



Animal memory: A review of delayed matching-to-sample data



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ABSTRACT

We performed a meta-analysis of over 90 data sets from delayed matching-to-sample (DMTS) studies with 25 species (birds, mammals, and bees). In DMTS, a sample stimulus is first presented and then removed. After a delay, two (or more) comparison stimuli are presented, and the subject is rewarded for choosing the one matching the sample. We used data on performance vs. delay length to estimate two parameters informative of working memory abilities: the maximum performance possible with no delay (comparison stimuli presented as soon as the sample is removed), and the rate of performance decay as the delay is lengthened (related to memory span). We conclude that there is little evidence that zero-delay performance varies between these species. There is evidence that pigeons do not perform as well as mammals at longer delay intervals. Pigeons, however, are the only extensively studied bird, and we cannot exclude that other birds may be able to bridge as long a delay as mammals. Extensive training may improve memory, although the data are open to other interpretations. Overall, DMTS studies suggest memory spans ranging from a few seconds to several minutes. We suggest that observations of animals exhibiting much longer memory spans (days to months) can be explained in terms of specialized memory systems that deal with specific, biologically significant information, such as food caches. Events that do not trigger these systems, on the other hand, appear to be remembered for only a short time.

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1. Introduction

Animal memory is the object of enduring fascination and debate (Suddendorf and Busby, 2003; Raby et al., 2007; Clayton and Dickinson, 1998; Roberts, 2002; Bouton, 2007; Pearce, 2013; Kendrick et al., 1986). Even a cursory look at the literature reveals that sometimes animals appear to remember events in detail, and for a long time, while sometimes they seem to forget surprisingly fast. For example, many jays (family Corvidae) can remember the location of hidden food for many months (Bossemma, 1979; Bednekoff et al., 1997), but have difficulty remembering simple color stimuli for more than 25–40 s (Olson et al., 1995). This is just one example of the great variation in memory performance that has led scholars to widely different conclusions. Some maintain that non-human animals have no explicit memories of past events, that is, they cannot recollect them in the same way as we do when we think about, say, childhood vacations (Roberts, 2002;

Suddendorf and Busby, 2003). Others, in contrast, conclude that we have evidence that animals have “episodic-like” memories perhaps not dissimilar from those of humans (Clayton et al., 2001a, 2001; Zentall, 2005). Comparison with human memory is central to the debate about non-human memory. Humans, in fact, appear capable of remembering practically arbitrary events for very long times without appreciable decline in performance, notably in tasks in which most other species perform poorly (Overman and Doty, 1980).

Here we review well-controlled experiments using the delayed matching-to-sample paradigm (DMTS, summarized below), one of a number of tasks that has been used to probe animals' working memory (Bouton, 2007; Pearce, 2013). By “working memory” we mean information about an event that is maintained for some time in the absence of reinforcement, and that can be used to guide behavior at a later time (Pribram et al., 1960; Baddeley, 1991). We are particularly interested in events without specific biological significance, such as colored lights, visual patterns, or sounds, as typically used in laboratory studies. We ask whether we can discern any species differences in working memory, and whether memory can be improved by training. We conclude by suggesting that animal memory is best characterized as the sum of specialized memory

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capacities, different across species and potentially lasting a long time, and a general memory capacity that works in essentially the same way in all non-human species, and which has a limited span ranging between a few seconds and a few minutes.

2. Methods

2.1. The delayed matching-to-sample (DMTS) paradigm

In a typical DMTS experiment a *sample* stimulus is presented for a short time, typically a few seconds. The sample is then removed and, after a delay, two *comparison* stimuli are presented, of which one is identical to the sample and the other is different. The animal is rewarded for choosing the comparison stimulus that matches the sample (several procedural variations are possible, such as requiring the animal to perform an action to remove the sample and initiate the delay). This paradigm has been used for many decades, for example to study whether animals possess conceptual or “symbolic” abilities (Finch, 1942; Yerkes and Nissen, 1939; Weinstein, 1941; Giurfa et al., 2001), or to study the effect of drugs or brain lesions on memory (Dunnett and Martel, 1990; Stanhope et al., 1995; Sloan et al., 2006; Horel et al., 1984 and many others). Here we are interested in DMTS as a probe into animals’ capacity to retain information about arbitrary events.

2.2. Estimation of memory parameters

We acquired over 90 data sets from published DMTS studies conducted with 25 species, each study using one or more delay intervals. Data sources are given in Appendix). Performance in DMTS is customarily measured in terms of % correct trials, i.e., % trials in which the animal chose the comparison stimulus matching the sample. Thus 50% represents chance performance and 100% perfect performance. We used DMTS data to estimate two performance parameters:

Zero-delay performance: Performance when comparison stimuli are presented immediately after the sample is removed. This condition imposes minimum requirements on memory.

Performance half-life: The delay for which performance has fallen halfway between zero-delay performance and chance performance (50% correct).

To estimate these parameters, we first transformed the percentage of correct responses into a measure of performance ranging between 0 and 1:

$$y = \frac{\%correct - 50}{50} \tag{1}$$

We then fitted an exponential function to each data set:

$$y(t) = M \exp\left(\frac{-t}{\tau}\right) \tag{2}$$

where t is the delay interval and M and τ are the fitted parameters. According to Eq. (2), performance at zero delay equals $50(1 + M)$, while its half-life equals $\tau \ln 2$. Thus fitting Eq. (2) to data enables us to estimate these parameters even if performance at the exact delays that define them (0 and $\tau \ln 2$) was not actually assessed. We used a simple exponential function for three reasons. First, it fits the data remarkably well. Across all experiments, the mean difference between observed and predicted performance is 5% per data point (median 4%, range 0–17%), with no detectable difference across species ($\chi^2_{16} = 10.06$, $p = 0.86$, Kruskal–Wallis test relating mean

squared error in fit to species). Second, Eq. (2) can be recast as a linear relationship by taking logarithms:

$$\ln y(t) = \ln M - \frac{t}{\tau} \tag{3}$$

Linear fits are numerically more robust than nonlinear fits (Björck, 1996). Lastly, while other functions have been used to fit working memory data (Rubin and Wenzel, 1996; Wickens, 1998), these have additional parameters and cannot be linearized, which makes them less suitable to fit data sets with few observations, typical of DMTS studies.

In fitting Eq. (3) to data, we encountered a few special circumstances. First, three studies observed performance slightly below 50% (in Fig. 2: bees 4, pigeons 5, macaques 3). We treated these observations as measurement error and considered all values ≤ 50 as equal to 51. We choose 51 rather than 50 because 50 would result in $\ln y(t) = -\infty$, which would prevent fitting. This choice very slightly overestimates DMTS performance at long delays. Second, some studies used only one delay interval, preventing estimation of performance half-life. For these studies, we used observed performance to estimate zero-delay performance, provided the delay interval was ≤ 1 s. Third, fitting Eq. (3) estimates an infinite half-life when performance over the probed range of delays is stable or increasing. This occurred in a black-capped chickadee study (maximum delay = 20 s, birds 1 in Fig. 2), one dolphin study (maximum delay = 60 s, dolphins 4), and two chimpanzee studies (maximum delay = 20 s in both, chimpanzees 1 and 2). While the claim of infinite memory is clearly untenable, simply ignoring these studies would bias our estimates toward shorter memory spans. As a compromise, we estimated performance half-life as twice the longest probed interval. This choice is arbitrary yet appears generous in light of other data with the same or similar species.

2.3. Delay titration studies

While most studies reviewed below presented a set of delay intervals determined by the experimenter, some studies used a subject-driven titration procedure in which the delay interval is lengthened whenever a subject meets a predetermined response criterion (e.g., two correct responses in a row). If the criterion is not met, the delay interval is shortened. These studies, although a minority, deserve special attention as they sometimes report striking long-delay performance. We detail here how we estimated memory parameters from titration data, and postpone to Section 4 their evaluation. Data from titration studies are not reported as delay-performance curves because performance is kept at criterion by adjusting the delay. Rather, the maximum delay achieved under a given performance criterion is reported. It is possible to estimate the M and τ parameters in Eq. (2) from such data exploiting the fact that, typically, animals are first trained with a small or zero delay until a performance criterion is met that is more stringent than what is maintained during titration. For example, Kangas et al. (2010) trained pigeons to 85% correct at zero delay, and maintained them at 67% correct during titration. Let (d_1, y_1) be the initial delay and performance, and (d_2, y_2) the delay and performance at the end of titration. According to Eq. (2), we have:

$$y_i = M \exp\left(\frac{-d_i}{\tau}\right) \quad i = 1, 2$$

or, according to Eq. (3):

$$\ln y_i = \ln M - \frac{d_i}{\tau} \quad i = 1, 2$$

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