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An analysis of immediate serial recall performance in a macaque

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Abstract There has been considerable research into the ability of nonhuman primates to process sequential information, a topic that is of interest in part because of the extensive involvement of sequence processing in human language use. Surprisingly, no previous study has unambiguously tested the ability of nonhuman primates to encode and immediately reproduce a novel temporal sequence of perceptual events, the ability tapped in the immediate serial recall (ISR) task extensively studied in humans. We report here the performance of a rhesus macaque on a spatial ISR task, closely resembling tasks widely used in human memory research. Detailed analysis of the monkey's recall performance indicates a number of important parallels with human ISR, consistent with the idea that a single mechanism for short-term serial order memory may be shared across species.

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Introduction

In research comparing cognition between nonhuman primates and humans, one area that has been of particular interest is the processing of sequences. In humans, the ability to encode and recall sequences of perceptual events is fundamental to language use, and in particular to language acquisition (Baddeley 2003; Martin and Gupta 2004). Thus, an obvious question is how sequence processing in nonhuman primates may compare.

Existing research on this question has revealed a considerable capacity for sequence processing across several primate species (Conway and Christiansen 2001; although see Fitch and Hauser 2004). Studies with monkeys have demonstrated an ability to memorize repeatedly presented sequences of images (Chen et al. 1997; Orlov et al. 2000; Terrace 2005) and locations (Hikosaka et al. 1999), and to immediately reproduce arbitrary sequences of locations (Barone and Joseph 1989; Funahashie et al. 1997) or shapes (Ninokura et al. 2003). And in experiments reported by Matsuzawa and colleagues (Inoue and Matsuzawa 2007; Kawai and Matsuzawa 2000), chimpanzees showed a surprising ability to recall, in the correct numerical order, the locations of briefly presented Arabic numerals.

Despite the richness of such data, there is an important gap in existing research, which limits comparisons between the sequence-processing capacities of nonhuman primates and those of humans in a particularly important domain. Specifically, to the best of our knowledge, there exists no experiment evaluating performance of nonhuman primates under conditions matching those involved in human studies on immediate serial recall (ISR).

Previous research

The majority of studies with nonhuman primates has focused on long-term memory for sequences rather than short-term or working memory, the focus of ISR experiments, or have examined item rather than order recall (Buchanan et al. 1981; Castro and Larsen 1992; Matzke and Castro 1998; Wright 1998; Wright and Roediger 2003; Wright et al. 1984). Memory for items has been evaluated primarily through free recall (e.g., Buchanan et al. 1981) or using probe recognition tasks (e.g., Castro and Larsen 1992; Wright and Roediger 2003; Wright et al. 1984). Results from such studies clearly indicate that non-human primates can retain information about multiple items, presented serially. However, the tasks involved do not require the animal to retain order information.

Petrides (1991) studied the behavior of macaque monkeys in an order judgment task. Here, a series of individual objects was presented, and then two those objects were presented side-by-side. The monkey's task was to select the item that had occurred earlier in the sequence (see Kesner and Novak 1982 for a similar task studied with rats). Although this task required animals to encode the ordinal position of items, interpretation is hindered by the fact that the task was blocked. Specifically, within each block of trials, items from two specific ordinal positions were presented, for example, the first and fourth items from each target sequence. This presentation schedule made it possible, at least in principle, for animals to perform the task by encoding the identity of only one item in each target sequence. For example, in blocks where only the first and fourth items in each sequence were presented as probes, it would suffice to encode the identity of the first item, and to select this item regardless of the identity of the other probe item.

This problem was avoided in studies by Barone and Joseph (1989), Funahashi et al. (1997) and Ninokura et al. (2003), which required monkeys to reproduce entire sequences after a brief delay. However, these three studies share a different limitation. This stems from the fact that the set of sequences used in each study was extremely small. In all three experiments, every sequence was contained the same three items (shapes or locations). As a result, monkeys dealt with a set of only six specific three-step sequences (i.e., *ABC*, *ACB*, *BAC*, *BCA*, *CAB*, *CBA*), practicing with these over the course of several months. This is an important difference from human studies using ISR, where the space of possible sequences is typically very large, with any particular sequence repeating rarely if at all across trials. Even when a closed set of stimulus *items* is employed (e.g., a set of consonants in verbal recall), this set and the list length used are typically large enough to yield a very large set of unique *sequence* stimuli.

Studies with both monkeys and humans studies have shown that, when a specific sequence is encoded and recalled repeatedly, a representation of the sequence becomes established in long-term memory (Conway and Christiansen 2001; Hitch et al. 2005). With massive repetition, sequences can come to be represented holistically, as "chunks" (Graybiel 1998). Clearly, the availability of such holistic representations in long-term memory fundamentally changes the task of serial recall. Specifically, it obviates the need to encode a set of arbitrary, trial-specific relationships between items and ordinal positions, the challenge ISR tasks are typically understood to impose. Use of a large set of target sequences, minimizing repetition of specific sequences, is thus desirable if the objective is to focus on short-term or working memory for sequence information.

The task Matsuzawa and colleagues (Inoue and Matsuzawa 2007; Kawai and Matsuzawa 2000) employed with chimpanzees did involve a large space of target sequences. However, the task differed in another way from the ISR tasks used in most studies with humans. In particular, it did not require the animal to encode a sequence of events, but rather the identities and locations of concurrently presented stimuli. As discussed by Inoue and Matsuzawa (2007), the task could thus, in principle, be performed based upon visual memory for a single display image.

The present work

In order to more directly assay short-term memory for temporal order, we trained a macaque monkey to perform a spatial ISR task. Like the ISR tasks used in studies of human working memory, the task we used involved a relatively large set of target sequences, avoiding massive repetition of any particular sequence. The task involved a fixed set of eight unique target items, and each sequence contained some subset of these. Target sequences of length three and four were presented, meaning that any given trial could involve any among thousands of possible sequences.

Also as in human ISR tasks, target sequences were presented as a series of non-overlapping events, whose order had to be encoded.

The items in our task were spatial locations within a visually presented grid. The monkey was thus faced with a spatial ISR task, very close in design to spatial ISR tasks that have been employed in human studies (e.g., Farrand and Jones 1996; Farrand et al. 2001; Fischer 2001; Fraser et al. 2004; Jones et al. 1995; Smyth and Scholey 1996).

Importantly, the comparability of the task with ISR tasks used in human research placed us in a position to evaluate our monkey's recall performance for several hallmark characteristics reliably seen in human serial recall. In particular, our analyses focused on the following seven effects routinely obtained in human studies:

The list length effect

A basic observation is that recall performance in ISR declines with list length (Crannell and Parrish 1957). In studies of spatial serial recall (Jones et al. 1995; Smyth and Scholey 1996), as in studies using other kinds of stimulus items, recall accuracy at each ordinal position is lower for longer lists. This effect is typically weakest at the earliest list positions, rising progressively thereafter.

Primacy and recency

In human ISR, a recall advantage is typically seen for items occurring near the beginning of target lists (primacy effect). In some circumstances—though, importantly, not all—an advantage is also seen for the last one or two items (recency; Jahnke 1963, 1965). The recency effect tends to be strongest when auditory stimuli are used, and is often absent in studies using visual stimuli, a pattern sometimes referred to as the *modality effect* (Crowder and Morton 1969). Nevertheless, recency has been observed in some studies of human spatial serial recall (e.g., Farrand et al. 2001).

Unlike other effects in the present listing, primacy and recency have been demonstrated in previous studies with nonhuman primates. In particular, each has been observed in numerous studies using serial probe recognition tasks (e.g., Castro and Larsen 1992; Matzke and Castro 1998; Wright and Roediger 2003; Wright et al. 1984). However, it is worth noting that, in human studies, very different serial position curves are obtained in ISR and probe recognition tasks; in particular, a much stronger recency effect is observed in the latter than the former (see, e.g., Avons et al. 1994). To our knowledge, primacy and recency effects have not been previously studied in nonhuman primates in the specific setting of ISR.

Transposition gradients

In human studies of ISR, memory for item identity is typically superior to memory for item order (Bjork and Healy 1974). That is, very frequently, the correct items are recalled but in the wrong order. Importantly, when an item is recalled in the incorrect ordinal position (a *transposition error*), there is a tendency for its position at recall to lie close to its position in the target list (Smyth and Scholey 1996). This tendency of transpositions to span short distances has been labeled the *locality constraint* (Henson et al. 1996).

Item confusion errors

When an item is incorrectly recalled in human ISR, there is a tendency for the item produced to resemble the item that occurred at the same ordinal position in the target list. In verbal recall, the resemblance is usually phonological (Conrad and Hull 1964); in spatial recall, it takes the form of spatial proximity (Hitch 1974). In studies of spatial serial recall, this inter-item similarity effect has been shown to interact with list position. Specifically, the magnitude of spatial errors has been shown to increase with ordinal position (Farrand and Jones 1996; Farrand et al. 2001).

Repetition errors

In human studies, a *repetition error* has typically been defined as the incorrect production, at recall, of an item already produced at an earlier list position. It has been noted that such errors occur in human recall at rates below what would be expected by chance, suggesting that humans keep track of the items they have already produced, actively avoiding repetitions (Henson et al. 1996).

Fill-in

In human recall, when an item is recalled at too early an ordinal position, there is a tendency for the next item selected to be the item that was displaced by the error, a phenomenon known as *fill-in* (Page and Norris 1998). Thus, if recall of the sequence *ABCDE* were to begin *AC*, the next item recalled would tend to be *B*. Both Henson (1996) and Surprenant et al. (2005) noted that fill-in errors in human ISR occur more often than 'infill' errors, where an item recalled early is followed by the item that followed it in the target list.

Protrusions

Another important finding from human ISR is that when an item 'intrudes' from the immediately preceding trial, it tends to be recalled at the same ordinal position it held in that trial, thus taking the form of a *protrusion error* (Conrad 1960; Henson 1996).

In order to further elucidate the relationship between serial order in monkeys and humans, the present study evaluated the ISR performance of a macaque for each of the hallmark effects above.

Methods

Subject

The subject was a 6-year-old male rhesus monkey (*Macaca mulatta*) named Jelly, who was born in the US in 1999 and housed at Northwestern University since 2003. At all times Jelly was housed and cared for according to all federal and

state guidelines. The experimental protocol, including the use of fluid restriction to ensure adequate motivation, and the use of restraint in preparation for planned neuronal recording experiments, was granted approval by the Northwestern University Institutional Animal Care and Use Committee (IACUC). The present experiment is the only one in which Jelly was involved.

Task and materials

The spatial ISR task required encoding, and then sequential selection, of a series of spatial locations. The monkey was seated in a primate chair that allowed free range of arm and hand motion, with his head held stationary in a humane manner (a measure taken in preparation for planned neurophysiological recording experiments). A plastic tube was positioned to deliver juice rewards directly into the monkey's mouth. The task apparatus, including a 15-inch computer display and a small joystick, was positioned directly in front of the chair. On the display appeared a set of nine square targets (25 × 25 mm), outlined in red, arranged in a three-by-three grid (total size 155 × 155 mm). The layout of the display, as well as the basic sequence of events, is illustrated in Fig. 1.

The onset of each trial was signaled by illumination of the center square, which cued the animal to move a blue circular cursor into this square, using the joystick. Success caused the cursor to turn yellow. Cursor movement was then suspended while a subset of the other (outside) squares was highlighted in red, one at a time, for 700 ms each. Target sequences never involved repetition of an item (square), and by the time of testing these sequences were all either three or four items in length. After a further 2,000 ms, the cursor returned to blue, cuing the animal to begin recall, starting from the beginning of the presented sequence. The joystick was used to select a first square, which was counted as acquired when the cursor has been held stationary, inside its borders, for at least 700 ms. Selection of a square caused the cursor to turn yellow and triggered a chime sound, along with delivery of a small (0.1 cc) juice reward, which was received regardless of response accuracy. After an interval ranging randomly between 1,700 and 2,200 ms, the cursor returned to blue, cuing the animal to select the second target.

The trial continued in this same manner until either three or four items were selected (depending on the length of the target sequence). If the sequence selected matched the target sequence, an additional 1 cc juice reward was dispensed at the end of the trial. If, on any step, the monkey failed to acquire a new target within 5,000 ms, a brief auditory cue was triggered, the trial was aborted, and a delay of 1,500 ms was added to the intertrial interval, which was otherwise 1000 ms.

Training and testing procedure

To ensure adequate motivation, Jelly was water-restricted during both training and testing, following procedures

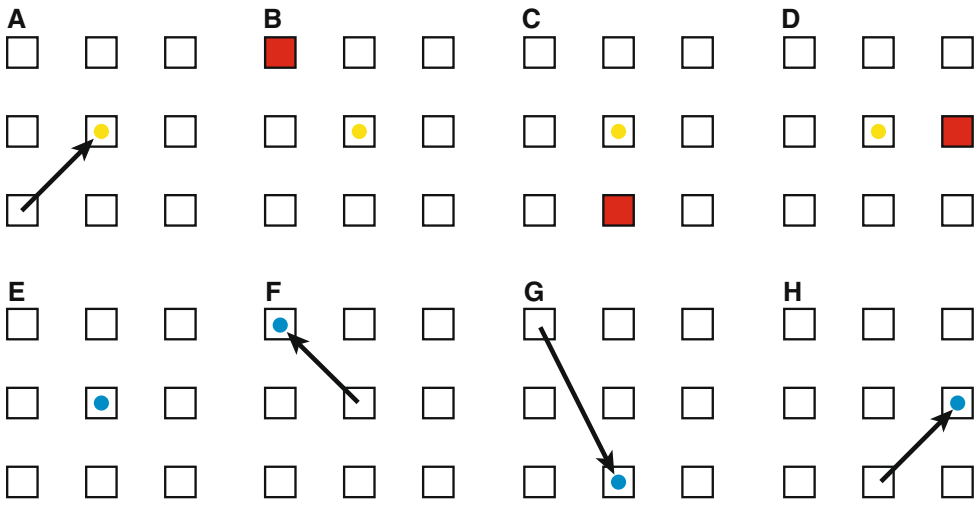

Fig. 1 Spatial immediate serial recall (ISR) task. **a** The onset of each trial was signaled by *illumination of the center square*, which cued the animal to move a *blue* circular cursor into this square, using the joystick. Success caused the cursor to turn *yellow*. **b**–**d** Cursor movement was suspended while a subset of the squares was highlighted in *red*, one at a time, for 700 ms each. **e** After a further 2,000 ms, the cursor returned to *blue*, cuing the animal to begin recall, starting from the beginning of the presented sequence. **f** The joystick was used to select a first square, which was counted as acquired when the cursor has been held stationary, inside its borders, for at least 700 ms. Selection of a square caused the cursor to turn *yellow* and triggered a chime sound, along with delivery of a small (0.1 cc) juice reward. **g** After an additional 2,200 ms, the cursor returned to *blue*, cuing the animal to select the second target. **h** The trial continued in this same manner until either three or four items were selected (depending on the length of the target sequence)

approved by the Northwestern University IACUC. During training sessions, a trial was aborted if the animal selected an incorrect target. In that event, the same target was repeated on the subsequent trial, up to a maximum of 12 repetitions. Training involved gradual incrementation of list length from one to four, as proficiency developed. Testing sessions were performed on separate days. Here, as described above, recall continued until the same number of targets had been selected as had appeared in the target sequence, regardless of recall accuracy, and targets were not repeated. Each testing block, several of which could occur on a single day, contained up to 200 trials. (Testing blocks were terminated at lower trial counts when the daily limit of juice had been dispensed or Jelly failed to initiate a trial for greater than 30 min). Ninety percent of testing trials involved four-item target sequences, ten percent three-item sequences. Target sequences were selected randomly but were never repeated within the same session.

Analysis

The final data set was drawn from 34 testing blocks, involving 468 four-item and 104 three-item trials. Chi-squared tests were used to compare recall accuracy at each ordinal position within each list-length against what would be expected by chance. Chance performance was defined as 0.125 (1/8) at ordinal position one, and 0.143 (1/7) at later positions, given the unlikelihood of selecting the same location on successive steps. Chi-squared tests were used to test for a difference in overall positional recall accuracy between three- and four-item lists and for a difference in recall accuracy across ordinal positions. The frequency of response repetitions—defined, following earlier studies (e.g., Henson 1998), as the incorrect selection of a location already selected at any earlier point in recall—was computed by ordinal position. Transposition gradients were constructed for four-item lists by tabulating the proportion of errors that involved movement of a target item from its ordinal position in the target list to a new position in the recalled list, separating out transpositions involving shifts of one, two, and three ordinal positions (in either direction). A chi-squared test was used to compare the resulting distribution to chance. In this and subsequent analyses, trials involving response repetitions were excluded from consideration, again following earlier human studies (e.g., Henson 1996). Spatial errors were scored by taking the Manhattan distance between each incorrect item and the item that should have been recalled at its ordinal position. The distribution across spatial distances was compared to chance using a chi-squared test, and was compared between three- and four-item lists, as well as across ordinal positions for four-item lists. Rates of fill-in, infill, and protrusion errors (all defined under Results) were quantified as in Henson (1996).

Results

Positional recall accuracy: list length, primacy and recency effects

Positional recall accuracy for three- and four-item lists is plotted in Fig. 2a. Recall accuracy at all ordinal positions within both list-lengths was significantly above chance ($P < 0.0001$ in all cases). Recall accuracy, pooled across ordinal positions, was better for three- than four-item lists, $\chi^2 = 47.70$, $df = 1$, $P < 0.0001$, reproducing the list-length effect observed in human serial recall (Jones et al. 1995; Smyth and Scholey 1996). Recall accuracy differed across ordinal positions, $\chi^2 = 49.63$, $df = 2$, $df = P < 0.0001$ (three-item lists), $\chi^2 = 719.46$, $df = 3$, $P < 0.0001$ (four-item lists), displaying a clear primacy effect, again as in human performance (Jones et al. 1995; Smyth and Scholey 1996). Interestingly, no recency effect was evident. In order to investigate whether a recency effect might be present in reaction times, if not in response accuracies, we computed the onset time for each action on trials involving four-item target lists, defined as the elapsed time between the 'go' signal (change in cursor color) and the onset of cursor movement (relative to a velocity threshold of 7.5 cm/s, approximately 10% of average peak velocity). Like error rates, mean reaction time rose monotonically with ordinal position at recall (449, 491, 544, and 615 ms for positions one through four).

Order errors: transposition gradient

As noted in the introduction, in human ISR, when items are recalled in the incorrect ordinal position, there is a tendency for such transpositions to span shorter distances (Smyth and Scholey 1996), an effect Henson and colleagues (1996) dubbed the locality constraint. The same pattern was observed in the present study. As shown in Fig. 2b, in four-item lists, the proportion of transposition errors that involved a shift of one ordinal position was greater than the proportion involving a two-position shift, and this was in turn greater than the proportion involving a three-position shift. The distribution of errors differed significantly from what would be expected to occur by chance, $\chi^2 = 151.95$, $df = 2$, $P < 0.0001$.

Effects of inter-item similarity: spatial errors

As discussed earlier, in human ISR, items produced in error tend to bear a resemblance to the item that should have been recalled at the same ordinal position, and in spatial recall the resemblance takes the form of spatial proximity (Hitch 1974). In our experiment, as shown in Fig. 2c, when an item was recalled incorrectly, the item selected tended to

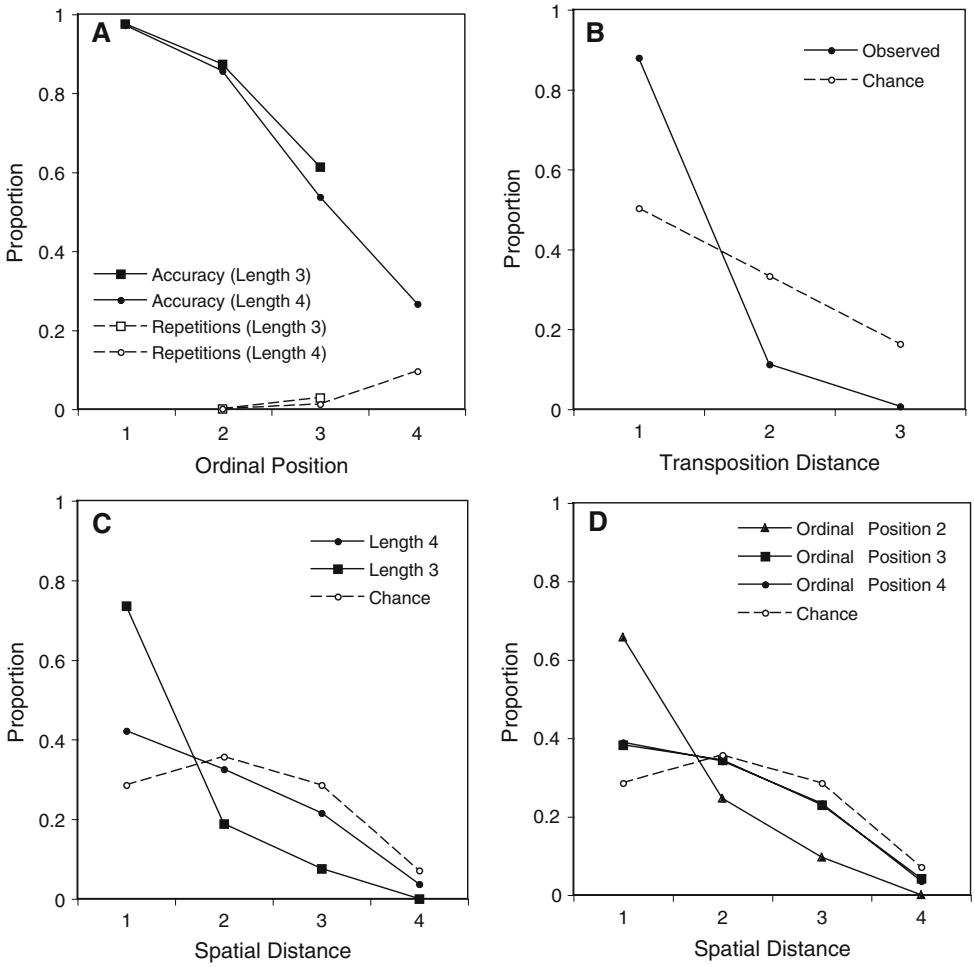

Fig. 2 **a** Positional recall accuracy for three- and four-item lists, and proportion of responses involving a repetition of any item previously selected. **b** Transposition gradient for four-item lists, showing the proportion of errors involving a shift of one, two or three ordinal positions in either direction. **c** The proportion of errors falling at different (Manhattan) distances from the location of the correct response, for three- and four-item sequences. **d** Distances as in panel **c**, but shown separately for the second, third and fourth items selected in four-item trials. Data for step one, where very few errors occurred, are omitted. For clarity, note that the data series for third and fourth items are nearly superimposed

lie relatively near the correct target. The distributions shown in the figure differed significantly from what would be expected by chance, $\chi^2 = 50.11$, $df = 3$, $P < 0.0001$ (three-item lists), $\chi^2 = 63.61$, $df = 3$, $P < 0.0001$ (four-item lists). For both list lengths, item errors were more likely to involve immediate neighbors to the correct target than items farther away, $\chi^2 = 50.43$, $df = 1$, $P < 0.0001$ (three-item lists), $\chi^2 = 58.87$, $df = 1$, $P < 0.0001$ (four-item lists). The tendency to choose near-neighbors was stronger in three-item than in four-item lists, as indicated by a significant difference between the error distributions for the two list lengths, $\chi^2 = 17.69$, $df = 3$, $P = 0.0005$. Consistent with data from humans (Farrand and Jones 1996; Farrand et al. 2001), the magnitude of spatial errors also varied across recall positions ($\chi^2 = 25.61$, $df = 9$, $P = 0.0024$), with the spatial gradient appearing sharper for early ordinal positions than late ones (Fig. 2d).

Repetition errors

Figure 2a shows the proportion of responses that involved a repetition of an item recalled anywhere earlier in the list. The frequency of such errors, as a proportion of all errors, was well below what would be expected by chance, consistent with data indicating that humans avoid repetitions in ISR (Henson et al. 1996).

Fill-in

'Fill-in,' as introduced earlier, refers to the finding that, when an item is recalled at too early an ordinal position, there is a tendency for the next item selected to be the item that was displaced by the error (Page and Norris 1998). The same pattern was evident in our monkey's performance, where fill-in events were more than four times more frequent than infills (46 vs. 10; $\chi^2 = 21.88$, $df = 1$, $P < 0.00001$).

Protrusions

As in human studies, when an item 'intruded' from the immediately preceding trial, it tended to be recalled at the same ordinal position it held in that trial, thus taking the form of a 'protrusion' error (Conrad 1960; Henson 1996). Of 157 between-trial intrusion errors on four-item lists, 51 (32.5%) were protrusions, a rate significantly above what

would be expected to occur by chance, $\chi^2 = 4.30$, $df = 1$, $P = 0.038$.

Discussion

Earlier research has demonstrated a considerable capacity for sequence processing in nonhuman primates. However, previous data do not allow an entirely direct assessment of how short-term memory for temporal order in nonhuman primates compares with that of humans. The present findings fill a gap in the existing literature, by reporting the performance of a macaque on an ISR task requiring a full encoding and reproduction of temporal order, and involving a set of stimulus items large enough to avoid frequent repetition of specific target sequences.

Beyond simply establishing an ability to perform the task at levels significantly above chance, the data also reflect several patterns that are characteristic of human ISR. These include a decrement in positional recall accuracy with list length and a clear primacy effect (see Jones et al. 1995 for analogous effects in human spatial ISR); a transposition gradient consistent with the 'locality constraint' (Henson et al. 1996); spatial errors increasing gradually in magnitude with recall position (Farrand and Jones 1996; Farrand et al. 2001); relative avoidance of repetition errors (Henson et al. 1996); and clear fill-in (Henson 1996; Page and Norris 1998; Surprenant et al. 2005) and protrusion (Conrad 1960; Henson 1996) effects.

The occurrence of fill-in and protrusions in the present study is particularly informative. These two effects have been considered (for example, by Henson 1996) to provide specific support for positional models of short-term serial order memory, in which item representations are transiently bound to independent representations of ordinal position (e.g. Botvinick and Watanabe 2007; Brown et al. 2000; Burgess and Hitch 1999; Henson 1998). There is already strong evidence for positional coding in long-term memory for serial order in macaques (Chen et al. 1997; Orlov et al. 2000; Terrace 2005). The present data indicate that positional accounts of short-term order memory, developed to account for human performance, may also be appropriate for understanding ISR in some nonhuman primates.

Interestingly, in contrast to many ISR studies with humans, and numerous studies using other list-memory tasks with nonhuman primates (Buchanan et al. 1981; Castro and Larsen 1992; Matzke and Castro 1998; Petrides 1991; Wright and Roediger 2003; Wright et al. 1984) no recency effect was evident in our data, either in terms of accuracy or RT. It is important to note that recency is a variable finding in human ISR studies (see e.g., Drewnowski and Murdock 1980; McFarland and Cacace 1995), a point that makes it difficult to draw strong conclusions from its absence in the present study. Nonetheless, it is worth considering some factors that may relate to this result.

A first consideration relates to the stimulus modality used. It is true that recency is typically weak or absent in human ISR studies using visual stimuli such as letters or numbers. However, it is difficult to attribute its absence in the present study to the visual nature of the task, since recency has been observed in human spatial ISR (e.g., Farrand et al. 2001). Furthermore, as just noted, recency has been obtained in monkey studies, several of which used visual stimuli.

Another thought is that recency might have been affected by the fact that steps of recall were interleaved with sequence-irrelevant events, including a tone and a small juice reward. While this is certainly a possibility, it is worth noting that such interleaving has not been found to affect recency in studies of human free recall; indeed, it is a defining aspect of the continuous distractor paradigm used to demonstrate 'long-term recency' (Bjork and Whitten 1974).

An alternative explanation for the absence of recency in the present study can be offered based on the relatively long duration of recall (mean 7.5 s for three-item targets and 10.9 s for four-item targets); in studies of human recall (e.g., Korsnes and Magnussen 1996), recency is sometimes reduced or eliminated when increasing delays are introduced between encoding and recall. In monkeys performing a visual serial probe recognition task, Wright et al. (1984) found that recency declined as the retention interval increased, disappearing altogether at delays in the tens of seconds. Based on these findings, it seems reasonable to speculate that the absence of recency in our study may be a consequence of the relatively long delay between the onset of recall and the production of the final list item. Having raised this possibility, however, it must also be noted that Wright and colleagues, in a different study (using auditory stimuli), actually observed a *growth* in recency with delay (Wright and Roediger 2003). Further clouding the implications of such data is the fact that recency effects can differ dramatically between serial probe recognition and ISR tasks (see, e.g., Avons et al. 1994). In view of these considerations, the absence of recency in the present study must be interpreted with caution. Further work will be necessary to elucidate this particular issue.

Before closing, it is important to acknowledge some limitations of our study. The first, and most obvious, is the fact that we studied only a single animal. This of course makes it impossible to say whether the patterns of recall behavior we observed would also be obtained from other members of the species. We take some reassurance from the fact that numerous previous studies have generated highly useful information about sequence memory, based on experiments with single animals (e.g., Buchanan et al. 1981; Kawai and Matsuzawa 2000; Wright and Roediger 2003). However, the findings we have reported would certainly benefit from

replication in a larger sample. Finally, as acknowledged in various places throughout the foregoing discussion, despite our effort to align the task used with tasks from human studies, several differences remained, including the long duration of the recall process, as well as the inclusion of small (non-contingent) rewards between steps of recall. Further research will be needed before firm conclusions can be drawn concerning the role of such factors in shaping the present results.

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