Memory of Ordinal Number Categories in Macaque Monkeys

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Abstract

■ What mechanism underlies serial order memory? Studying preverbal serial memory shows that macaque monkeys reproducing a sequence of items can acquire knowledge of item ordinal position. In our previous experiment, macaques were repeatedly presented with image lists (first shown sequentially and then simultaneously on a touch screen together with a distractor chosen randomly from other lists). The task was to touch list images in the correct order. The monkeys' natural tendency was to categorize images by their ordinal position or number because their most common error was touching the distractor when it had the same ordinal number (in its own list) as the correct image. Item-to-item associations were used to complete the categorization strategy. Proposing a dynamic image-salience hypothesis for serial recall (based on category-to-image influence and a salience computation for identifying touch targets), we now study the category label characteristics in the context of this hypothesis.

We found that these category labels are absolute, ordinal-number-based categories (first, second, etc.), not relative memorized as relative distance from the beginning and the end of the list, and not based on fixed ranking of reward contingency/image familiarity. Even isolated from item–item associations, the categories demonstrate category tuning (as well as the corresponding overlap of adjacent ordinal number codes). Moreover, monkeys choose images by proximity of their category to the current touch number, irrespective of the accuracy of the preceding choice. Category tuning itself is symmetric relative to correct ordinal position, but is skewed by other factors (reward, etc.). Tuning width increases with list length, with a concurrent increased use of item-to-item associations for determining touch order. ■

INTRODUCTION

A number of recent studies have found that monkeys are able to encode and retrieve ordered lists of up to seven arbitrary stimuli (Terrace, Son, & Brannon, 2003; Orlov, Yakovlev, Amit, Hochstein, & Zohary, 2002; Colombo and Frost, 2001; Orlov, Yakovlev, Hochstein, & Zohary, 2000; Chen, Swartz, & Terrace, 1997; Swartz, Chen, & Terrace, 1991, 2000; D'Amato and Colombo, 1988, 1989, 1990; Terrace, 1986). Monkeys trained on a series of images (e.g., A-B-C-D-E) successfully report the order of a random pair of images, including nonsequential pairs (A-C, B-E, etc.; Terrace et al., 2003; Swartz et al., 1991, 2000; D'Amato and Colombo, 1988, 1990). Similarly, monkeys trained on a sequence of pairs (A-B, B-C, etc.) are able to retrieve the order of any pair (A-C, etc.; Treichler and van Tilburg, 1996). We now ask what mechanism underlies this serial order memory.

Surprisingly, these nonverbal subjects reproduce sequences of items by relying on the memory of each item's ordinal position rather than on chaining and associations between adjacent list items (Terrace et al., 2003; Orlov, Yakovlev, Amit, et al. 2002; Orlov, Yakovlev, Hochstein, et al., 2000; Chen et al., 1997) despite their being highly skilled in generating such paired associations (Erickson and Desimone, 1999; Murray, Gaffan, & Mishkin, 1993; Sakai and Miyashita, 1991). A number of studies showed that monkeys acquire this ordinal position concept during list learning. For example, in a pioneering study, Chen et al. (1997) trained monkeys on several four-item lists (photographs of natural objects), with their task being to touch the subsequently simultaneously presented images in the correct order. When the monkeys had mastered this task, new lists were formed by shuffling the items, taking one from each list, so that in some of the derived lists the ordinal position of the items was maintained, whereas in others it was not. Lists with maintained ordinal position were acquired rapidly and virtually without error, whereas lists with items in changed positions were as difficult to learn as lists with novel items. In another experiment, it was found that after monkeys were trained on lists of up to seven items of photographs, they could immediately report the order of any random pair chosen not only from a given list (Swartz et al., 1991, 2000; D'Amato and Colombo, 1988), but also from different lists (e.g.,

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the first item from List 6 and the fifth item from List 2; Terrace et al., 2003). This transfer to derived lists or pairs supports the conclusion that the monkeys had acquired knowledge about each item's ordinal position.

In a previous study, we addressed the contribution of different mnemonic strategies in the recall of ordered fractal patterns. Monkeys were trained to report the order of several three-item lists of samples shown repeatedly in fixed temporal order (Orlov, Yakovlev, Amit, et al. 2002; Orlov, Yakovlev, Hochstein, et al., 2000). On each trial the monkeys viewed one list, first shown one after another and then simultaneously on a touch screen, together with a distractor image (chosen randomly from the remaining triplets). The task was to touch the simultaneously presented images in their original order, avoiding the distractor. Surprisingly, the most common error was touching the distractor when it had the same ordinal position (in its own list) as the correct image, demonstrating that the monkeys' natural and dominant strategy was to categorize images by their ordinal position in the list. In learning the task, this categorization strategy was established first, and only later did the monkeys attain additional strategies of association memory between adjacent items and sample-stimulus working memory, and these were used only in situations when categorization was insufficient to eliminate the distractor.

Ordinal category assignment is based on an abstract label common to all images of the same category, as shown by the above test with derived lists and the distractor error pattern (Orlov, Yakovlev, Amit, et al. 2002). In addition, when we reassigned the original images to new categories (with images in Category 2 being assigned Category 1, Category 3 to 2, and Category 1 to 3) we found that monkeys needed retraining on these new category assignments. However, after retraining was accomplished on half of the images, we found a degree of generalization that affected subsequent learning of this new assignment to the other half of the set. This finding, too, supports the conclusion that monkeys are able to form an abstract concept of ordinal position that can be generalized to other stimuli. We hypothesized the existence of "category label" neuron populations, which encode separately each ordinal position in long-term memory. Thus, viewing or choosing a particular item in a sequence may be reflected in the activity of two neuronal populations—one representing the individual image (presumably in the inferotemporal cortex; Miyashita & Hayashi, 2000; Yakovlev, Fusi, Berman, & Zohary, 1998; Tanaka, 1997; Miller, Li, & Desimone, 1993; Miyashita & Chang, 1988) and the other representing its ordinal category (presumably located in parietal, prefrontal, or high-order motor areas; Isoda & Tanji, 2004; Ninokura, Mushiake, & Tanji, 2004; Sawamura, Shima, & Tanji, 2002; Clower and Alexander, 1998). However, a mechanism linking item and order memory is yet to be proposed.

Based on these findings and those of the current article, we propose a *dynamic image-salience* hypothesis of serial recall, based on top-down (category-to-image) influence and a salience computation for identifying potential target choices during performance of the serial touch task (see Discussion for details). According to this hypothesis, the ordinal position of the upcoming touch is signaled by ordinal number neurons (perhaps similar to parietal number-selective neurons found by Sawamura et al., 2002). These neurons activate image representation neurons, increasing the salience of images belonging to this particular category. As a result of a salience computation, a single image—represented by the most active neuron population—is foveated and touched. This top-down-mediated image salience is dynamic in that ordinal number neurons are updated after each touch. That is, active populations are inactivated and those representing the following ordinal number become active, shifting salience to the next set of image neurons. Thus, during the course of a single trial, with the same images present on the test screen throughout, each particular image will be highly salient when the animal is about to perform one touch and less salient when it plans another. Dynamic salience may be aided by additional strategies especially when two presented images belong to the same ordinal number category (i.e., in the presence of a distractor). These include working memory of images just seen as samples and image–image associations, that is, enhancement by each image representation of the neurons representing the image that usually follows it.

In the current article, we study category label characteristics in the context of this proposed dynamic salience hypothesis and compare it to a fixed salience alternative. Fixed salience could result from properties such as reward salience or familiarity. In previous studies, these correlated with ordinal position in the sequence. For example, in the above-mentioned experiments of Chen et al. (1997), where knowledge of ordinal position was tested by shuffling lists with maintained and nonmaintained ordinal categories, initial list training was accomplished using progressively longer lists, with one item added at a time. Such training leads to the situation that the degree of reward salience and familiarity will be greater for earlier ordinal categories, that is will correlate with ordinal category number. In other experiments demonstrating ordinal position memory, images from all ordinal categories were presented from the start of training, but trials were aborted following an erroneous touch (Terrace et al., 2003; Orlov, Yakovlev, Amit, et al. 2002; Orlov, Yakovlev, Hochstein, et al., 2000). Thus, earlier categories were again presented more often and they had higher probabilities of being followed by a reward (because each correct touch was rewarded: Orlov, Yakovlev, Amit, et al. 2002; Orlov, Yakovlev, Hochstein, et al., 2000, or was followed by visual/auditory feedback: Terrace et al., 2003).

In all of the above cases, correct image order could have been retrieved without direct memory of ordinal position per se by successively selecting the most salient image while suppressing all already touched images. Furthermore, the two-item subset test becomes trivial even with skips and derived lists: The monkey needs simply to touch the more familiar image of the presented pair. Because image familiarity would correlate with ordinal position, the distance effect (improved discriminability for pairs with more distant ordinal positions; Terrace et al., 2003) may have been a result of the better ability to discriminate between two images as the difference in their familiarities increases. Similarly, the two-item test magnitude effect (slower discrimination between adjacent items in a list as their ordinal position increase) may be based on slower discrimination of equally distant but less familiar items. In fact, monkeys actually used a fixed salience strategy at first, but quite rapidly, they switched to position-based ordinal categories (Orlov, Yakovlev, Amit, et al. 2002).

We now avoid differences in image familiarity and reward contingency by allowing monkeys to proceed with the trial following an erroneous touch in order to test whether fixed-salience categorization is needed, at least at first, to trigger temporal order categorization. We find that monkeys learn just as well, excluding fixed salience as the source of serial recall and proving that the order categories that are established during list learning are indeed memory of ordinal position.

The second issue we address is whether long-term memory of nonverbal ordinal position categories is actually based on ordinal number, that is, on the absolute item position from the beginning of the list (Henson, 1999), or is memorized as relative distance from the beginning and the end of the list. Instead of absolute categories, first, second, third, and so forth, monkeys could learn the relative labels "initial," "intermediate," and "last" for three-item lists. By splitting the "intermediate" category to "closer to initial" and "closer to last" for four-item lists, and so forth, relative categories may serve as an alternative to absolute categories for any list length. Interestingly, using short-term memory recall, Henson (1999) found that humans indeed use relative encoding. We now ask if absolute encoding becomes effective when a long-term memory option is available. To identify which of these encoding schemes is actually used, we use lists of different lengths in the same experiment and test monkeys' categorization abilities in trials when items from lists of different length are intermixed.

To understand the nature of ordinal number category representation, we study its tuning width and shape (symmetry) characteristics. The ordinal number neurons that we hypothesize as guiding the dynamic salience may be similar to those found in experiments where monkeys tracked the number of its hand movements (Sawamura et al., 2002). The tuning characteristics of these neurons would support gradient of category uncertainty in both the forward and backward directions (along the list), and forward–backward symmetry. By excluding factors that bias or mask positional uncertainty (familiarity or reward salience, item–item associations, etc.), we are able to determine fundamental ordinal category tuning. More important, while studying positional errors, we also find evidence for the most basic prediction of our hypothesis—that image salience actually changes during serial recall by activation of its ordinal category.

The final issue of our study concerns the balance among mnemonic routines. As found earlier, item-to-item associations are established in three-item lists but are not used for order retrieval (Orlov, Yakovlev, Amit, et al. 2002; Orlov, Yakovlev, Hochstein, et al., 2000). We expect that the impact of item-to-item chain memory will grow with increased list length, as a result of increased ordinal position uncertainty. We test task performance with longer (four-item) lists, while enabling or disabling access to chain memory, and study monkey post-error behavior by allowing them to proceed with the trial following erroneous touches. If item–item associations guide behavior, one error will lead to another, whereas if monkeys rely on positional memory, they will tend to touch the correct image, even following an error.

In summary, the overall goal of the present set of experiments is to isolate ordinal category memory from other memory strategies that contribute to order retrieval and to study its characteristics in the context of the dynamic salience hypothesis. (Some of these results have been published in abstract form; Orlov, Amit, Yakovlev, Zohary, & Hochstein, 2003; Orlov, Amit, Zohary, & Hochstein, 2003).

METHODS

Subjects and Apparatus

Two adult male macaque monkeys, *Macaca fascicularis* (G, 6.9 kg; S, 6.8 kg) participated in the experiments, which were performed in accordance with NIH and Hebrew University guidelines for use of laboratory animals. We used operant conditioning to train the monkeys on a memory task, giving a fruit juice reward. The monkeys sat in a primate chair 30 cm from a computer color monitor equipped with a touch screen. Trial events, stimulus presentation, and data recording were computer controlled.

Previous Experience

Previously, monkeys G and S were trained to perform a *delayed sequence recall* task with a number of three-item lists of fractal images (Orlov, Yakovlev, Hochstein, et al. 2000). A set of 30 images, divided into 10 triplets,

was presented repeatedly in fixed temporal order. In each trial, the monkeys viewed one triplet, that is, three sequentially presented sample stimuli, followed by a test stimulus that included the previous three images as well as a distractor (chosen from the remaining 27 stimuli), shown simultaneously at random positions on a touch screen. The monkeys were rewarded for touching the three images in the order of their sample presentation, avoiding the distractor, and each correct touch was rewarded with juice. Touching a wrong image (an out-of-order image or the distractor image) terminated the trial and the next trial, with the following triplet, was initiated. As part of shaping towards performance of this task, the monkeys had been presented with three images on the touch screen, and were rewarded for touching them in any order; a repetition terminated the trial.

Stimulus Images

In the present experiment the same monkeys were trained on the similar delayed sequence recall task with quadruplets. We used a set of 24 fractal images, divided into six constant nonoverlapping quadruplets (Figure 1, bottom). Both the order of presentation of images within each quadruplet and the order of the quadruplets were kept fixed. Successive quadruplets from K to P were presented in a repeating cycle: (K1, K2, K3, K4; L1, L2, L3, L4; ... P1, P2, P3, P4; K1, K2, K3, K4; ...). Each trial consisted of four sample images, each with a fixed ordinal position in its quadruplet (first, second, third, or fourth). During each trial, a given quadruplet was displayed twice: first, sequentially, as a sample sequence, with a delay interval separating successive images, and then, simultaneously, during the test presentation (Figure 1, top). Monkeys S and G were trained on different 24-item sets of images, one of which is presented in Figure 1, bottom.

Experiment I: Basic Behavioral Task

The scheme of the basic task is given in Figure 1 (top). Following the appearance of a fixation spot on the screen, the monkey pressed a lever. This initiated presentation of a sequence of four sample stimuli (a quadruplet), in fixed temporal order. Each sample image was shown at the center of the screen for 500 msec followed by a 1-sec interstimulus interval. Then the same four images were presented together at *random* positions on the screen. This test display was a "go" signal for the monkey to release the lever and touch the four images of the sample sequence, in the order of their sample presentation. No distractor was included in the test presentation of the basic task version. It was added

Figure 1. Task scheme and image set. Top: example of trial. Each trial began with a sequential presentation of four images of a given quadruplet. Each sample image was shown for 500 msec followed by a 1-sec blank interval. The subsequent test presentation included the same four stimuli, shown simultaneously at random positions on a touch screen. The monkeys' task was to touch the four images in the order of their sample presentation. They were allowed to perform four touches per trial irrespective of accuracy. Each correct touch was rewarded with juice and erroneous touches were followed by an audio signal. Bottom: 24 fractal images, organized into six constant nonoverlapping quadruplets were used (columns K–P). Each image "belonged" to one of the six quadruplets and also to one of four abstract temporal-order categories, according to its fixed ordinal position in the quadruplet (1st, 2nd, 3rd, and 4th).
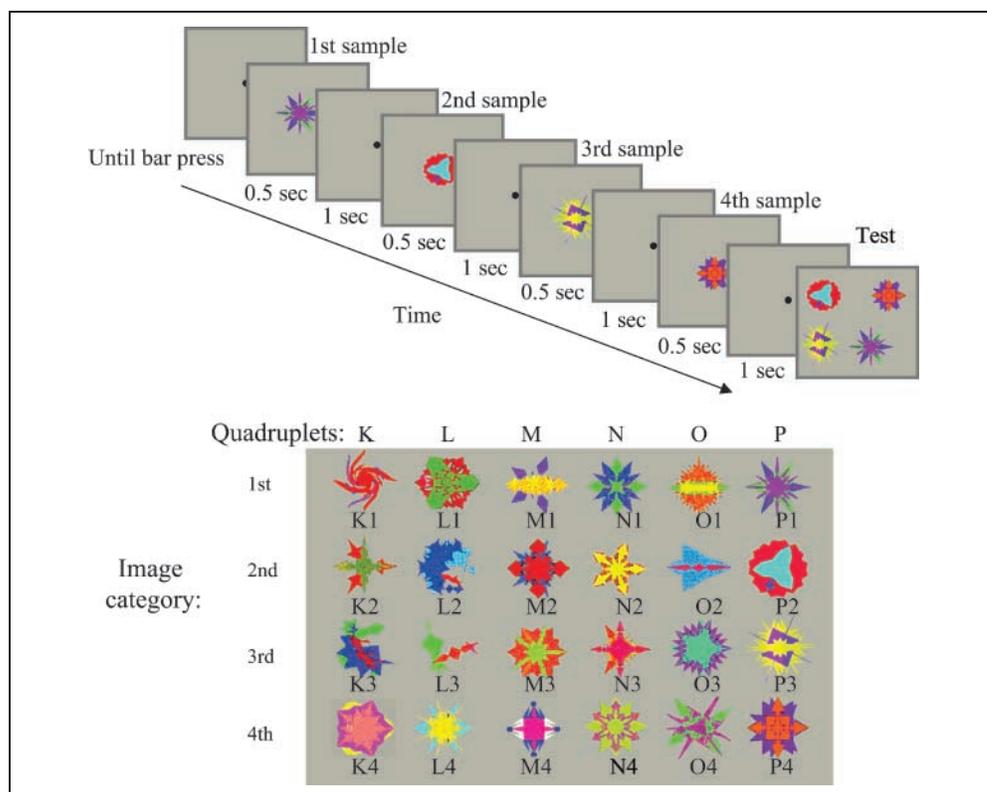
only after the monkeys had reached a high performance level (see below). Monkeys were allowed to perform a total of four touches in each trial, irrespective of their accuracy. The fourth touch terminated the trial, and the next trial, with the succeeding quadruplet was initiated. Each correct touch was rewarded with juice, and erroneous touches were followed by an audio signal. The monkeys performed as many trials as they wished in a given session (one session per day; total number of trials: monkey G: 1018, S: 1058; averaging 170 and 176 trials per quadruplet/image, respectively).

Experiment II: Two-Sequence-Length Test for Category Label Identification

After two-stage training—first with triplets and then with quadruplets—the monkeys successfully learned to retrieve the order of the images and they were tested on a two-length-sequence test (Figure 2A). For this test, they were not presented with sample images, so that working memory of samples was disabled. Furthermore, during the test phase of each trial, four images were chosen from different sequences: Three of them were from the trained triplet sequences (blue circles) and one was from the trained quadruplets (red circles). Target images for each triplet were chosen randomly from different triplets, so that intratriplet associations were also not available. The fourth image was chosen randomly from the quadruplets and introduced as a distractor. The monkeys were rewarded for touching correctly the three images of the shuffled triplet, avoiding the distractor. Note that the monkeys had learned the triplet and quadruplet sequences with an interval of several months and they were not retrained on the triplets before this two-sequence-length testing. Immediately after they finished training with the quadruplets, they were tested with the two-sequence-length test. Monkeys G and S performed 268 and 320 trials, respectively, with distractors from the first to the fourth categories (~67 and ~80 trials per distractor category, respectively).

Experiment III: Task Variations following Training on the Basic Task

We explored the balance between different memory strategies in the basic task with quadruplets *without a distractor* image in the test presentation. Like in the paradigm with triplets (with another pair of monkeys— J and R) we measured task performance, disabling access to one or two of the possible mnemonic routines (Orlov, Yakovlev, Hochstein, et al. 2000). The additional task versions were as follows:

(a) *Trials with no samples*: Touch-order performance was tested in the absence of sample stimuli, thus eliminating the effects of sample working memory. The sample sequence of four images was replaced by a sequence of four gray rectangles, to maintain the temporal structure of the trial (Figure 3A, NS).

(b) *Trials with images shuffled among quadruplets:* The images *within each category* were shuffled to form new quadruplets on each trial. This shuffling maintained the ordinal category of each image but destroyed the internal membership of the integral quadruplet, thus eliminating intraquadruplet associations. The same shuffled quadruplet of images was presented in both the sample and test stages of the trial, enabling use of working memory (Figure 3A, SH).

(c) *Trials without samples and with images shuffled among quadruplets* combined the two previous manipulations, disabling access to both mnemonic routines: The shuffled triplets of images were displayed only during the test presentation (Figure 3A, NS + SH).
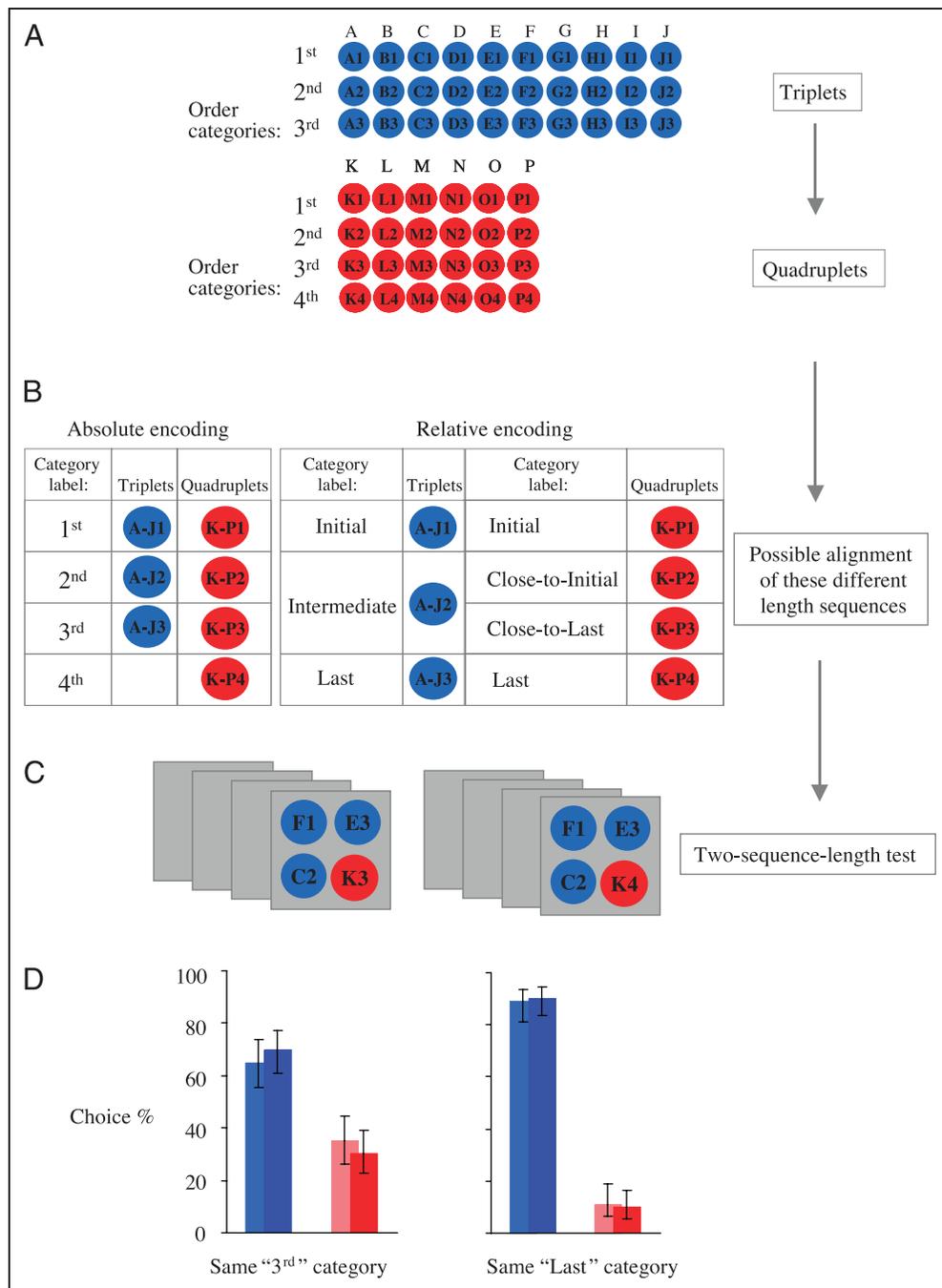
Monkey G and S performed 420 and 240 trials, respectively, with the four task versions (including the basic task, ~105 and ~60 trials per task, respectively; each task version was presented during an entire session, with one session per day). Tasks were presented in the following order: BT → NS → SH → NS + SH, and then BT was presented once again to control general performance.

Experiment IV: Task Variations following Training on the Basic Task in the Presence of Distractor

When the monkeys had learned to touch the quadruplets correctly (Experiments I, II, and III, above; performance > 90% correct for each touch), we returned to the basic task and added a distractor image to the four images in the test stimulus. Monkeys G and S were trained until accuracy of distractor avoidance became significantly greater than random for all touches and average accuracy across all touches reached the level attained in the similar experiment with triplets with monkeys R and J (Orlov, Yakovlev, Hochstein, et al. 2000). Note that monkeys G and S were previously trained on the basic task with triplets but were not tested on the triplet task variations because we felt that this testing might bias the results of the upcoming two-sequence-length test. Thus, to compare properly the tests on task variations between triplet and quadruplet lists, we took into account the results of monkeys R and J when tested with triplets. After a relatively short period of training (300 and 500 trials for monkeys G and S, respectively) on the basic task *with the distractor*, the monkeys were tested on the task variations, as in Experiment III (Figure 3A) in the presence of a

**Figure 2.** Scheme and results of two-sequence-length test. (A) Monkeys were trained successfully on triplets (indicated by blue circles marked A–J) and quadruplets (indicated by red circles marked K–P). (B) If encoding is absolute (left), monkeys would actually label images as first, second etc. If it is relative, they might be categorizing images as "initial," "intermediate," and "last" for triplets or "initial," close to initial,"close to last," and "last" for quadruplets (right). To differentiate between these options, monkeys performed a two-sequence-length test. (C) Two test trial examples are presented schematically. Animals were not shown sample images, so that sample working memory was disabled. For the test phase of the trial, four images were chosen from the triplets and quadruplets, as follows: three targets from the triplets (indicated in blue) and one distractor, randomly chosen from the quadruplets (red). Target images were chosen randomly from different triplets, so that intratriplet associations were not available. Monkeys were rewarded for touching correctly the three images of the shuffled triplet, avoiding the distractor from the quadruplet. Without working memory and intratriplet association clues, we expect many erroneous touches of the distractor instead of the target of the same category. If encoding is absolute, monkeys are expected to err by touching the distractor when it belongs to the same ordinal number category as the correct image, for example, to touch distractor K3 for a third touch (left). If encoding is relative they would confuse correct and distractor images if these stimuli belong to the same relative ("last") category, choosing as their third (and final) touch, distractor K4 (right). (D) Proportion of correct (blue) and distractor (red) image choices for the third touch of the two-sequence-length test. Trials with a distractor from the third (left) and fourth (right) categories were analyzed. Note that monkeys mainly confused correct and distractor images if they belonged to the same absolute (3rd)—rather than to the same relative ("last")—ordinal category. Monkeys S and G: dark and light bars, respectively (error bars, 95% confidence interval for proportions).

A

	A	B	C	D	E	F	G	H	I	J
1st	A1	B1	C1	D1	E1	F1	G1	H1	I1	J1
2nd	A2	B2	C2	D2	E2	F2	G2	H2	I2	J2
3rd	A3	B3	C3	D3	E3	F3	G3	H3	I3	J3

Order categories:

	K	L	M	N	O	P
1st	K1	L1	M1	N1	O1	P1
2nd	K2	L2	M2	N2	O2	P2
3rd	K3	L3	M3	N3	O3	P3
4th	K4	L4	M4	N4	O4	P4

Order categories:

Triplets

Quadruplets

Possible alignment of these different length sequences

Two-sequence-length test

B

Absolute encoding

Category label:	Triplets	Quadruplets
1st	A-J1	K-P1
2nd	A-J2	K-P2
3rd	A-J3	K-P3
4th		K-P4

Relative encoding

Category label:	Triplets	Category label:	Quadruplets
Initial	A-J1	Initial	K-P1
Intermediate	A-J2	Close-to-Initial	K-P2
		Close-to-Last	K-P3
Last	A-J3	Last	K-P4

C

F1 E3 C2 K3

F1 E3 C2 K4

D

Choice %

Same "3rd" category   Same "Last" category

distractor. Note that when we add a distractor to variant (c), that is, for trials without samples and with shuffled images ("no samples + shuffled," Figure 3B, NS + SH), no strategy is available for discriminating between the correct image and the distractor of the same category,

and monkeys were rewarded for either choice. Monkeys G and S performed 1200 and 1400 trials, respectively, with the four task versions and four different distractor categories (~75 and ~87 trials, respectively, per task version with each distractor category).

Figure 3. Behavioral task variants. Top: schematic illustration of specific trial image set for the different task versions, with (right) and without (left) shuffling. K, L, ..., P correspond to the quadruplets of images; 1st, 2nd, 3rd, and 4th correspond to the ordinal number categories. White circles: images to be touched; black circle: distractor. (A and B) Schematic diagrams of an example trial for each task variant in the absence (A, Experiment III) or presence (B, Experiment IV) of a distractor image. Without a distractor (A), sequence order categorization suffices for performance of the task for all task variants, but in (B), discriminating between the correct image and the distractor requires an additional strategy, as illustrated below. "Basic task" trial (BT): a quadruplet of fixed-order images is presented: for example, M1, M2, M3, M4. In (B), besides identifying the images of the first category, the monkey also needs to discriminate between the correct image, M1, and the distractor, L1, for its first touch. This illustrates a choice between images that belong to the same
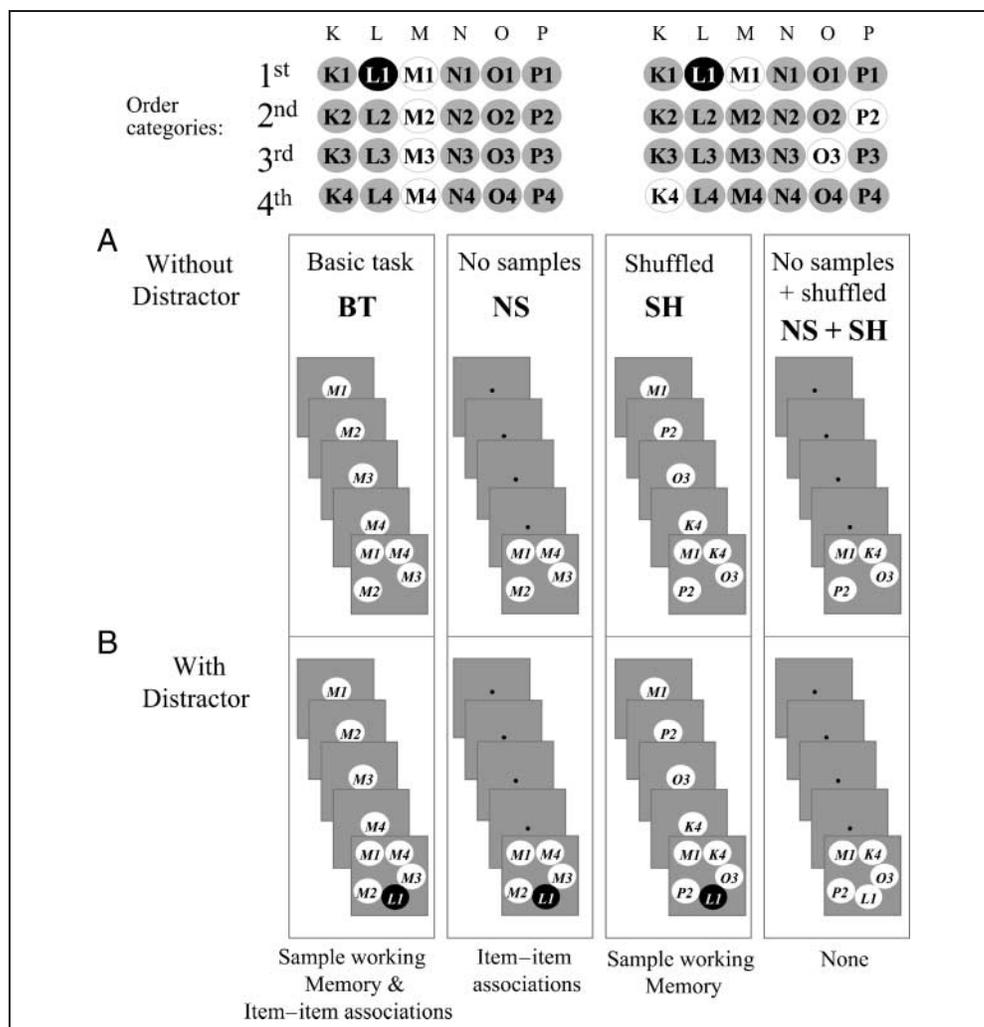
ordinal category. Two supplementary strategies are available: Working memory: M1 just appeared as a sample stimulus while L1 did not. Associations: because the same quadruplet was shown over and over again, associations between quadruplet members could be used to avoid the distractor. "No samples" trial (NS): The four-sample image sequence is substituted by four successive blank rectangles and images are only shown simultaneously in the test phase so that working memory is unavailable. However, the integrity of the quadruplets is maintained. The monkeys can therefore differentiate between the correct image and the distractor belonging to the same category on the basis of associations between successive images formed during the learning stage. "Shuffled" trial (SH): Item–item associations are precluded by presenting images from different triplets (e.g., M1, P2, O3, K4) while maintaining the correct category order. The correct choice can be made using sample working memory. "No samples + shuffled" trial (NS + SH): Combining both manipulations, no strategy is available for discriminating between stimuli from the same category (in fact, there was no difference between correct and distractor images in this case, and monkeys were rewarded for either choice from the correct ordinal category).

RESULTS

Is Category Encoding Ordinal-number Based (Absolute) or Relative?

If encoding of the image ordinal position is absolute (ordinal-number based), monkeys would actually label images as first, second, third, and so forth. If encoding is relative, with image ordinal position remembered in terms of relative distances from the beginning and the end of the sequence, category labels might more accurately be termed "initial," "intermediate," and "last" for three-item lists and "initial," "closer to initial," "closer to last," and " last" for four-item lists. To differentiate

between these possibilities we trained two monkeys that had participated in the experiment with triplets on six four-item sequences, shown in Figure 1. (See below, Methods, and supplementary material.) When they reached a constant level of 85–95% correct performance, we tested them on the two-sequence-length test. The scheme of this experiment is shown in Figure 2A–C. We reverted here to the triplets that the monkeys had previously learned and added a distractor image from the quadruplet sequences.

As we had done before (Orlov, Yakovlev, Hochstein, et al., 2000), we tested the monkeys without showing them sample images and shuffled the images among the

triplets; that is, the three images were chosen randomly from different triplets, making sure, however, that there was one image of each category (Figure 2A and C, blue; see also Figure 3, no samples + shuffled paradigm, NS + SH). Thus, the only strategy left for determining image touches was retrieval of ordinal number categories. The monkeys were rewarded for touching correctly the three images of the shuffled triplet, avoiding the distractor. Without sample working memory and intra-triplet association clues, we expect many erroneous touches of the distractor instead of the target of the same category. But how are the categories of triplets and quadruplets related? The following options are possible: If triplets and quadruplets do not share common ordinal labels, we predict random distractor choices, irrespective of the relationship between image and distractor category ordinal numbers. If they share *absolute* labels (Figure 2B, left), the monkeys are expected to touch the distractor when it matches the ordinal number category of the correct image, for example, to touch distractor K3 for a third touch. On the other hand, if triplets and quadruplets share *relative* order labels (right), the animals would be more likely to choose as their third (and final) touch, distractor K4.

To differentiate between these possibilities, trials with a distractor from the third and fourth categories were analyzed. Graphs of Figure 2D show the proportions of correct (blue) and distractor (red) choices during the third touch of each monkey in such trials. The percent distractor choice is significantly larger, and performance accuracy lower, for either monkey if a distractor from the third category was present than if a distractor from the final fourth category was present ($p < .01$ for correct and distractor choices of both monkeys, z test for proportions). Hence, it is clear that monkeys mainly confused correct and distractor images if they belonged to the same absolute (third) rather than to the same relative ("last") ordinal category. We conclude that images belonging to triplets and quadruplets share common ordinal category labels (even when these were learned with different reward schedules); and that these categories are based on ordinal numbers (absolute position) for three- and four-item item lists.

Identification of Strategies Underlying Retrieval of Quadruplet Image Order

To preclude the option of classifying images according to their fixed salience from the onset of learning we changed the reward schedule of the basic task so that the monkeys were allowed to make four touches on each trial, irrespective of their accuracy, preventing differences between reward contingency/familiarity of images (see Supplementary Material). We ask: Would monkeys categorize images according to their ordinal number with the new schedule? In addition, in the experiment with three-item lists, retrieval of ordinal

categories was the crucial strategy for recall of image order. We now increased the list length and asked if this categorization strategy is still dominant with quadruplets? To answer these questions, we reexamined the categorization phenomena and the contribution of different memory strategies (categorization, item–item associations, and working memory of samples) in retrieval of image temporal order of four-item lists. The approach used here was the same as that of the paradigm with triplets: we measured task performance, disabling access to one or two of the possible mnemonic routines (Orlov, Yakovlev, Hochstein, et al., 2000).

We first tested monkeys without a distractor image in the test presentation so that any changes from performance with triplets (with a distractor) to quadruplets (without a distractor) could not be due to a change in the number of items on the test screen: There were always four items on the screen. Then we added to the test presentation a distractor image, chosen randomly from among the other quadruplets, to test performance when the distractor was from the same, or from a different category as the image to be chosen. Again, training was first done on the basic task, and then the monkeys were tested on the different task variants. They were examined with and without a distractor: (1) in the absence of sample stimuli (eliminating the effects of sample working memory; "no samples" paradigm; Figure 3A and B: NS); (2) with the images shuffled within each ordinal category (disabling associations between quadruplet members; "shuffled" paradigm; SH); and (3) without samples and with images shuffled among quadruplets, combined the two previous manipulations (disabling access to both mnemonic routines so that the only strategy left was retrieval of ordinal categories; no samples + shuffled paradigm; NS + SH).

Figure 4A (top) describes monkey behavior for the different versions (with a distractor of the same category [left], of a different category [center], or without a distractor [right]), comparing this performance to that of two other monkeys (J and R) who performed the same versions of this task with triplets (Figure 4A, bottom; see Orlov, Yakovlev, Hochstein, et al., 2000). An ANOVA revealed significant effects for main factors: distractor category (same vs. different, $F = 38, p < .001$); task type ($F = 13; p < .001$), and touch number ($F = 3; p < .05$), but not monkey identity. The only significant interaction term was Distractor Category × Task ($F = 3; p < .05$), reflecting a greater difference between task variants for the same cases or a greater difference between same and different for the shuffled task variants. Together these factors accounted for 93% of the total performance variance. The same factors were significant in the performance data of J and R on the triplet task.

The main effect of distractor category reflects the finding that the most common error for all task versions with quadruplets was touching the distractor if it belonged to the same ordinal category as the correct

Figure 4. Contribution of different mnemonic strategies to the ordered recall of quadruplets compared to triplets. (A and B) Monkey touch choices following task manipulations *with* (left and middle) *and without* (right) the presence of a distractor, averaged across touches/ monkeys. Same and different: distractor is from the *same* category as the correct image and from a *different* category, respectively. Upper graphs: quadruplet task (monkeys S and G); bottom graphs: triplet task (J and R; Orlov, Yakovlev, Hochstein, et al., 2000). Task versions as in Figure 3. Error bars, *SE*. (A) Gray, dark, and white bars indicate percent choice of correct, distractor and other images. Note that in the triplet task we aborted the trial after any mistaken touch so that all errors were the first in the touch sequence. For the quadruplet task, monkeys were allowed to continue making touches even after an error. To properly compare performance of different list sizes, we selected for analysis

only distractor choices, which were first errors in the quadruplet touch sequences, as well. (B) Contribution of intralist associations (black line) and sample working memory (gray line) as a function of touch number. We plot the absolute difference of the percent image choice between trials with a strategy active and trials when it is disabled. Thus, for the association strategy, we compare "basic task" and "no samples" trials versus "shuffled" and "no samples + shuffled" trials. This strategy is used for triplets only for "same" trials, and for quadruplets also for "different" trials, for intermediate touches. For the sample working memory strategy, we compare "basic task" and "shuffled" trials versus "no samples" and "no samples + shuffled" trials. This strategy is used only for the first touch and only for "same" trials. (Asterisks indicate significant impact for strategy/touch pair).
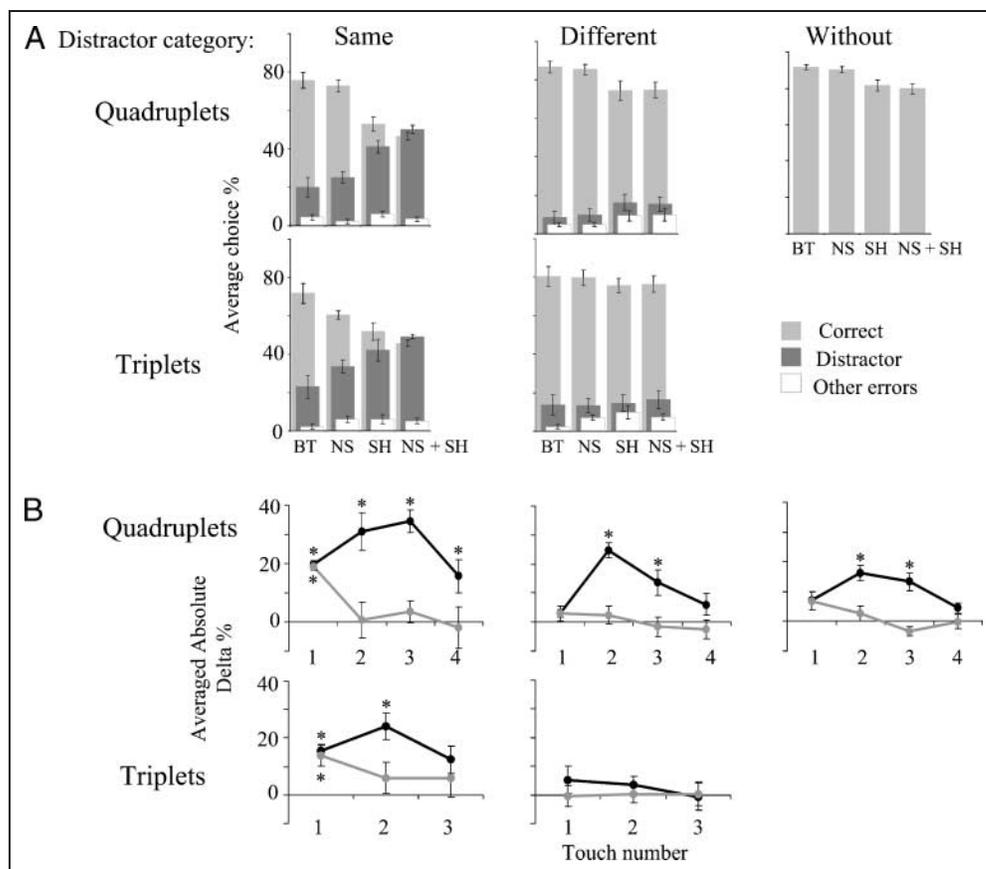
image (Figure 4A). The main effect of task type reflects the degradation of performance with removal of the associations or working memory strategies, and especially for removing them both, leading to chance (50%) performance for "same" trials; (in fact, there was no difference between correct and distractor images in this case, and monkeys were rewarded for either choice from the correct ordinal category). The average sum of these choices exceeded 90% suggesting that the monkeys knew well the correct ordinal category of these images but they had no strategy available to discriminate between the two exemplars of the same category and to eliminate the distractor image. This behavior in the presence of a distractor provides clear evidence that monkeys categorize images of quadruplets according to their ordinal position. We conclude that ordinal number categories can be developed in conditions when a trial is not stopped after an error.

Figure 4A demonstrates that the categorization strategy is *crucial* and nearly sufficient for retrieval of quadruplet order. That is, when the correct item and

the distractor differed in ordinal category, memory of the samples and intraquadruplet associations provided only moderate additional benefit in average performance irrespective of distractor presence/absence. That is, performance was high (mean error rate $\pm$ *SE*: $77 \pm 4\%$ and $80 \pm 3\%$; with and without distractor, respectively) even with both of these strategies disabled, leaving only the ordinal number categorization strategy (Figure 4A, top, middle, and right columns, NS + SH trials).

A detailed picture of the separate effects of item–item associations and sample working memory on image order retrieval is seen in Figure 4B as a function of the touch number, which the monkey is currently performing. This figure demonstrates that while categorization suffices for nearly perfect performance, associations between items contribute significantly to order retrieval in the middle of four-item lists, but not with three-item lists (Figure 4B, middle and right columns, black line). That is, disabling associations in tests with (Figure 4B, top middle) or without a distractor (Figure 4B, right) mainly hampered recall of images for the second and

third positions (average difference ± SE with a distractor: 25 ± 3% and 14 ± 4%; ANOVA, $p < .001$ and $p < .05$, respectively; without: 16 ± 2% and 13 ± 3%; $p < .01$ for both). The effect of presentation of the sample images on order retrieval was not found (Figure 4B, middle and right columns, gray line) in any touch. Nevertheless, monkeys use both additional mnemonic routines for distractor elimination (i.e., in the "same" case) in quadruplet list tests as with triplet lists. Disabling associations decreased performance for all touches (Figure 4B, left, black line: 16–34%; ANOVA, $p < .001$ for the second and third touches; $p < .05$ for the first and fourth touch) and disabling working memory mainly affected the first touch (Figure 4B, left, gray line: 18.9%; $p < .05$).

We conclude that (1) categorization is still the dominant strategy in establishing image order in four-item lists, but item–item associations contribute significantly to order retrieval in the middle of the list so that the dominance of the categorization strategy is not as complete as with three-item lists; (2) the impact of association memory is not a result of a change in the number of items on the test screen; (3) monkeys use both additional mnemonic routines—item–item associations and working memory of samples—for distractor elimination in either list. The associative strategy was similarly helpful in every touch but the effect of sample working memory was mostly restricted to its influence on the first touch.

Tuning of Ordinal Category Memory

To evaluate tuning of ordinal category, we studied the uncertainty of item category memory, focusing on errors made when touching the distractor rather than quadruplet items in the wrong order (see below). An initial, dichotomous analysis of distractor choices was helpful above in examining the categorization strategy, when we found that the distractor image was chosen when it belonged to the "same" ordinal number category as the correct image to be touched and ignored if it was from a "different" one. We now analyze in more detail the different case, and find variability in the statistics of the degree of avoiding it. As Figure 5A shows, the most

Figure 5. Monkeys' categorical choices as a function of distance of positional error. (A) Percent of distractor choices in the 1st to 4th touches, as a function of distractor category. (B) Gray line: the same distractor choices as a function of distance between correct category and category of distractor actually touched. Distance 0 indicates that distractor and correct image belong to the same category (e.g., touching distractor F2 during the second touch). Other distances correspond to "different" cases. Negative distances specify backward errors (e.g., touching distractor F1 during the second touch), while positive ones correspond to forward errors (e.g., touching distractor F3 during the second touch). Black line: average distractor choices following normalization, that is, multiplying by the fraction
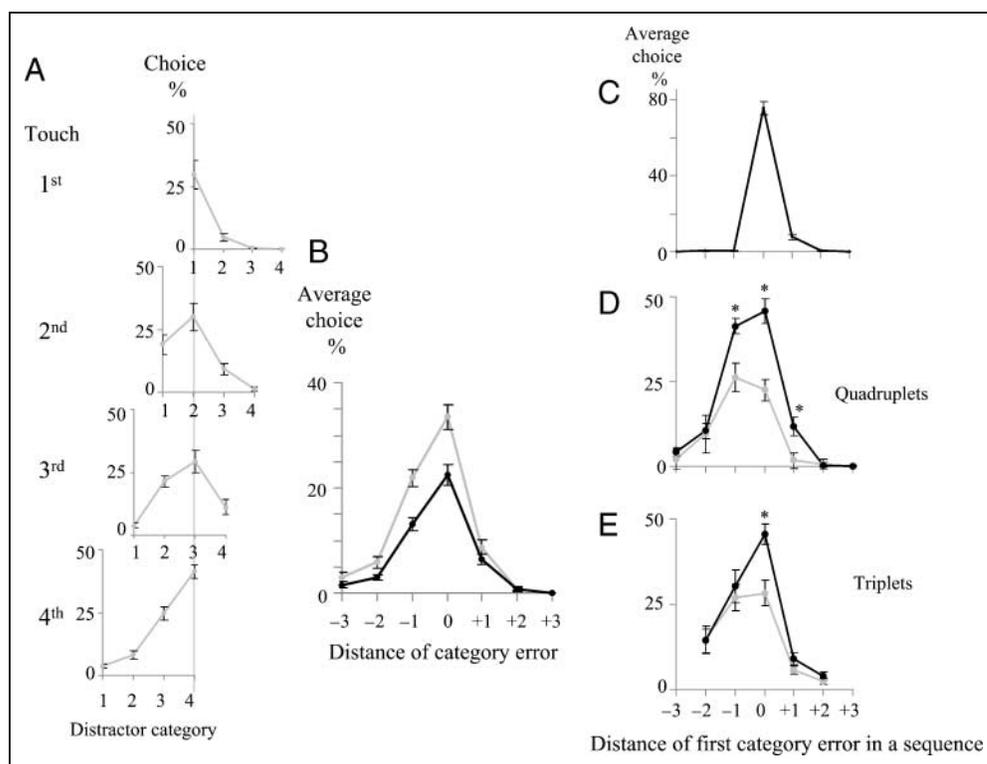
of items on the screen not ruled out by inhibition of return. (Data are averaged across task versions/monkeys; error bars, *SE*). (C) Positional uncertainty curve based on first errors made in the touch sequence—by touching the wrong *list member*. Distance 0 indicates touching the correct image, while negative and positive distances specify backward and forward errors, respectively (e.g., touching the 1st or the 3rd quadruplet member for the second touch). Note that the inhibition-of-return strategy eliminated backward errors in this case (distance −1; item repetition), whereas the distractor positional errors (A, both lines) are present in both directions. That is, monkeys made repeat touches of the same ordinal category with another exemplar of the category, but did not touch the same image twice. (D and E) Proportion of *distractor choices* for different distance errors in trials with item–item associations active ("basic task" and "no samples," gray) or disabled ("shuffled" and "no samples + shuffled," black), for task with quadruplets (D) or triplets (E). Note that we only took into account distractor choices that were first errors in the touch sequence. Asterisks denote significant differences (ANOVA, $p < .005$ for all differences).

commonly chosen distractor category is that of the correct image touch, reflecting the categorization strategy. At the same time, choice of a nonmatching category depends on the numerical distance of this category to the correct one: Distractors from adjacent categories confuse the monkey much more than remote ones.

Figure 5B (gray line) presents the percent of distractor choices, averaged across touches as a function of distance error. Erroneous choices cluster around the correct ordinal category and the probability of a choice declines gradually with increasing distance from the correct category, suggesting a positional uncertainty gradient in judging image ordinal position, in both the forward and backward directions along the sequence. Even though ordinal position encoding is imperfect, its fuzziness is mostly restricted to touching the nearest forward or backward category. Disabling the item-to-item association strategy, which is relevant for ordered retrieval of quadruplets, influences selectively the proportion of category errors at different distances. Figure 5D and E exhibits the percent of distractor choices in trials with item–item associations active (gray line) and disabled (black line). Disabling associations—hampering categorical judgment in quadruplets (D) but not triplets (E)—leads mainly to choosing an adjacent ordinal category in the forward or backward direction (ANOVA, $p < .005$ for both).

Why do we rely on the distractor categorical errors? Monkeys rarely returned to images that were already touched during the trial (e.g., touching the first image again as the second touch or touching the third image correctly after touching it in error as a first touch), most probably keeping in memory their identity and/or location. We call this an ''inhibition-of-return'' strategy, which in general is useful for list retrieval, helping to produce sequential choices (see Supplementary Material). It severely diminished the rate of backward errors (item repetitions) leaving intact the forward ones (skips of a correct list item; Figure 5C). However, the distractor positional errors are free of this bias; that is, monkeys that strongly avoid repeat touches of an individual image easily make repeat touches of the same ordinal category with another exemplar (Figure 5A, B, D, and E). Thus, the key feature of our paradigm, the presence of a distractor during the test phase of the trial, which also has the ordinal category assignment similar to the list members, allowed us to acquire all types of category errors and to estimate category tuning.

In summary, we found uncertainty in judging image ordinal category, which declined with increasing forward or backward distance from the correct category. Nevertheless, the fuzziness of the category encoding is mostly restricted to touching the nearest forward or backward category. These specific errors are the main targets of applying the intraquadruplet association strategy. This ordinal category tuning (and correspondent overlap of

adjacent number codes) is independent of item–item associations.

Tuning Asymmetry of Ordinal Category Memory

Returning to Figure 5B (gray line), it is apparent that the uncertainty gradient is not symmetric: monkeys tended to make more backward positional errors (''−1, −2, −3'' touches, including category repetitions by choosing another exemplar of a category already touched) than forward errors (i.e., category skips). For example, when monkeys touched correctly the first quadruplet member for their first touch, then, for their second touch, they often had a tendency to choose the distractor if it was from the same first category (19%), and less so if it was from the third category (9%). We now study possible sources of this asymmetry.

Because later touches allow more negative distances, while earlier ones allow more positive distances, this asymmetry could be a result of the inhibition-of-return strategy (see above and Supplementary Material). That is, by using this strategy alone, the chance of touching each of the as yet untouched images on the screen for the first to fourth touches gradually increases (and is 20%, 25%, 33%, and 50%, respectively). Figure 5B (black line) denotes the average normalized distractor choices, taking into account this varying chance level; normalization was equivalent to reducing the number of items on the screen to those not ruled out by inhibition of return. Clearly, the resulting error rate at *each* negative distance is still significantly larger than at the equivalent positive distance (ANOVA, $p < .002$ for each distance). Item-to-item associations may prevent this asymmetry (i.e., touching correctly category 2 may initiate recall of the next category 3 but not category 1). However, the asymmetry is present with (Figure 5D, gray line) or without (black line) these associations.

Because each correct touch in our experiment was rewarded, we test the hypothesis that this reward is responsible for the asymmetry. In this case, the asymmetry should depend on the outcome (presence or absence of reward) of the preceding touch: Monkeys should make repeated choices of the same category only if this category was previously correct and rewarded. According to our dynamic salience hypothesis, the mechanism underlying the repetition tendency may then be understood as an increase in salience of the touched image's category representation, and through it, all exemplars of the same category by reward. This necessarily depends on a top-down signal from category label to image neuronal population.

An alternative explanation, that is, fixed salience hypothesis, might be that ordinal positions themselves are encoded as relative ranks, with decreasing rank associated with increasing ordinal number. In this case, monkeys would tend to touch images of earlier categories

first, thus increasing the proportion of backward errors. The current experiment was designed to reduce the probability of such a ranking, by allowing the monkeys to continue the trial after error touches. However, there could be a residual (or inherent) ranking.

To differentiate between these possibilities (ranking or reward), we evaluated the proportion of −1 (backward) errors made by touching either the distractor or a quadruplet member, taking into account the accuracy and reward contingency of the preceding touch. We computed the proportion of touches of each category for four types of preceding touches: (I) correct category and image, with reward; (II) correct category but wrong (distractor) image; (III) wrong (skip) category; and (IV) wrong (repetition) category. Table 1 lists the possible instances of Types I–IV. We chose for analysis only trials where there was an appropriate distractor allowing backward errors. Furthermore, in order to have the monkey's choices depend only on the categorization strategy, the test was performed with ''shuffled'' trials (eliminate the image association strategy) and looking at touches 2–4 where working memory effects have been found to be irrelevant (Figure 4B, top, gray line).

Table 1. Trial Types for Analysis of Positional Uncertainty Asymmetry

|	Previous Choice			Next Choice Options			
Group	Categories	Accuracy	Reward	−1	0	1	2
I	1-?	Correct	Reward	1*	2	3	4
	1-2-?	Correct	Reward	2*	3	4	
	1-2-3-?	Correct	Reward	3*	4		
II	1*-?	Correct	No reward	1	2	3	4
	1-2*-?	Correct	No reward	2	3	4	
	1-2-3*-?	Correct	No reward	3	4		
III	2-?	Skip	No reward	1	2*	3	4
	2*-?	Skip	No reward	1	2	3	4
	1-3-?	Skip	No reward	2	3*	4	
	1-3*-?	Skip	No reward	2	3	4	
	1-2-4*-?	Skip	No reward	3	4		
	1-2-4-?	Skip	No reward	3	4*		
IV	1-1*-?	Repetition	No reward	2	3	4	
	1*-1-?	Repetition	No reward	2	3	4	
	1-2-2*-?	Repetition	No reward	3	4		
	1-2*-2-?	Repetition	No reward	3	4		
	1*-1-2-?	Repetition	No reward	3	4		
	1-1*-2-?	Repetition	No reward	3	4		

1, 2, 3, 4—touch target categories; 1*, 2*, 3*, 4*—distractor categories.

Figure 6A displays the proportions of categorical choices at different error distances averaged across touches and monkeys for each of the Types I–IV. The reward effect is evident because the error rate for distance −1 is significantly greater than that for +1 only for trials of Type I (blue, ANOVA, $p < .001$), and not of Types II–IV (green, red, yellow; $p > .05$ for all). The rank effect hypothesis fails because following a skip error (e.g., touching categories $1 \rightarrow 3$ or $1 \rightarrow 4$) monkeys tried to touch the correct category (correct image: $1 \rightarrow 4 \rightarrow 3$ or distractor: $1 \rightarrow 3 \rightarrow 3*$), and did not return to the untouched image with the highest rank ($1 \rightarrow 3 \rightarrow 2$). As a result, the proportion of correct category choices was larger than the error proportion for distance −1 (red, $p < .001$). Thus, the uncertainty is biased in the backward direction by a reward, which leads to repetitive touches of a category if this category was rewarded in the preceding touch; this demonstrates a top-down effect of the category label on the individual representations of category members.

In addition to the reward effect, three other characteristics of category memory become clear: (1) Retrieval of ordinal number category is equally effective irrespective of whether the previous category choice was correct or erroneous (Figure 6A, distance=0; green vs. red and yellow; $p > .4$ for both). Thus, monkeys choose images by appropriateness to the current touch number, independently of previous choice accuracy. (2) ''Pure'' category memory (without reward or associations) has a symmetric uncertainty curve (Figure 6A, green, red, yellow). This suggests that categories are not stored as absolute rank ($1 > 2 > 3 > 4$), which would introduce an asymmetry even in the absence of a reward, but as a dynamic category salience enhanced by activation of the category label, that is shifted from touch to touch. Thus, the symmetric uncertainty curve and reward effect demonstrate that the salience of a specific image actually changes during serial recall, by activation of its ordinal category, either by advancing from category to category, or by reward. (3) The half-width at half maximum of the positional uncertainty curves is 0.95, suggesting that ordinal number category tuning is sharp enough to encode separately each ordinal position.

Category tuning characteristics are drastically changed if the association strategy becomes available (Figure 6B, ''basic task'' and ''no samples''). If the previous choice was correct, this strategy cooperates with categorization, increasing the proportion of correct category choices (Figure 6B, blue, 69.6 ± 3%; compared to Figure 6A, blue, 49.2 ± 2%; ANOVA, $p < .001$). If the preceding choice was erroneous, for example, a skip of the correct category, the association strategy competes with categorization leading to many forward errors (Figure 6B, red, 56.4 ± 6% and 14.7 ± 5% for distances +1 and −1; $p < .001$) On the other hand, note that the tendency to continue the chain after a category repetition error is not statistically significant (yellow, $p = .09$). Thus, if item–item associations

Figure 6. Category tuning dependence on previous categorical choice. (A and B) Proportions of categorical choices at different error distances for each of four conditions (I–IV, as shown schematically in the upper: results averaged across monkeys and touches 2–4): I (blue): preceding category choice was correct and rewarded; II (green): choice of distractor of correct category, so nonrewarded; III (red), IV (yellow)—erroneous choice with category skip (red) or repetition (yellow). (A) Proportions of choices without associations, isolating the categorization strategy (''shuffled'' trials). Note large number of −1 errors, but only when category was previously rewarded (blue compared with green). Except for this reward bias (blue curve), graphs are symmetric, reflecting equal number of positive and negative distance errors. (B) Proportions with associations strategy enabled (''basic task'' and ''no samples'' trials). Note

that following a rewarded touch, monkeys continue the chain, rather than repeating the category (as in A), and thus make a correct touch (compare blue and green). Similarly, following a skip error, monkeys erroneously continue the chain and make a second +1 error (red). The case of ''no samples + shuffled'' is not included in this analysis because monkeys were rewarded for either correct category choice, preventing analysis of case II. Error bars, *SE*.
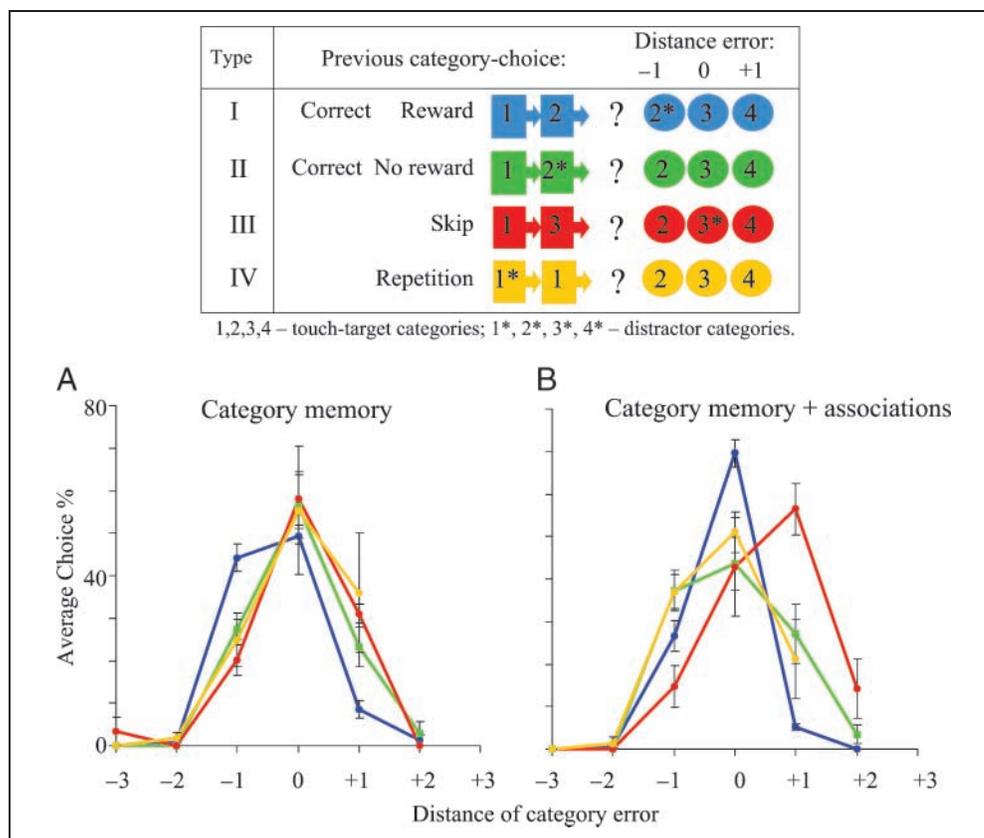
are available, the uncertainty is biased to the forward direction following a skip error, indicating that directed item–item associations are used for ordered retrieval, in quadruplets. (The mechanism may be that of Erickson and Desimone [1999] in pair-associate learning and modeled by Mongillo, Amit, and Brunel [2003]).

Summary of Results

The new experiment with quadruplets found the following categorization characteristics:

1. Ordinal number categories can be learned even under conditions when trials are not stopped after an error.

2. Ordinal numbers are abstract categories: Images belonging to different length sequences share common labels even when learned with different reward schedules.

3. Ordinal categories are absolute (ordinal-number-based, labeled first, second, etc.), rather than relative (initial, intermediate, last).

4. Monkeys choose images by proximity of their category to the current touch number, irrespective of the accuracy of the preceding choice.

5. Even isolated from item–item associations, ordinal numbers demonstrate category tuning, with a resulting fuzziness restricted mainly to the nearest forward or backward categories.

6. Category tuning itself is symmetric relative to the correct ordinal position.

7. Category tuning can be skewed by other mnemonic factors—reward-contingency and item–item associations—suggesting interaction of ordinal category memory with other memories.

8. The tendency to make repetitive choices of a rewarded category is a top-down (category to image) effect.

The other issue addressed by our study is the balance between mnemonic routines. We revealed the following findings:

1. With four-item lists, item–item associations contribute significantly to order retrieval for midlist items, so that the dominance of the categorization strategy is not as complete as with three-item lists. Thus, when associations are disabled, fuzzy tuning of ordinal numbers with four-item lists leads to occasional choice of adjacent (forward or backward) categories.

2. When the distractor is of the same category as the correct image, then categorization is useless and monkeys depend on both item–item associations and sample working memory to select the correct image. The balance between strategies for distractor elimination did not change significantly with list size. Working memory is mainly used for the first image of the sequence while associations are used for all list images.

3. Following a skip of the correct category, monkeys try to continue the chain using item–item associations, which compete with categorization. This finding supports the suggestion that monkeys use associations for quadruple order retrieval. When associations are disabled, this bias is no longer present.

DISCUSSION

Characteristics of Category Memory

Clear evidence that monkeys did not use fixed individual image salience for determining image order comes from their choosing images by the proximity of their ordinal number category to the current one, rather than choosing the available image with the lowest ordinal number. We found that tuning of pure categorical memory is clearly symmetric relative to the correct category and that there are no more backward than forward errors (in the absence of reward), suggesting that categories are not stored as fixed absolute rank ($1 > 2 > 3 > 4$). Furthermore, when monkeys were allowed to proceed with the trial following an erroneous touch, this radical paradigm change did not prevent ordinal category learning. Taken together, these findings support a failure of the fixed-property-salience hypothesis demonstrating that labels stem—even originally—from item ordinal position, and not from some other fixed item property. Concluding that the type of image salience that is relevant here is not a fixed salience, we propose a dynamic image salience hypothesis to explain serial recall of images (see below).

We found that ordinal category labels are absolute, ordinal-number-based (first, second, etc.; having only one starting point, the beginning of the list). This characteristic of ordinal position memory is important for understanding positional encoding, as it implies that transitions from category to category may be accomplished by a process that is somewhat similar to a (nonverbal) counting-like enumeration. Gelman and Gallistel (1978) suggested that children's early counting behavior follows five principles: one to one correspondence (one and only one tag, "1," "2," etc., is assigned to each counted object); stable order (tag order is invariant across counted sets); abstraction (objects of any kind can be counted); cardinality (the value of the final tag represents the quantity of items); and order irrelevance (items within a given set can be tagged in any sequence). We propose that the first three principles are shared by the assignment of ordinal number labels.

What is the possible neural correlate of ordinal number categorization? In fact, ordinal position can be read out simply from an analog numerical system or "mental number line" for cardinals, which is shared by human and nonhuman primates, having preverbal origin and obeying Weber's law (Dehaene, Molko, Cohen, & Wilson, 2004; Piazza, Izard, Pinel, Bihan, & Dehaene, 2004; Hauser, Tsao, Garcia, & Spelke, 2003; Nieder & Miller, 2003, 2004; Nieder, Freedman, & Miller, 2002; Brannon & Terrace, 2000; Gallistel & Gelman, 2000; Dehaene, Dehaene-Lambertz, & Cohen, 1998). This system may produce general number category labels that may be used for either cardinals or ordinals. For example, the final number in a counting sequence may be assigned to the numerosity of a set of objects, while the set of sequential ordinal category labels would be assigned to the items belonging to an ordered sequence. Recent primate studies reported number-tuned neurons in monkeys trained to keep track of how many times they performed a given hand movement (Sawamura et al., 2002). We suggest that these, or similar cells, may be used for coding and retrieval of serial order categories in our experiment. The responses of these neurons are tuned around the correct ordinal position, a characteristic that may be responsible also for the distance effect found for pairwise testing as an improved discriminability for pairs with more distant ordinal positions (Terrace et al., 2003).

Because monkeys make fewer backward than forward errors following list learning (Orlov, Yakovlev, Amit, et al. 2002; Orlov, Yakovlev, Hochstein, et al., 2000; Swartz et al., 1991, 2000; and current experiment), we tested if this asymmetry reflects a natural category tuning characteristic or is the result of another strategy—a type of inhibition of return—whereby monkeys avoid backward errors by memorizing images that have already been touched during the trial. We found evidence for this later strategy, based on short-term memory of touched images (see Supplementary Material). We then studied the uncertainty of item category memory, relying on distractor categorical errors rather than on order errors of sample list items. We found that backward errors, which reflect natural category tuning, did not disappear with learning. Rather, they were inhibited by an inhibition-of-return mechanism. We also isolated ordinal category memory from other factors, which could bias or mask this tuning, such as familiarity or reward contingency, item–item associations, and so forth. This revealed a symmetric uncertainty gradient of pure category memory, similar to the symmetric tuning of number-selective neurons (Sawamura et al., 2002). This tuning (and corresponding overlap of adjacent number codes) exists independently of item–item associations, thus being an inherent characteristic of these categories.

During retrieval of list order, different additional strategies can help ordinal category memory, decreasing positional uncertainty. For example, whereas inhibition-of-return influenced uncertainty by eliminating backward errors, item–item associations are particularly effective in eliminating forward errors. However, this arrangement is not perfect. That is, inhibition of return fails if several members of the same ordinal category are presented during the test. Moreover, if a positional error is made (i.e., a skip of the correct category), item–item associations acting alone can drastically worsen monkey performance because they facilitate forward errors (each error automatically will lead to another error). In this case, only positional memory can save the situation, allowing monkeys to touch the correct image irrespective of the accuracy of the preceding choice. Additionally, positional uncertainty can be worsened by a reward effect, which increases proportion of backward errors.

Possible Mechanism for Ordinal Number Encoding

We now address the related issues of the sequencing of these ordinal number-representing neurons (i.e., that 4 comes after 3), and the source of their tuning. Given that cell populations that code for ordinal numbers will often be activated sequentially, correlated activity in these populations would naturally ensue (e.g., by a mechanism similar to that found for symmetric pair-association activation; Mongillo et al., 2003; Erickson & Desimone 1999; Sakai & Miyashita, 1991). Synapses between successive ordinal number category populations would form in both the forward and backward directions, resulting in some width to the tuning curves. Symmetry would be a natural consequence of overlapping activation (in the absence of a biasing effect such as reward). A nonsymmetrical transition model based on simple Hebbian learning and ordered sequential experience has been suggested that may lead to an asymmetry in the synapses, potentiating more synapses from k to $k + 1$ than in the other direction. This would leave the tuning curves symmetric, but create an asymmetry in dynamic transitions (Amit, 1988).

Another mechanism has been proposed in the form of an accumulator model (Gallistel & Gelman, 1992; Meck & Church, 1983; each counted item is encoded by an impulse of activation, which is added to an accumulator, with the total analog magnitude at the end of the count representing the number). Number-selective neurons (Sawamura et al., 2002) may act in a similar way, being leaky integrate-and-fire neurons that accumulate sustained (delay) activity inputs (which are in turn individually activated following each list item presentation) and respond when accumulated inputs reach an appropriate threshold (Amit & Brunel, 1997). The threshold level of each neuron would be correlated with the category number that it represents.

The above mechanisms provide approximate detection of the ordinal number of an item, as is characteristic of an analog magnitude process. This analog representation is supported by the distance effect found in a pairwise test (Terrace et al., 2003) and by symmetric category tuning (current experiment). Saturation of either delay activity or threshold levels with increasing ordinal number can explain the Weber law behavior in human and animal nonverbal counting (number representations get fuzzier in proportion with the number represented; Whalen, Gallistel, & Gelman, 1999; Plat & Johnson, 1971), the magnitude effect found in the pairwise test (Terrace et al., 2003) and increased ordinal position uncertainty with a concurrent growing impact of item-to-item chain memory when list size is enlarged (current experiment). The fact that similar effects are found for cardinals (Dehaene, Molko, et al. 2004; Piazza et al., 2004; Nieder & Miller, 2003; Nieder et al., 2002; Brannon and Terrace, 2000; Gallistel & Gelman, 2000; Dehaene, Dehaene-Lambertz, et al., 1998; Moyer and Landauer, 1967) suggests a common basis for ordinal and cardinal number encoding.

Balance of Strategies Underlying Retrieval of Image Order in Three- and Four-item Lists

We found changes in the balance of mnemonic routines for image order retrieval when the list size was increased from three to four items. With more items, tuning widths increased, and there was a concomitant increased reliance on directed item–item associations for determining touch order. This effect of item–item associations is seen in the results of four-item list tests without a distactor but not in those for three-item tests with a distactor (maintaining the same number of items on the test screen so that changes in the effect of item–item associations cannot be due to a change in the number of items; Figure 4B, rightmost graphs). We also obtained this effect studying monkey post-error behavior: When item–item associations were available, the positional uncertainty was significantly biased in the forward direction following a skip error, clearly indicating that monkeys try to continue the associative chain.

We predict that the impact of chaining memory on order retrieval for fractal lists would grow further with increases in list length, because longer lists result in increased ordinal position uncertainty. Possibly, at some critical list size, positional encoding will be so fuzzy that it will not suffice for encoding absolute ordinal category. Consequently, associations might become the dominant strategy for memorizing long lists.

This tendency of positional uncertainty to grow with list size is consistent with the magnitude effect found in the two-item-subset test (i.e., slower discrimination between adjacent items in a list as their ordinal positions increase; Terrace et al., 2003). On the other hand, in that situation, there was no significant impact of item–item

associations even for rather long (seven-item sequences), as evidenced by equivalent ordering performance for pairs chosen from the same or from different lists. We explain the lack of use of item–item associations in that test condition as deriving from the use of only two items to be ordered. In our case, too, there was no impact of item–item associations for the first or last touches. We propose that chaining helps to continue a chain, once the first item has been chosen, but is useless for choosing the first item. Note also that in the two-item test, fixed salience familiarity effects were not excluded.

Top-down Label Effect

An important categorization characteristic found here is that category retrieval accuracy is independent of the accuracy of previous categorical choices. This supports the suggestion that retrieval of a specific ordinal category is top-down mediated and that following each touch, the category label neuronal population (working as a *top-down pointer)* signals the next touch target in the sequence, disregarding the category of the previous choice.

We also revealed direct evidence of this top-down label effect in that monkeys had a tendency to make repetitive touches of a category, if the initial choice of this category (with another image) was rewarded in the previous touch. We propose that a rewarded choice of a category member automatically augments salience of this and all other (non-touched) exemplars of the category for some period of time—via the ordinal category population.

The Dynamic Image Salience Hypothesis for Serial Order Recall

We postulate that the image representation neuron populations (with visual responses selective to individ-

ual images) and ordinal number populations (with activity selective to the ordinal position of the anticipated touch during the test phase) are critical for image serial recall, as represented schematically in Figure 7. A correct (or incorrect) touch resulting in a reward (or nonreward) will lead to long-term potentiation (or depression) of synaptic connections between ordinal number and individual image representations. This account emphasizes learning during the test stimulus presentation (rather than during the sample presentation), because here the reward potentiates the learning. Parsimony leads us to propose a two-level model; however, a third, perhaps intermediary, level may be present not only to especially integrate reward contingencies, but also, perhaps, to allow for a task-specific representation of ordinal number neurons.

The novelty of our proposal is that a preattentive salience-computation mechanism—suggested for visual search in natural scenes (Amit, 2002; Koch & Ullman, 1985)—is used to find potential touch targets during serial image recall. The serial recall scenario is as follows, as shown in Figure 8: During planning of each touch, the corresponding category population signals the next touch target in the sequence by increasing salience of images belonging to this category. Category representation tuning leads to activation of several items (the currently correct and neighboring categories) and competition for being touched. Attention mechanisms detect the most salient image, which is foveated and touched. If this touch is correct, it results in a reward, which in turn adds to the salience of all items associated with the current category.

Following a touch, the salience map is updated. This occurs by top-down influence from the ordinal number populations, which are themselves updated, perhaps by one of the two order-encoding mechanisms discussed above. Salience of the next category images is then

Figure 7. Scheme of neural connectivity expected following ordinal category learning of a serial recall task with triplets and quadruplets. Image representation neurons with selective visual response to images from triplets (A1–J3) or quadruplets (K1–P4); ordinal number neurons with activity selective to the ordinal position of anticipated touch during the test phase of the task. Arrows denote synaptic connections potentiated during learning. Dashed lines between image representations correspond to item–item associations.
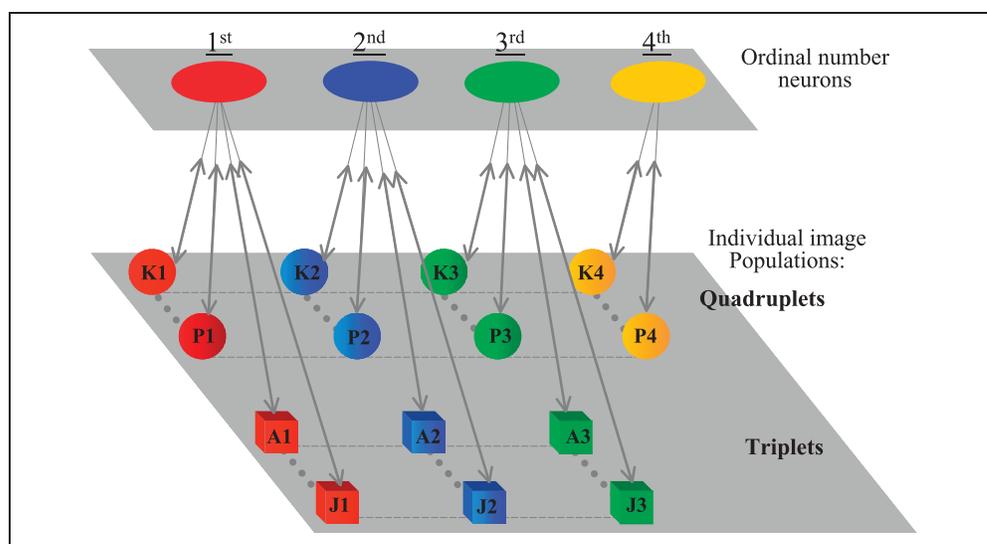
Figure 8. Dynamic image salience hypothesis for serial recall touch performance. Schematic diagram of activity and salience map during sequential stages of image ordered recall: (A and C) planning the first and second touches; (B) after a correct first touch; (D and D′) after correct or erroneous second touch. Square represents salience map with image salience represented by circle diameter. P1–N4: images of a quadruplet in the "shuffled" task version. During planning of each touch (A, C, D, D′), ordinal number neurons increase salience of images belonging to the appropriate ordinal category. Following a touch (B, C, D, D′), currently attended target is transiently inhibited (by inhibition-of-return mechanism). Touch reward increases the salience of the touched (P1, K2) and nontouched (distractor, L2*) exemplars of the category (C, D), via the category neurons. As a result, monkeys may make repetitive category (but not image) touches if the initial choice of this category is rewarded (D).
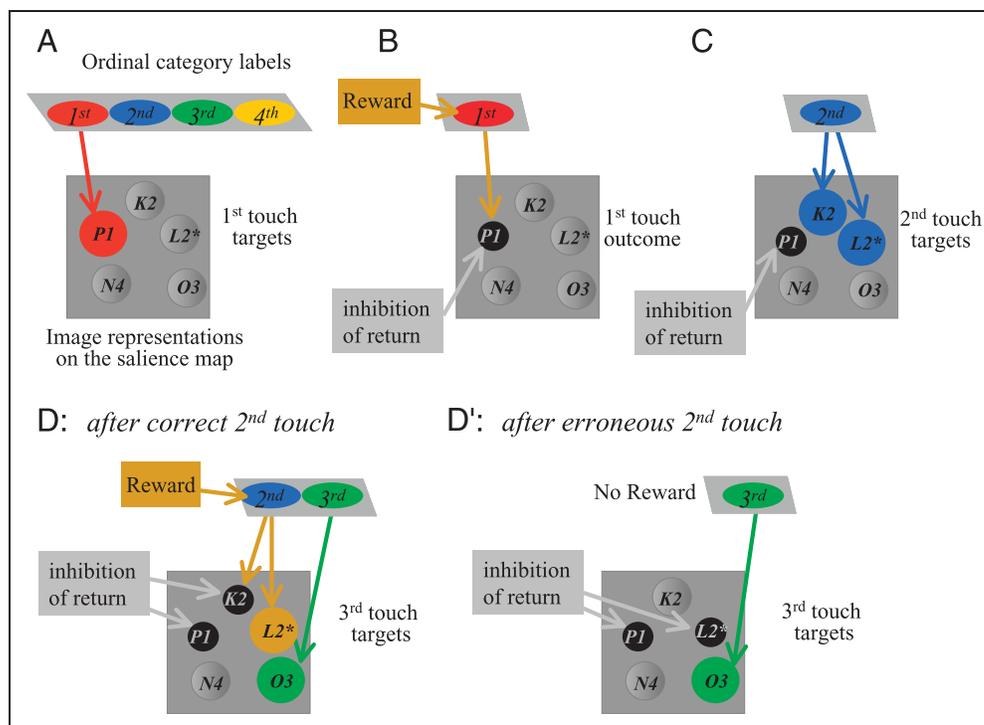
enhanced by activity of these ordinal number neurons. Therefore, a single image can have high salience for one particular touch and low for others—during the same trial. An inhibition-of-return mechanism may transiently reduce the salience of a touched item, facilitating the shift of attention to the next most salient item. In addition, the salience map may be shaped by other inputs, such as supplementary memory strategies and reward effects. Thus, the proposed mechanism integrates memories of a variety of origins (category, reward, item–item association, sample working memory, inhibition of return), via a single salience computation, into a unitary behavior in high-level associative cortical areas (e.g., lateral intraparietal cortex and frontal eye fields; Bichot & Schall, 1999; Gottlieb, Kusunoki, & Goldberg, 1998).

The pairwise test of Terrace et al. (2003) could also be performed by monkey subjects using a similar dynamic salience mechanism: When the two images are presented, the order neurons of the first category would be activated, which may add salience to the earlier of the two items if its category falls within the tuning width of the first ordinal number category. This would suffice for selection of the earlier item if its category is sufficiently early and sufficiently distant from the second. Alterna-

tively, activation within the ordinal number neurons may proceed sequentially to the next categories adding salience to the related images, until a sufficient salience differential in favor of the earlier item is achieved. Dominance of the earlier image of a specific pair would be more prominent for earlier image pairs in a sequence or for pairs with more distant images, providing better first-touch performance for these pairs (the magnitude and distance effects, respectively; Terrace et al., 2003). Subsequent ordinal category neurons will then be activated, sequentially, until the second item's salience is enhanced, following a time that depends on the distance between the test pair items. Accordingly, the second-touch reaction time would be slower with increasing interitem distance (the missing item effect; Swartz et al., 1991; D'Amato & Colombo, 1988). With training, this effect may decrease (Swartz et al., 1991) as the second item is touched by default (i.e., as the only remaining item, as found in humans by Colombo & Frost, 2001).

Because eye movements follow object salience, a prediction of the dynamic salience hypothesis is that, following training on the item list, subjects will shift their attention and their eyes according to this dynamic salience map. One should be able to measure such eye movements on an eye-tracking system.

Note

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