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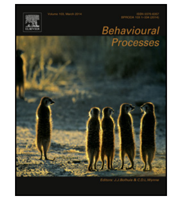

Pigeon visual short-term memory directly compared to primates

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ABSTRACT

Three pigeons were trained to remember arrays of 2–6 colored squares and detect which of two squares had changed color to test their visual short-term memory. Procedures (e.g., stimuli, displays, viewing times, delays) were similar to those used to test monkeys and humans. Following extensive training, pigeons performed slightly better than similarly trained monkeys, but both animal species were considerably less accurate than humans with the same array sizes (2, 4 and 6 items). Pigeons and monkeys showed calculated memory capacities of one item or less, whereas humans showed a memory capacity of 2.5 items. Despite the differences in calculated memory capacities, the pigeons' memory results, like those from monkeys and humans, were all well characterized by an inverse power-law function fit to *d*' values for the five display sizes. This characterization provides a simple, straightforward summary of the fundamental processing of visual short-term memory (how visual short-term memory declines with memory load) that emphasizes species similarities based upon similar functional relationships. By closely matching pigeon testing parameters to those of monkeys and humans, these similar functional relationships suggest similar underlying processes of visual short-term memory in pigeons, monkeys and humans.

1. Introduction

Visual short-term memory (VSTM) refers to the ability to transiently store visual information for brief time intervals of seconds to several minutes. VSTM (also called visual working memory) underlies numerous cognitive and motor functions including: detecting changes in the environment, planning and executing goal directed movements, and combining information across eye movements (e.g., Brouwer and Knill, 2007; Irwin, 1991; Henderson, 2008). Over the past 27 years, the task of choice for investigating human VSTM has been change detection where subjects are presented with an array of visual stimuli and following a short delay they report which stimulus changed or whether (or not) there was a change (e.g., Alvarez and Cavanagh, 2004; Cowan et al., 2001; Eng et al., 2005; Luck and Vogel, 1997; Pashler, 1988; Rensink, 2002). More recently, the emphasis has been on identifying the nature of VSTM limitations in terms of capacity or accuracy (Anderson et al., 2011; Bays and Husain, 2008; Devkar et al., in press; Donkin et al., 2013; Elmore et al., 2011; Gorgoraptis et al., 2011; Keshvari et al., 2013; Pashler, 1988; Rouder et al., 2008; Sims et al., 2012; Van den Berg et al., 2012; Wilken and Ma, 2004; Zhang and Luck, 2008, 2011).

Despite considerable effort and research to characterize the nature of human VSTM, similar studies of nonhuman animal VSTM have only recently been conducted (Buschman et al., 2011; Devkar et al., in press; Elmore et al., 2011, 2012; Elmore and Wright, 2015; Gibson et al., 2011; Heyselaar et al., 2011; Lara and Wallis, 2012; Lazareva and Wasserman, 2016; Wright et al., 2010). Among the reasons for the lag in animal VSTM research, is that training nonhuman animals to perform these demanding memory tasks is very time consuming, often requiring a year or more of training to achieve stable accurate performance with delays and as many as six to-be-remembered items. Nevertheless, it is important to understand how VSTM works in species other than humans for evidence about differences and similarities, including evolutionary continuity of such a fundamental processes as VSTM. Indeed, all visual memory (including long-term visual memory) begins with VSTM.

Training difficulties notwithstanding, we (and others) have developed procedures to train monkeys and pigeons to achieve reasonably accurate performance in tasks similar to some of those used to test humans. Although rhesus monkeys are not typically as accurate as humans in these tasks, nevertheless, both species have shown progressive and systematic declines in accuracy as the

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number of to-be-remembered items is increased (e.g., Elmore et al., 2011; Elmore and Wright, 2015; Heyselaar et al., 2011). In some of these tasks, the basic change-detection procedure (change vs. no change; 2-stimulus test vs. all array stimuli) for animals has differed compared to that used for humans. In addition to differences in basic change-detection procedures, there are often parameter differences (item types, item number, visual angle, viewing times, delay times, intertrial times, etc.), that complicate direct species comparisons in VWM, particularly across laboratories, but even within the same laboratory. Indeed, in our experiments with monkeys we initially had used longer presentation times and shorter delay times than with humans, to promote accurate monkey performance (Elmore et al., 2011). But later we redid the experiment with those parameters matched to those used with humans, including making the items the same shape (squares) and same colors for more direct species' comparisons (Elmore and Wright, 2015).

The results from the Elmore and Wright (2015) study showed differences in accuracy and capacity that emphasized species differences, but a continuous-resource account provided a simpler and more straightforward explanation based upon similar functional relationships that emphasize species similarities. Memory sensitivity (d') declined precisely as an inverse power law function of N (display size) and the functions from both species were well fit by power law functions that accounted for 85% of the variance. By closer matching of monkey testing parameters to those of humans, conclusions based upon the similar functional relationships strengthened the evidence for similar VSTM processing between monkeys and humans.

The purpose of the experiment presented in this article was to test pigeons with colored-square stimuli with the same basic change-detection procedure (2-stimulus test) and the same parameters previously used to directly compare monkeys and humans (Elmore and Wright, 2015).

2. Methods

2.1. Subjects

Three White Carneaux pigeons, 5–9 y.o., from the Palmetto Pigeon Plant (Sumter, SC) and Double T Farm (Glenwood, Iowa) participated in the experiment. They had been trained and tested in a change-detection task with colored circles (Elmore et al., 2012; Wright et al., 2010). In the experiment presented here, testing was conducted 5 days per week. Pigeons were maintained at 85% of their free-feeding weights with free access to grit and water in their individual home cages. A 14–10 h light–dark cycle was maintained in the room containing the home cages. All animal procedures conformed to the National Institutes of Health guidelines, and were approved by the Institutional Care and Use Committee at the University of Texas Health Science Center at Houston.

2.2. Apparatus

Pigeons were tested in a custom designed and built wooden testing chamber (35.9-cm wide × 45.7-cm deep × 51.4-cm high) equipped with a custom-built wooden grain hopper tray containing mixed grain that was centered below a 17-in Eizo T550 color monitor (800 × 600) and was accessed by pigeons through an opening (5.1 × 5.7 cm) centered in the front panel 3.8-cm above the chamber floor. An infrared touch screen (Carroll Touch, Round Rock, TX) detected responses and interfaced with the computer. An exhaust fan was located at the back of the chamber. A houselight (Chicago Minature #1829, 24 V) located in the center of the ceiling illuminated the pigeon's portion of the chamber during intertrial intervals (ITI).

Custom software written with Visual Basic 6.0 on a Dell Optiplex GX110 recorded and controlled all events in the operant chamber. A video card (ATI 3D Rage Pro AGP 2X, Ontario Canada) controlled graphics generated by the computer and a computer-controlled relay interface (Model no. PI0-12, Metrabyte, Taunton, MA) operated the grain-hopper, hopper light, and chamber light.

2.3. Stimuli & displays

The stimuli were six approximately 1.4-cm colored squares (RGB 24 bit values: aqua—0, 255, 255, blue—0, 0, 255, green—0, 255, 0, magenta—255, 0, 255, red—255, 0, 0, yellow—255, 255, 0) like those shown in Fig. 1. The stimuli were presented in random locations on an invisible 4 × 4 matrix (9 cm horizontal and 7 cm vertical). (These stimuli and displays were sized to compensate for the pigeons' closer proximity to the screen than monkeys and humans.)

2.4. Testing procedures

Following extensive training to steady-state performance accuracy, the pigeons were tested for 12 (pigeon G345 and P8040) or 13 (pigeon P8893) consecutive sessions with 96 trials per session. Trials began with a 1000 ms presentation of 2, 3, 4, 5, or 6 colored squares in random positions within the 4 by 4 matrix. The number of items in the sample display (display size) was random-

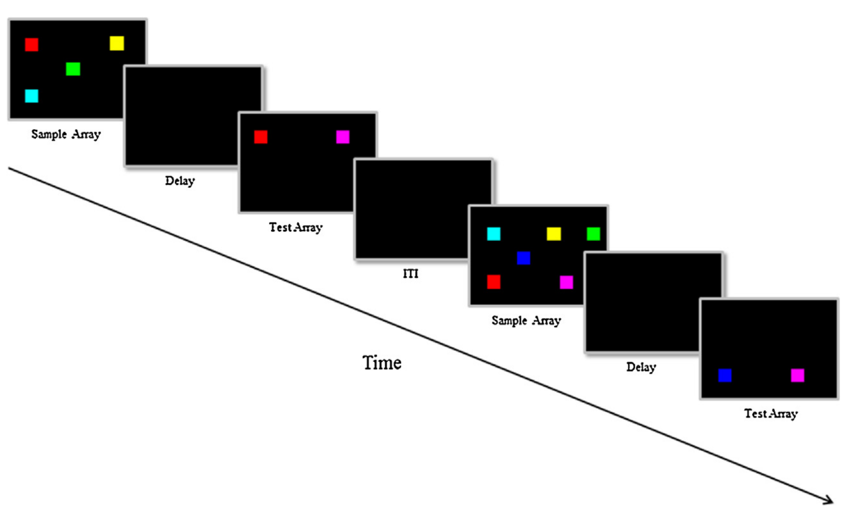

Fig. 1. Progression of events for two trials with colored squares in the change detection task.