). This high level of relatedness is apparent from physical and behavioral similarities across great apes and confirmed by considerable overlap in DNA (see Shumaker & Beck, 2003). Studies of cognitive processes in nonhuman great apes often address a specific cognitive skill using research from human children or adults to guide the investigation (Shumaker & Swartz, 2002).

Our studies of list memory in nonhuman primates are based on phenomena previously demonstrated in humans, using an experimental procedure that is modeled after the procedure used with humans. In a typical free-recall list memory task, human subjects are presented with a list of words and asked to recall the list items, in any order, following presentation of the entire list (free recall). Over the course of several trials, subjects become able to produce most of the list items, adopting strategies to improve performance. If some of the list items are associated with one another (e.g., dog, cat) or if they fall into the same category (e.g., apple, orange), those items are clustered during recall (Bousfield, 1953, 1958). Even with lists of words that have low associations with one another, humans will begin to organize the list items into clusters based on the individual's subjective associations. This strategy has been called subjective organization (Tulving, 1962). In our first study of list memory with orangutans we addressed subjective organization (Swartz, Himmanen, & Shumaker, 2006) using the same procedure reported in the present study. This first study is discussed in more detail below.

One of the most robust effects reported in human memory is the serial position effect (Ebbinghaus, 1885/1964; Murdock, 1962). The serial position effect refers to the U-shaped function obtained when accuracy is plotted as a function of the serial position of individual items in a serial list memory task. When humans are asked to recall a list of words that have been presented in the same serial order on every trial (serial, or ordered presentation), and they are free to report these items in any order they wish (free recall), they typically report the last items first and are most accurate on these end items (recency effect). They also are more accurate on items at the beginning of the list (primacy effect), with items in the middle of the list being learned more slowly.

There are several proposed explanations for this recency and primacy effects (see Crowder & Greene, 2000; Lewandowsky & Murdock, 1989). Galver (Galver & Cunitz, 1966; Galver, 1972) proposed that the recency effect occurs because subjects report the contents of short-term memory (STM) store immediately at the beginning of the recall period while they are still contained in this time-limited store. The primacy effect in this explanation is based on the transfer of earlier items to long-term memory (LTM) through rehearsal. Items early in the list have more time dedicated to their rehearsal, but as the list lengthens there is less time to rehearse all items and items in the middle of the list are less likely to receive sufficient rehearsal to place them in LTM. Other explanations based on associative mechanisms, interference effects, and distinctiveness have been proposed. Lewandowsky and Murdock (1989) present a comparison of some of the models proposed to explain recency and primacy effects of the serial position effect in humans. Some of these models are based on semantic, hence verbal, attributes of the stimuli. The presence of a serial position effect for list memory in nonverbal organisms should have implications for such theories.

In a study of serial position effects with what they call a "free recall" procedure, Buchanan, Gill, and Braggio (1981) presented a list of lexigrams to Lana, a language (lexigram) sophisticated chimpanzee. Lana was then asked to report the list items by using her lexigram board. She was provided with lists up to eight items, with data reported on 4- to 8-item lists. Lana showed a serial position effect but it was not as extensive as that of humans. Whereas humans show a recency effect for as many as eight items on long lists (Murdock, 1962), Lana's recency effect was limited to the last position. However, she did report that last item first during the report of the list. Lana's primacy effect was also limited to the item in the first serial position, compared to three positions found in long lists with humans (Murdock, 1962). Buchanan *et al.* (1981) suggested that the finding that Lana's primacy effect was limited to the first item did not suggest that rehearsal had taken place. They suggested other possible mechanisms, including distinctiveness of the first position or interference on other early items from items presented later in the list.

Despite the large number of lexigrams from which Lana selected list items, her performance cannot be termed recall. Recall memory is difficult to examine in nonverbal nonhuman organisms, as it requires that the subject generate the list items, rather than simply recognizing them. Fujita and Matsuzawa (1990) developed a procedure with Ai, a lexigram-sophisticated chimpanzee, that allowed her to report a previously presented lexigram by constructing it from its elements. Ai's lexigrams were composed of three elements superimposed on one another. She was presented with a lexigram and, following a retention interval that varied from 0 to 32 seconds, she was provided with the nine elements that comprised the 84 3-element lexigrams used in the study. Her task was to construct the 3-element lexigram that had previously been presented. Ai's performance level varied according to retention interval, ranging from 100% at a 0-second delay to 80% at a 32-second delay.

In a second experiment Fujita and Matsuzawa (1990) tested whether delayed reconstruction of lexigrams would vary according to meaningfulness of the lexigrams. Two sets of novel lexigrams were presented to Ai in the same delayed reconstruction

task described above. Her performance did not differ across the two sets, showing that baseline performance levels for both sets were equivalent. Following that, the lexigrams in one set were each paired with a particular food in a naming task (a procedure designed to impart meaning to these lexigrams) while the lexigrams in the second set were presented in a match-to-sample task that equated experience with the lexigrams in each set. In the delayed reconstruction task, Ai's performance was equivalently high on both of these lexigram sets, with no effect of naming training on performance. Humans provided with the same naming and matching experience prior to delayed reconstruction showed better performance on the set of lexigrams that had been used in the naming task. It is unclear whether the naming lexigrams were insufficiently meaningful to Ai following this particular course of naming training, or whether she simply did not make use of the acquired meaning to facilitate her delayed reconstruction performance. Fujita and Matsuzawa (1990) differentiated the delayed reconstruction task from a delayed recognition task, but did not refer to it as recall memory. It is possible that her performance was based on recognition of individual elements rather than recall of the entire lexigram during reconstruction

Wright and his colleagues (Sands & Wright, 1980; Wright, Santiago, Sands, Kendrick, & Cook, 1985) developed a recognition memory task to address serial memory in nonhuman organisms, including monkeys and pigeons. Their serial probe recognition (SPR) procedure was modeled after a task used by Wickelgren and Norman (1966) in which a list of items is presented followed by the presentation of a single stimulus (probe item) that may or may not have been in the list. The subject's task is to indicate that the item either was or was not included in the list previously presented.

While humans can use verbal responses ("yes" or "no") to indicate, nonverbal animals can be trained to produce discriminative responses. Monkeys were trained to move a lever to the right or left to indicate that the probe item was or was not in the list presented previously; similarly, pigeons pecked a response key on the right or left to indicate that the item had or had not occurred in the list previously presented. Wright et al. (1985) found similar serial position functions in humans, monkeys, and pigeons. They also found that they were able to manipulate the shape of the retention function by manipulating the time delay between list presentation and presentation of the probe stimulus. With a 0-second delay, there was a strong recency effect and no primacy effect in all three species. Increasing the delay served to eliminate the recency effect while improving the primacy effect. These results were similar across species, but with differences in the effective time delay to eliminate recency. For pigeons, that delay was 10 seconds; for monkeys, 30 seconds; and for humans, 100 seconds.

Similarities across species as diverse as birds and primates in an abstract task like serial list memory demonstrate the fundamental nature of particular cognitive phenomena across organisms. The focus of the present study was to explore the nature of the serial position effect in nonlinguistic but cognitively complex organisms. The orangutans who participated in the present study had no linguistic training or exposure although they did appear to understand some spoken English in the context of daily interactions with humans.

The present study was one of a series of studies investigating organization of memory in orangutans (*Pongo sp.*). In a previous study (Swartz *et al.*, 2006) we found that orangutans could learn lists of items presented in a manner similar to that used to present words to humans in a list memory study. Rather than words, the orangutans were presented with photographs of objects. Individual list items were presented successively on a touch-sensitive video monitor. Once the list had been presented, all list items appeared in a random array on the screen along with items that had not occurred in the list (distractor items). The animal's task was to report the list items by touching each of them in any order while avoiding the distractor items. In our initial study, list items were presented in random order on each trial which eliminated the possibility of using serial order to facilitate acquisition. This procedure was followed in order to investigate whether orangutans would develop subjective organization of list items, an organizational strategy similar to that shown by humans under the same conditions (Tulving, 1962).

In that first study, there was no evidence of subjective organization of list items. However, the orangutans did develop a specific response strategy that involved an organized response pattern, but not one based on organizing items, as was expected. Rather, a general strategy was developed based on spatial organization. That is, the animals began each trial at the same general location on the touch screen and reported items in a systematic spatial pattern. Both animals began to search on the right side of the screen and moved progressively to the left, identifying list items as they encountered them. There was no evidence that individual items were searched for as the list was reported. Location on the screen appeared to organize specific responses. This strategy was applied to all novel lists beginning at the 5-item stage for both animals.

Although this strategy was simple, it did provide structure that served to reduce cognitive load by providing a response "anchor" that organized responses. It provided a starting point to which the orangutan returned if an item was missed during the first pass through the list. Although not directed at organizing individual list items during report, the use of the spatial strategy was a cognitive solution to the problem, which provided a structured response path that reduced the cognitive load for the orangutans. Because it is item-independent, this response path could be applied to all novel lists. An item-based organizational strategy might lead to longer acquisition because it would require acquisition of individual items and their relationships based on inter-item associations and/or perceptual similarities. Using this strategy, the basis for organization would change with different lists. The spatial strategy maximizes the use of recognition memory and does not require an overall representation of the list at the beginning of a trial. This reduces the load on reference memory as there is no necessity of planning the list at the start of a trial, and on working memory as there is no need to remember which items had been previously touched.

However, in lists that maintain the same serial order on every trial, the use of order information could facilitate performance. In the present study, the question was whether these orangutans would continue to use the spatial response strategy, or, in light of the robust nature of serial position effects, would shift their response strategy to the use of serial order information to report those lists.

METHOD

Subjects

Subjects were two captive-born female orangutans (*Pongo spp.*), Iris, who is currently 18 years old, and Bonnie, who is currently 29. Both animals live at the Smithsonian National Zoological Park in Washington, DC. At the time they began the study, both had had extensive experience with the list learning procedure used in the present study (Swartz *et al.*, 2006).

Apparatus

The apparatus consisted of a 14-in (36 cm) diagonal Sony color video monitor equipped with a CarrollTouch infrared touch frame. The computer equipment, including the video monitor for stimulus presentation, was enclosed in a 166.52 cm tall x 95.40 cm wide 65.56 cm deep custom-made cabinet. The cabinet's total height was adjustable to allow the screen to appear directly in front of the subject's face. For each experimental session, the cabinet was wheeled up to the enclosure and positioned appropriately for each animal. A wire grid that defined the 25 possible stimulus locations (5 columns and 5 rows) was situated in front of the screen as a template to encourage discrete responses to each stimulus. Animals used a rod to touch the screen, which triggered the touch frame. Stimulus presentation and data collection were accomplished by a Pentium II computer using software written for the project.

Stimuli.

Stimuli were 5.54 cm x 4.45 cm digitized color images of naturally-occurring objects and individuals taken from our extensive collection of digitized images. Those images were obtained from a variety of sources including magazines, books, calendars, and the Internet The general categories that comprised the stimulus set included amphibians, fish, flowers, fruit and vegetables, insects, mammals, mountains, people, rocks, seashells, and general outdoor scenery.

Procedure

The task was a variant of the Matching-to-Successive-Samples task (MTSS; Devine & Jones, 1975) which can also be conceptualized as a list memory or list learning task based on recognition memory. At the beginning of a trial a start stimulus (a blue outline of a triangle that appeared in the center of the screen) was presented. This stimulus remained on the screen until the subject touched it. When the animal touched the triangle, it disappeared and the first list item (sample) appeared in a randomly-determined location, which began the list presentation phase. As the animal touched each list item, that item was high-lighted with a red border, indicating that the item had been successfully touched, then the item disappeared. In the case of lists longer than

one item, another list item immediately appeared at another location on the screen. The list items (samples) were presented one at a time, in randomly determined locations on the screen and in a randomly determined presentation order for each trial, until all list items had been touched.

The report phase immediately followed the presentation and touching of the final list item. All list items were displayed on the screen in a randomly determined array, along with items drawn from the same pool of items as the list items, but which had not been presented in the list (distractors). The animal's task was to touch the list items in any order without touching a distractor item. For Iris, the first touch of each list item produced a green border around that item which appeared briefly and only once for each item. For Bonnie, the green border remained around a stimulus for the duration of the trial once it had been touched. Following the first touch of each list item, additional touches (retouches) were permitted and recorded, but produced no feedback.

Successful completion of the list on each trial was accompanied by a brief chime and the presentation of a small piece of fruit. Touching a distractor stimulus ended the trial with a buzzer and no food reward. Failure to touch a list item during the list presentation phase or to complete a list during the report phase ended the trial with a third sound. A session consisted of 50 trials with the same list items and distractors presented on each trial. Once the animal performed at 70% or higher accuracy in one session, a novel list was introduced in the following session.

Each orangutan was presented with eight novel lists, four of which were ordered and four, unordered. The unordered lists were presented as described above; each trial began with a different randomized order of list items that were presented individually prior to the report phase of the trial. In ordered lists, all items were presented in the same sequence on all trials.

Bonnie was presented with 5-item lists with three distractors and Iris, with 6-item lists with 4 distractors. The number of distractors differed across the two subjects as a function of the training protocol in which number of distractors was increased as number of list items was increased, but the number of distractors was smaller in order to ensure that the longer lists could be more easily acquired. Preliminary analyses from another study (Swartz *et al.*, 2006) showed that there were no differences in acquisition of lists as a function of the number of distractors. Ordered and unordered lists were presented in an ABBA (or BAAB) design in which A refers to unordered lists and B refers to ordered lists. Two lists of each type were presented in each condition. Iris received the ABBA sequence and Bonnie, the BAAB sequence.

RESULTS

Acquisition

Completed trials to criterion (TTC) for each of the four lists in the two presentation conditions were compared for Bonnie and Iris using a paired-samples t-test. There was no significant difference between acquisition of ordered presentation lists and unordered presentation lists for Bonnie [$t(3) = -0.04$, $p < 0.97$] or Iris [$t(3) = 0.77$, $p < 0.50$].

More detailed analyses of acquisition of these lists were conducted to determine whether specific aspects of performance differed across ordered and random presentation. For the first analysis, acquisition of each list was divided into halves and the percentage of correctly completed trials for each half was calculated for each. A summary of these data are presented in Figure 1. For each animal, a 2 x 2 repeated measures ANOVA for list type (ordered presentation vs. random presentation) and half was conducted. The results showed no significant differences in performance between the ordered and random presentation lists [Bonnie: $F_{(1,3)}= 0.16$, $p< 0.72$; Iris: $F_{(1,3)}= 0.04$ $p< 0.85$], and no interaction between presentation type and half [Bonnie: $F_{(1,3)}=0.03$ $p<0.87$; Iris: $F_{(1,3)}= 0.02$ $p< 0.90$] for either orangutan. Both subjects showed significant differences in percent correct between halves [Bonnie: $F_{(1,3)}= 1177.43$, $p< 0.0001$; Iris: $F_{(1,3)}= 56.6$, $p< 0.005$].

The second analysis of the progression of acquisition addressed the number of items each orangutan correctly reported before making an error. A correct trial required correctly identifying all five or six items in a list while avoiding the distractors. Although overall percent correct was usually low on the first day of acquiring a novel list, accurate performance of some list items did occur on many trials. The number of items correctly reported before making an error is indicated by conditional probabilities, which refer to the number of correct items at each point in the list as a function of the
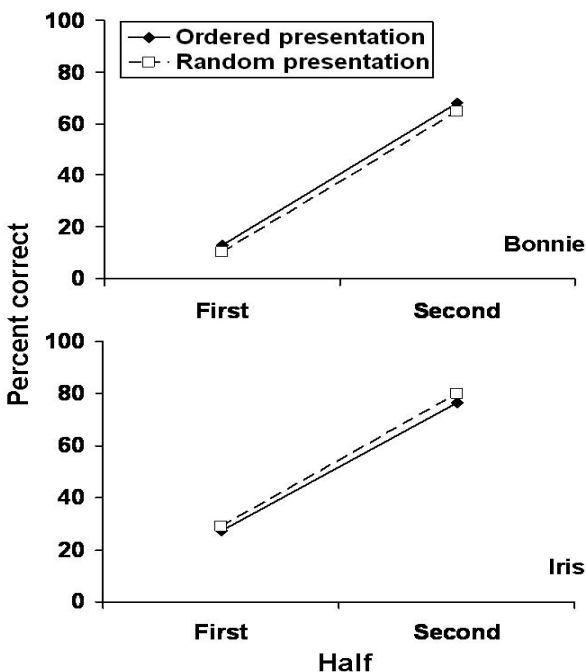

Figure 1. The proportion of correct trials for the first and second halves of acquisition for ordered and random presentation lists are shown in this figure.

number of opportunities to respond at that point in the series. For example, the conditional probability for the first response segment (one item) shows the proportion of correct one-item responses out of the total number of trials started. Given that a percentage of correct responses occurred in the first response segment, the conditional probability of two items consists of the proportion of correct responses in the second response segment out of the total number of possible responses (the number of correct one-item responses).

Figure 2 presents conditional probabilities for correct choices across lists with ordered and random presentation, on the first and second half of acquisition for Iris' 6-item lists and Bonnie's 5-item lists. Three-way repeated measures ANOVAs (2 x 2 x 5 for Bonnie and 2 x 2 x 6 for Iris) on the conditional probabilities for list type, half and response segment were conducted for each orangutan. Neither subject showed a significant difference in conditional probabilities depending on list type [Bonnie: $F_{(1,3)}=$ 0.966, $p< 0.398$; Iris: $F_{(1,3)}= 0.399$, $p< 0.571$]. Both subjects showed a significant effect of first half versus second half [Bonnie: $F_{(1,3)}= 158.507$, $p< 0.001$; Iris: $F_{(1,3)}=$ 23.938, $p< 0.016$] and a significant main effect of response segment [Bonnie: $F_{(4,12)}=$ 48.773, $p< 0.0001$; Iris: $F_{(5,15)}= 16.249$, $p< 0.0001$]. A Tukey's LSD analysis showed that for Bonnie, the conditional probability for Response 3 was significantly different from Response 2, the conditional probability for Response 4 was significantly different from Responses 1 and 2, and the conditional probability for Response 5 was significantly different from Responses 1, 2, 3 and 4. For Iris, the Tukey's LSD post-hoc analysis revealed that the conditional probability for Response 5 was significantly different from Response 4, and the conditional probability for Response 6 was significantly different from Responses 1, 2, 3 and 4.

In addition, both subjects showed a significant interaction between half and position [Bonnie: $F_{(4,12)}= 16.836$, $p< 0.0001$; Iris: $F_{(5,15)}= 8.308$, $p< 0.001$]. A simple main effects analysis of this interaction for Bonnie showed that the conditional probabilities for the first half versus the second half were significantly different for all positions. For Iris, a simple main effects analysis on the interaction between half and position showed that the conditional probabilities for the first half for Responses 1, 2, 3 and 5 were significantly different from the conditional probabilities for the second half.

Serial position

For ordered lists, the percentage of correct responses for each stimulus was calculated to determine if there were any serial position effects. A Friedman analysis of the percentage of correct responses to each stimulus was done for each orangutan. No evidence for a serial position effect was found for Bonnie [$Fr_{(4)}= 1.385$, $p< 0.847$] or Iris [$Fr_{(5)}= 7.667$, $p< 0.176$]. In order to investigate whether a possible serial position effect was obscured by a high level of responding in the last half of acquisition, the percentage of correct responses for each serial position was divided into halves, shown in Figure 3.

For Bonnie, a 2 x 5 two-way repeated measures ANOVA showed a significant main effect of first half versus second half, $F_{(1,3)}= 334.000$, $p< 0.0001$. As the figure shows, performance on the second half was significantly higher overall than performan-

ce on the first half. Bonnie showed no significant main effect for position [$F(4,12)=$ 0.376, p< 0.821] and no significant interaction between half and position [$F(4,12)=$ 0.697, p< 0.608].

Iris showed a similar pattern of results as Bonnie. A 2 x 6 two-way repeated measures ANOVA on her serial position data showed a significant main effect of half, $F(1,3)= 29.671$, p< 0.012, with overall percent correct for the second half significantly higher than for the first half. Iris also showed no significant main effect of position [$F(5,15)= 0.839$, p< 0.545] and no interaction between half and response position [$F(5,15)=$ 0.554, p< 0.733].

Response pattern

The response screen was divided into a 5 x 5 matrix with stimulus location during the report phase randomly distributed across these 25 positions. To determine whether there were any systematic response patterns as the animals reported the list, the column and row locations of each response were recorded. For each of the N responses in a list (where N equals the number of items correctly reported in the list), the proportion of times a response occurred in each row and in each column location was determined. Because stimuli were randomly located on the screen, an even distribution of response locations would be expected. Analyses were performed on response distributions across
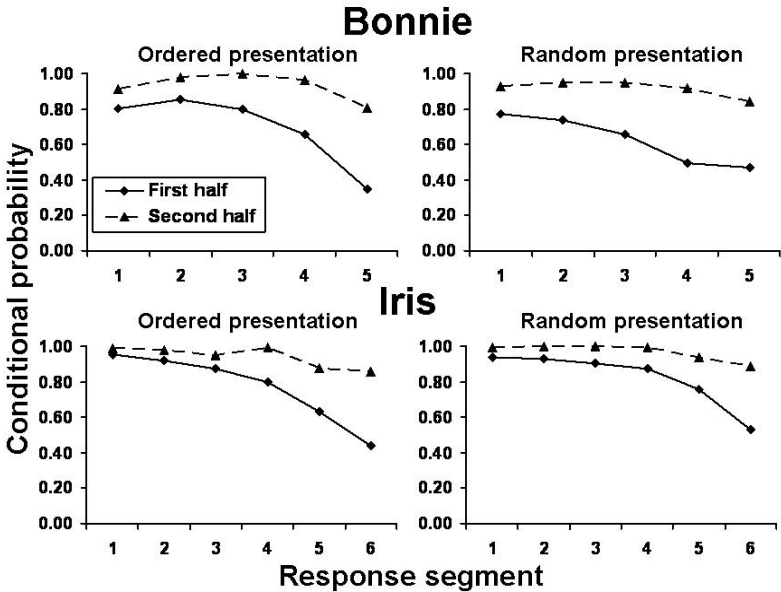

Figure 2. The conditional probabilities of a correct response at each response segment. Conditional probability is the number of correctly reported items as a over the number of opportunities to respond at each point in reporting the list. The data from both halves of acquisition are presented.

columns and across rows for all correct responses, regardless of whether the trial was correct or incorrect. No significant patterns were shown in the row data; however, the analyses of response patterns across columns did show systematic effects.

The proportion of responses to each column at each response segment are presented in Figure 4. To determine if the pattern of responses at each response segment was significantly different from chance (an even distribution of responses across columns), responses were recoded as "left side" if they occurred in the first two columns, and "right side" if they occurred in the last two columns. Data from the third column (the center column) were omitted. A binomial analysis of right-side vs. left-side revealed that Iris showed a significant tendency to touch items on the right side of the screen at the beginning of a trial, and a significant tendency to touch items to the left side of the screen at the end of the trial. This response pattern occurred regardless of presentation type. Bonnie showed the same response pattern as Iris for Random Presentation lists. For Ordered Presentation lists, Bonnie showed a significant side-preference only at the first and fourth responses.
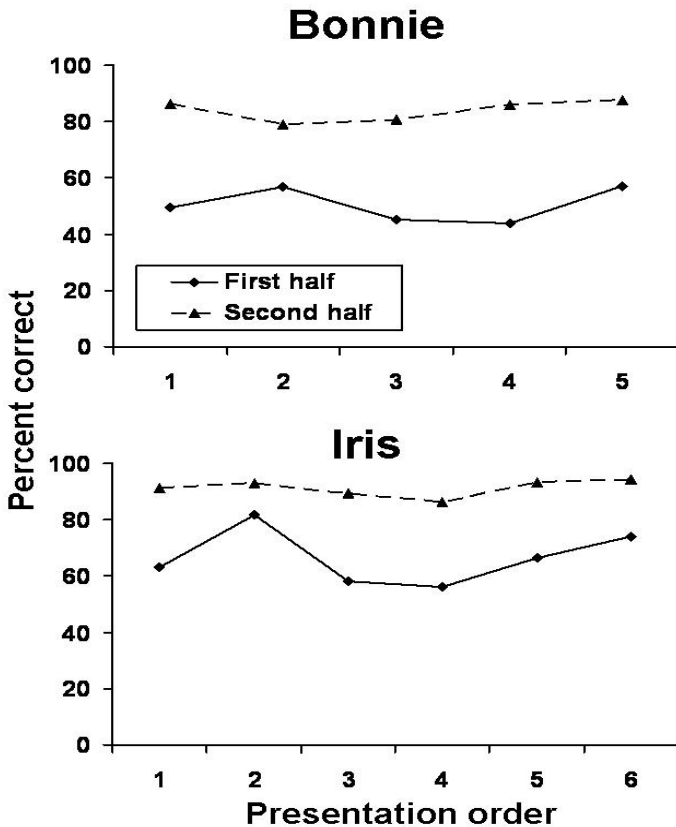

Figure 3. The mean percentage of correct responses at each position for ordered lists for each half of acquisition.
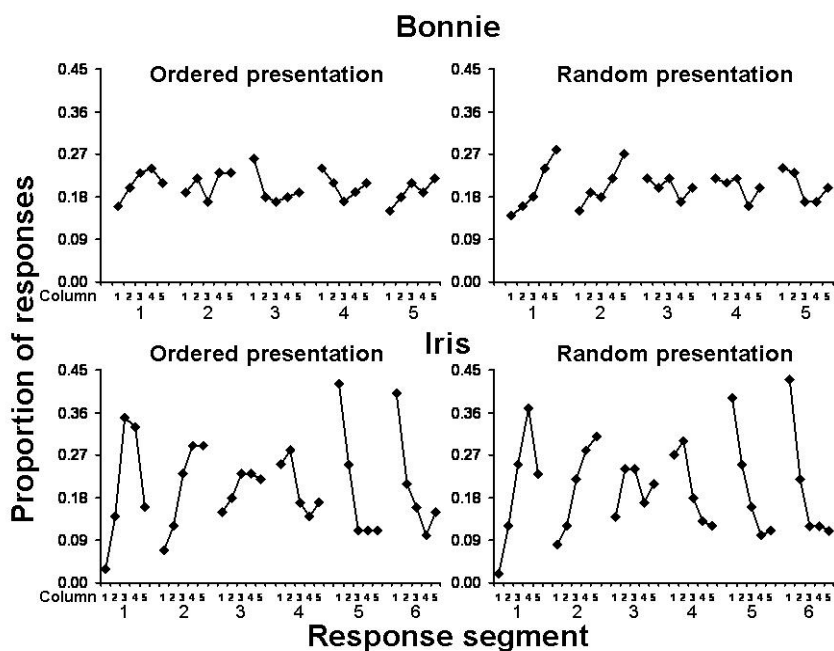
Figure 4. The proportion of responses to each column of the video screen. Columns are numbered 1-5 with 1 indicating the left-most column and 5, the right-most. Response segment refers to each response, from first (1) to last (5 for Bonnie; 6 for Iris) during a trial. All correct responses are included regardless of the outcome of the trial.

Since there appeared to be a difference between Bonnie and Iris' response patterns on this task, the binomial analysis was further broken down for individual lists. These data are presented in Figure 5 for Bonnie and Iris. Instead of a distribution of responses across the five columns (such as the data shown in Figure 4), these figures present the proportion of responses that occurred to the left and to the right side of the screen on each response segment for each of the eight lists learned. The figures present the lists in the order they were learned to illustrate the progression of changes for Bonnie. Iris' data are presented as a basis for comparison. Positions at which the orangutans showed a significant side preference are indicated by black functions, and those positions in which there was no side preference are gray functions.

DISCUSSION

In the present study, acquisition of lists with ordered and random presentations was equivalent with respect to the progression of correct responses. Further, with a global measure of acquisition, TTC, these lists did not differ from one another.

Two noteworthy findings arise from the present study. First, there was no evidence
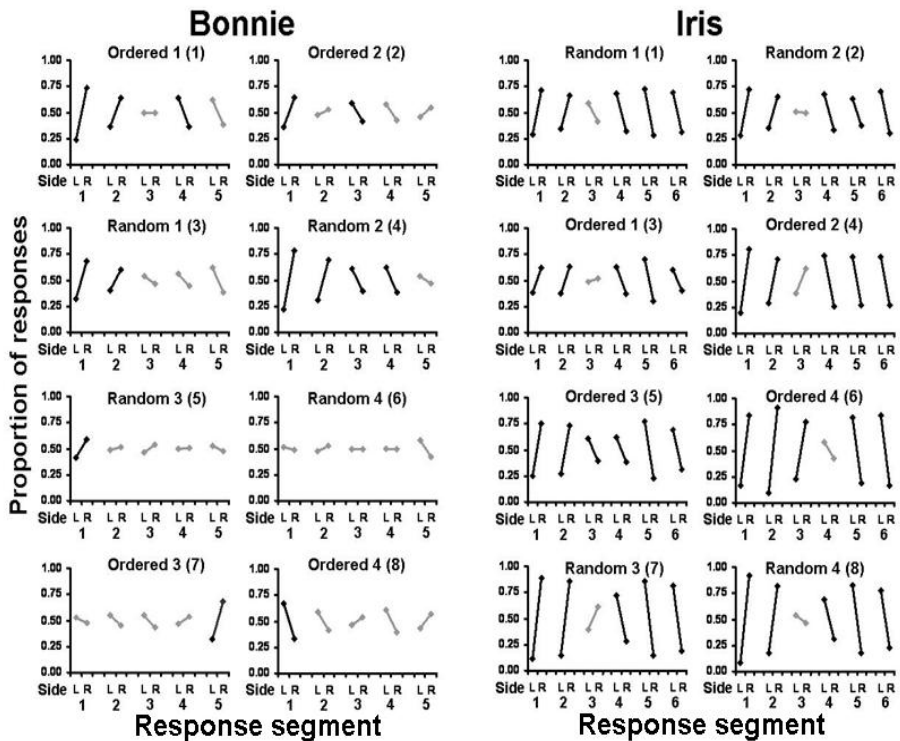
Figure 5. The proportion of responses that occurred to the left-most and right-most columns of the video screen for each response segment. Each list is presented individually, and in the order learned by each animal. Positions at which there was a statistically significant preference are indicated in black, while those that were not significant are gray.

for a serial position effect. Although there have been no previous studies investigating whether the serial position effect is shown in the present task by nonhuman primates, there is evidence that in another recognition memory task, serial probe recognition, monkeys showed a serial position effect that was similar to that shown by humans in the same task (Sands & Wright, 1980; Wright *et al.*, 1985). One major difference between our procedure and that of Wright and his colleagues is that we presented the same list items and distractors on every trial during a session whereas Wright presented a different list on each trial. Clearly, performance of Wright's animals was based on memory for items on that particular trial, and that procedure may have facilitated the use of serial order information relative to our procedure. In particular, the changing order in the random presentation condition of the present study would not be expected to produce a serial position effect.

In our task, a list could have been learned in three possible ways. First, the list items could have been learned during the list presentation phase. In that case, a serial position effect should have been demonstrated on lists with ordered presentation. Second,

the list presentation phase might have been irrelevant to guiding responses during report, and the animals could have been learning the list items through trial-and-error during the report phase by differentiating those items that led to termination of the trial from those that led to reward or continuation of the trial. In that case, there would be no reason to expect a serial position effect with ordered presentation. Third, the list items could have been learned through a combination of both, which might be expected to lead to inconsistent results with respect to serial position.

Neither animal appeared to make explicit use of serial order information. However, the obtained results do not allow disambiguation of the three above possibilities, especially in light of the obtained individual differences across the two animals. Iris used the right-to-left spatial pattern reported in acquisition of previous lists (Swartz *et al.*, 2006). That response pattern was clearly shown by Iris throughout the present study, with both ordered and random presentation. That Iris continued to use this pattern to report lists is not surprising in light of the strength of her right-to-left response pattern as she progressed beyond 5-item lists to acquire 6- and 7-item lists (Swartz *et al.*, 2006).

Second, in contrast to the consistency of Iris' response pattern, Bonnie showed considerable variability in the extent to which she used the right-to-left pattern that she had shown previously with 5-item lists (Swartz *et al.*, 2006). The overall response pattern presented in Figure 4 shows that Bonnie began most trials in the random presentation condition on the right side of the screen but did not progress to the left side as she had previously done. Response patterns on the third to fifth response were flat, suggesting that she did not move systematically across the screen. Further, she showed no consistent overall pattern with ordered lists.

However, analyses of individual lists showed a more variable pattern (see Figure 5). For the first five lists, the only consistent finding is that the first response is most likely to occur to a stimulus on the right of the screen. In our previous study we suggested that the consistent location of the first response provided an "anchor" for the orangutans that allowed them to know where they started on each trial in the event that they lost track of which stimuli had been touched or failed to touch a stimulus as they responded across the screen. This response strategy was independent of the stimuli in each list, as well as the particular configuration of stimuli on each trial. Having a constant starting point reduced working memory load during the report phase. In the present study, Bonnie maintained the first-response anchor on the first five lists. On the last three lists, however, she showed no systematic pattern.

The shift in response pattern following experience with ordered lists might be because Bonnie was influenced by serial order information, which interfered with the formerly-developed response pattern. If this is a transition from one response strategy to another, there may be no clear evidence for either one. The abandonment of the right-to-left pattern did not occur immediately, as evinced by the continuation of the right side location for the first response through the first five lists. It would appear that serial order affected Bonnie's response strategy, but that the abandonment of the previous strategy took place gradually over lists. This change in strategy, while happening slowly, was not specific to presentation condition, as the order of list conditions presented to Bonnie was two ordered lists followed by four random lists and ending with two

ordered lists (BAAB design in which A refers to random presentation and B refers to ordered presentation). The abandonment of the initial response on the right occurred on the last random list and continued through the last two ordered lists, but the overall response pattern was attenuated before that.

This shift in strategy in one animal and not the other may be related to the fact that Bonnie had less experience in using the right-to-left response pattern than did Iris, who had previously applied it to lists longer than five items. For Iris, who had successfully used the spatial response pattern with lists as long as seven items, this strategy remained effective. If Bonnie's shift away from the spatial response strategy was related to the transition to another response strategy, perhaps one that was based on serial position, it would be expected that she will continue to refine the new strategy with additional lists, a question we are currently addressing.

These data represent the first time we have discovered individual differences in strategies developed to solve a complex cognitive task. In our previous studies with rhesus monkeys (Swartz, Chen, & Terrace, 1991; Chen, Swartz, & Terrace, 1997) and orangutans (Swartz *et al.*, 2006) we obtained differences in acquisition rate or final level of performance across individuals. However, in contrast to the findings of the present study, the previously obtained differences were those of quantity rather than quality. The qualitative differences obtained in the present study may reflect fundamental differences across individuals in flexibility or in attention to variables included in lists. A strategy based on spatial position that can be applied independent of the individual list items may facilitate list learning overall, but it may not be efficient in capitalizing on additional attributes of items within the list that can facilitate performance beyond that provided by the more global strategy.

The failure to find evidence for a serial position effect does not provide any insight into the nature of either the primacy or recency effect in the current recognition memory paradigm with orangutans. However, the results do highlight that orangutans develop cognitive response strategies that can be applied to such a task and modified as aspects of the task change.

NOTES

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