



## Research paper

## Effect of acoustic similarity on short-term auditory memory in the monkey

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## ABSTRACT

Recent evidence suggests that the monkey's short-term memory in audition depends on a passively retained sensory trace as opposed to a trace reactivated from long-term memory for use in working memory. Reliance on a passive sensory trace could render memory particularly susceptible to confusion between sounds that are similar in some acoustic dimension. If so, then in delayed matching-to-sample, the monkey's performance should be predicted by the similarity in the salient acoustic dimension between the sample and subsequent test stimulus, even at very short delays. To test this prediction and isolate the acoustic features relevant to short-term memory, we examined the pattern of errors made by two rhesus monkeys performing a serial, auditory delayed match-to-sample task with interstimulus intervals of 1 s. The analysis revealed that false-alarm errors did indeed result from similarity-based confusion between the sample and the subsequent nonmatch stimuli. Manipulation of the stimuli showed that removal of spectral cues was more disruptive to matching behavior than removal of temporal cues. In addition, the effect of acoustic similarity on false-alarm response was stronger at the first nonmatch stimulus than at the second one. This pattern of errors would be expected if the first nonmatch stimulus overwrote the sample's trace, and suggests that the passively retained trace is not only vulnerable to similarity-based confusion but is also highly susceptible to overwriting.

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## 1. Introduction

Studies of auditory memory in nonhuman primates consistently report extremely slow learning of the rule for delayed match-to-sample (D'Amato and Colombo, 1985; Fritz et al., 2005; Wright, 1999) and short sample-stimulus forgetting thresholds (~30 s), whether the task utilizes only two sounds (Colombo et al., 1996) or trial-unique sounds (Fritz et al., 2005). These findings suggest that although monkeys are easily able to form long-term memories in vision and touch (Mishkin, 1978; Murray and Mishkin, 1983), they may be unable to do so in audition, and are therefore limited acoustically to short-term memory (Fritz et al., 2005). More recently, we obtained evidence that even this type of auditory memory in the monkey is sharply limited (Scott et al., 2012), as it is likely to be dependent on a passive form of short-term memory (pSTM). This passive form can be distinguished from the active form (viz., working memory, WM) in that it relies exclusively on

passively retained sensory traces rather than on activation of previously stored neural representations either of particular sounds or of sound categories, e.g. tones, vocalizations, environmental sounds, etc.

The proposition that monkeys may lack auditory long-term memory (LTM), and by extension WM, may appear to be inconsistent with the monkey's ability to react appropriately to species-specific communication calls, or to learn auditory discrimination tasks by instrumental conditioning. However, the first of these behavioral abilities is likely to rely instead on cross-modal association (in which a call activates the stored representation of a visual associate), and the second, on the formation and strengthening of stimulus–response habits, with neither of them depending on auditory LTM *per se* (Scott et al., 2012). Our definition of auditory LTM requires that a current sound be recognized, i.e. that it reactivate the stored representation of the same sound heard previously, as demonstrated by delayed matching-to-sample.

In an earlier study, we tested auditory STM in two rhesus monkeys using a serial delayed-match-to-sample (DMS) task (Scott et al., 2012). Two lines of evidence supported the proposal that the monkeys' performance relied on a pSTM trace rather than on a more robust representation retrieved from long-term memory. First, performance was particularly poor for a match stimulus that followed the nonmatch 'distracters', indicating that the memory

Abbreviations: LTM, long-term memory; STM, short-term memory; pSTM, passive short-term memory; WM, working memory; DMS, delayed-match-to-sample; DI, discrimination index; FA, false alarm.

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trace was fragile and so was easily overwritten by subsequent stimuli (i.e., highly susceptible to retroactive interference). Second, this low level of performance prevailed despite a task design in which the nonmatch stimuli were drawn from sound categories different from that of the sample, so that simply matching to category would have enabled perfect performance.

In fact, the monkeys' DMS performance did show an effect of sound category, but in a counter-intuitive direction: Performance was better for tones and narrow band-passed noise stimuli than for natural sounds, including vocalizations. Thus, under our task conditions, ethological significance of the stimuli did not seem to be a relevant factor in the monkeys' performance, leading us to speculate that their delayed matching was based solely on the sensory qualities of the stimuli. If so, then degree of acoustic similarity between sample and test items should predict DMS performance, and focusing the analysis on this variable should lead to identification of the relevant acoustic feature(s) for which sample-test similarity predicts the behavioral outcome.

The present study addressed this hypothesis by examining the patterns of errors made by our subjects over many tens of thousands of trials of auditory DMS. The analysis revealed that their errors resulted primarily from confusion between pairs of sounds with similar spectral content independent of the degree of their temporal-envelope similarity. These findings suggest that the monkey's short-term memory is based solely on passive retention of an acoustic trace dominated by spectral content, and this impoverished trace could conceivably reflect a limitation of auditory memory among nonhuman primates generally.

## 2. Methods

### 2.1. Subjects and apparatus

Subjects were two adult male rhesus monkeys (*Macaca mulatta*). One monkey (F) was naïve prior to this study, whereas the other monkey (S) had been trained in an earlier study on an auditory discrimination task (Yin et al., 2008); the possible influence of that training on monkey S's performance in the present study is discussed below (discussion, Section 4.2). Testing took place within a double-walled, sound-attenuating booth (IAC, Bronx NY), with the monkey seated in a primate chair fitted with a metal contact bar. A sipper tube was positioned for delivery of liquid reward (typically water) under computer control (Crist Instruments, Hagerstown, MD). Because the behavioral task was coupled intermittently with electrophysiological recording sessions, the monkey's head position was fixed during testing by a titanium head-holder secured to the primate chair.

The data in this report, however, were collected during daily sessions when only behavioral testing was conducted.

The behavioral task was controlled by NIMH Cortex software (Laboratory of Neuropsychology, NIMH; <http://dally.nimh.nih.gov/>), which triggered sound playback via a custom-built interface with a second computer running SIGNAL software (Engineering Design, <http://www.engdes.com/>). The output of the SIGNAL buffers was flattened across frequency (Rane RPM 26v parametric equalizer, Mukilteo WA), attenuated (Agilent HP 355C and 355D), amplified (NAD, Pickering, Ontario), and delivered via a loudspeaker (Ohm Acoustics, NY) located 1 m directly in front of the animal's head. Sound level was calibrated with a Brüel and Kjær 2237 sound-level meter using A-weighting. Task-relevant events were collected on a CED 1401 acquisition system controlled by Spike2 software (Cambridge Electronic Design, UK). Data were exported to MATLAB (Mathworks, Natick, MA) for analysis, and statistics were computed by the MATLAB Statistics Toolbox.

### 2.2. Delayed match-to-sample task

Preliminary training on the DMS rule was described in the earlier study (Scott et al., 2012). Once the rule was acquired, the task proceeded as follows. The animal initiated a trial by holding a contact bar for 300 ms (Fig. 1A). This triggered presentation of a sample stimulus (~300 ms in duration and drawn randomly from a set of 21 stimuli; see below), followed by 1–3 test sounds with a variable interstimulus interval (ISI) of 800–1200 ms. When the test sound was the same as the sample (a match), the animal was required to release the bar within a 1200-ms response window beginning 100 ms after the onset of the match sound. A correct response (a "hit") earned a few drops (0.3–0.5 mL) of liquid reward after bar release. A response within the first 100 ms following match onset was considered an "early-release" error. Failure to release the bar by the end of the response window was counted as a "miss" error. If the test sound was a nonmatch, the animal was required to hold the bar (a "correct rejection") until the match stimulus was presented. Release to the nonmatch stimulus was counted as a "false alarm" (FA) error. Any type of error aborted the trial and was penalized by a 3-s timeout in addition to the standard 3-s intertrial interval; the penalty was intended to discourage animals from aborting trials with multiple nonmatches. Each trial ended after release of the bar, but if the bar was released during stimulus presentation, the full stimulus played out before the trial was reset. Trials with zero, one, or two nonmatch sounds were randomly generated with equal probability. In an attempt to reduce the memory demands of the DMS task, the nonmatch stimuli were always drawn from categories different from that of the sample, which were otherwise selected randomly on each trial. Trials were organized in blocks such that each stimulus in the set served as the sample in a pseudorandom order before the same stimulus appeared as the sample again.

### 2.3. Stimuli

The set of 21 sounds is illustrated in Fig. 1B. All sounds were recorded at 16-bit resolution at a sampling rate of 32 kHz, except for the Mvocs, for which the sampling rate was 24 kHz. The rhesus vocalizations were collected from a colony on Cayo Santiago, Puerto Rico (provided courtesy of Marc Hauser), so the individual callers were unfamiliar to our two subjects. All stimuli were equalized in root-mean-square amplitude to have approximately equal loudness and were presented at 60–70 dB SPL.

In a control experiment, designed to determine which stimulus dimension (spectral or temporal) was the more important for performance, we used a version of the stimulus set in which the sounds were manipulated to contain information in only one or the other dimension. These data were collected in a separate block of sessions after collection of the DMS data described above. The 'temporal-only' stimuli were constructed by applying the envelope of the original sounds (as extracted by the Hilbert transform) to Gaussian noise. The 'spectral-only' stimuli were generated by measuring the frequency spectrum of the original sounds (power spectral density by the Welch method, 50% overlap, 64 sample segment length, Hamming window) and constructing a noise stimulus with the same spectrum. At each frequency  $\geq 60$  Hz, a sine function of random phase was generated with an amplitude proportional to the power spectral density at that frequency; the summed signal had a flat envelope (300-ms duration, with a 10-ms linear on/off ramp) and was normalized in root-mean-square amplitude to the original sound. The spectra of the resulting stimulus and the original stimulus were overlaid to confirm that they were spectrally identical. Some sounds in the original set had identical temporal envelopes or spectra, so the redundant stimuli

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