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Sudden Death and Gradual Decay in Visual Working Memory

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Abstract

General Douglas MacArthur famously remarked that "Old soldiers never die; they just fade away" (General Douglas MacArthur, April 19, 1951). For decades, researchers have concluded that visual working memories, like old soldiers, fade away gradually, becoming progressively less precise as they are retained for longer periods of time. However, these conclusions were based on threshold estimation procedures in which the complete termination of a memory could artifactually produce the appearance of lower precision. Here we use a recall-based visual working memory paradigm that provides separate measures of the probability that a memory is available and the precision of the memory when it is available. Using this paradigm, we demonstrate that visual working memory representations may be retained for several seconds with little or no loss of precision but that they may terminate suddenly and completely during this period.

Keywords

Recall; short-term memory; working memory; decay; capacity; all-or-none

Although the brain stores some memories for a lifetime, it also maintains temporary, disposable, scratch-pad memories that serve a variety of complex cognitive tasks (Cowan, 2005). It is well known that these short-term, working memories (Luck & Hollingworth, 2008) are lost rapidly (e.g., Posner & Keele, 1967). But do they fade away gradually, or do they die a sudden and complete death? For decades, researchers have concluded that visual working memories decay gradually, becoming progressively less precise as they are retained for longer periods of time (Cornelissen & Greenlee, 2000; Lee & Harris, 1996; Paivio & Bleasdale, 1974). However, most of these studies used threshold estimation procedures that are inappropriate when representations may completely terminate. Here we use a new method that can, for the first time, distinguish between gradual decay and sudden death.

Sudden death and gradual decay reflect two very different classes of mathematical and physical systems. Gradual decay typically occurs in passive systems that decline by a fixed percentage for each unit of passing time (e.g., the fading peal of a bell). In contrast, all-or-none processes (Ferrell & Machleder, 1998; Lau & Bi, 2005), such as sudden death, typically occur in active, feedback-driven systems that fail when some threshold is exceeded (e.g., a computer that suddenly shuts down after gradually overheating). Working memory appears to be an active, feedback-driven system that relies on all-or-none reverberatory neural activity (Durstewitz, Seamans, & Sejnowski, 2000; Lau & Bi, 2005), and we therefore expected it to exhibit sudden death rather than gradual decay. This would be consistent with a growing body of literature indicating that many aspects of cognition rely

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on thresholded representations (Sergent & Dehaene, 2004; Yonelinas, 1994), which may be important for making the transition from subsymbolic to symbolic representations (Hummel & Holyoak, 1997).

Distinguishing between gradual decay and sudden death requires the ability to separately measure the precision of the memory representation (which should decline over time if the memories gradually decay) and the probability that the representation continues to exist in working memory (which should decline over time if the memories suddenly terminate). To achieve this, we used a short-term recall paradigm in which observers attempt to retain three colored squares in working memory (Zhang & Luck, 2008). After a variable delay, one of the items is cued, and the observers report its color by clicking on a color wheel (Figure 1a). If the cued item is present in working memory at the time of the cue, the reported value should tend to be near the original color, with a bell curve probability distribution (Figure 2a). The width of the bell curve reflects the precision of the memory representation, which is directly related to its strength (Kinchla, 1973). If, however, the cued item is not present in memory, then the observer should have no information about the color and will guess randomly. This uniform distribution of guesses will create a constant vertical offset to the distribution of responses, and the height of this offset reflects the probability that the cued item is no longer available in working memory (which we denote as *p(failure)*).

To establish the generality of our findings, we conducted a second experiment examining memory for shape (Figure 1b). Because our method requires stimuli that vary along a known, quantitative dimension, the shapes were quantified with the Fourier descriptor method, which has been validated in psychophysical (Cortese & Dyre, 1996) and neurophysiological studies (Schwartz, Desimone, Albright, & Gross, 1983).

METHOD

Participants

Separate groups of twelve healthy young adults (18–35 years) participated in the color experiment and the shape experiment. The participants provided informed consent and received course credit or monetary compensation. All reported having normal color vision and visual acuity.

Stimuli and Procedure

The sample array consisted of three colored squares (see Figure 1a and Zhang & Luck, 2008 for details). The test array contained a color wheel and an outlined square at the location of each item from the sample array. One square was thicker than the others, indicating the item to be recalled. The color wheel consisted of 180 colors that were distributed in equal perceptual steps.

The sample array was presented for 100 ms, followed by a blank delay of 1, 4, or 10 seconds, and then the test display. Observers reported the color of the cued item by clicking on the color wheel with a mouse. We obtained 150 trials at each retention interval, in random order. A concurrent articulatory load of three digits was used to discourage verbal encoding (see Zhang & Luck, 2008 for details).

The shape experiment was identical to the color experiment except as follows. Each of 180 shapes was defined by the sum of two Fourier descriptors, and the shapes differed in the phase of one of these descriptors (see Figure 1b for details). The sample array (1000 ms) contained three of these shapes, and the test array contained a cue and a circular array that showed 30 samples of the 180 shapes, evenly distributed around the shape space. Observers reported the cued shape by clicking on this array (interpolating between shapes when necessary). They first received a 60-trial training block, in which the sample and test arrays were presented simultaneously, so that they could become familiar with the shapes and interpolation task.

Data Analysis

A quantitative model (Zhang & Luck, 2008) was used to estimate the probability that the cued item was present in memory at the time of test and the precision of this representation when it was present. This model assumes that the observer has a noisy memory representation of the cued item on some trials and no memory of the cued item on other trials. When the observer has a memory of the cued item, the response will tend to be near the value of the original stimulus, and the distribution of responses over trials will be normally distributed around the original value (a von Mises distribution was used because of the circular stimulus space). The standard deviation (SD) of this distribution is inversely proportional to the precision of the representation; a wider distribution is equivalent to a less precise representation. The SD is sensitive to any type of gradual decline in the quality of the memory representation, including changes in the breadth of the neural tuning, drifts in the averaged remembered value, and declines in the strength of the internal memory activity. If the cued item is unavailable in working memory, the response will be a random guess, leading to a uniform distribution over trials. Because the observer sometimes remembers and sometimes fails to remember the cued item, the observed data for a given observer in a given condition is a mixture of these two distributions, weighted by the probability that the cued item was remembered.

Maximum likelihood estimation (Myung, 2003) was used to fit this model to the group data and to the data for each observer in each condition, with three estimated parameters: (1) μ, the mean of the von Mises distribution, which represents any systematic drift in the representation; (2) SD, the width of the von Mises distribution, which represents the precision of the representation; and (3) p(failure), the height of the uniform distribution, which represents the probability that the cued item was unavailable for report. Note that 1-p(failure) equals the probability that the cued item was present in memory (termed P_m by Zhang & Luck, 2008),

The μ parameter did not vary significantly from zero and will not be discussed further.

The gradual decay hypothesis predicts that the SD parameter will increase as the delay interval increases. The sudden death hypothesis predicts that the p(failure) parameter will increase as the delay interval increases.

RESULTS

The model provided a good fit to the color recall data (Figure 2a). It accounted for 99%, 100%, and 98% of the variance (adjusted r^2) for the 1-, 4-, and 10-s delay conditions, respectively. The mixture model could not be rejected for any delay at the group level or for any of the individual observers at any delay (Kolmogorov-Smirnov test, $p > .10$ for all cases). A gradual decay model, in which SD can vary but p(failure) is held constant at the value estimated from the 1-s delay, was also fit to the data. Although this model fit the data extremely well at the 1-s and 4-s delays, it could be rejected for the 10-s delay at the group level ($p<.001$) and for 11 of the 12 individual observers ($p<.05$).

Figure 3a shows the mean p(failure) and SD values. SD increased very slightly between the 1- and 4-s delay conditions and then remained constant between the 4- and 10-s delay conditions. A one-way analysis of variance (ANOVA) indicated that these differences were

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not significant ($F<1$). Thus, there was little or no evidence of memory decay over a 10-s period.

P(failure) was essentially constant at the 1- and 4-s delays but increased sharply at the 10-s delay ($F(2,22)=5.10$, $p<0.02$). This can also be seen in Figure 2A as an increase in probability of extreme errors in the 10-s delay condition. Follow-up tests showed no difference between the 1- and 4-s delays ($F<1$) and a significant increase between the 4- and 10-s delays ($F(1,11)=7.71$, $p<0.02$), with a 50% increase in memory failure between 4 and 10 seconds. Memory performance was somewhat lower in this procedure than in the more typical change-detection procedure, but these two procedures yield highly correlated estimates of the number of items stored in memory (Zhang & Luck, 2008).

Similar results were obtained when observers were asked to remember shape (Figure 2b & Figure 3b). The model accounted for 99%, 96%, and 99% of the variance (adjusted r^2) for the 1-,4-, and 10-s delays, respectively. The model could not be rejected for any delay at the group level or for any of the individual observers at any delay (Kolmogorov-Smirnov test, $p > .05$ for all cases).

SD exhibited a slight increase across delays, but this effect was not statistically significant ($F(2,22)=2.64$, $p>.10$). In contrast, p(failure) increased significantly across delays ($F(2,22)=3.76$, $p<0.05$). The increase in p(failure) between 1 and 4 seconds was small and statistically insignificant ($F<1$), but the increase between 4 and 10 seconds was large and significant ($F(1,11)=4.68$, $P<0.05$). Thus, just as for color, we found little or no decline in memory precision as the delay interval increased, but we found a substantial increase in the probability that the cued item was lost from working memory between 4 and 10 seconds.

DISCUSSION

The present study has provided a new view of the nature of forgetting in visual working memory. We found that colors and shapes can be held in short term memory for at least 4 seconds with little loss in either quantity or quality. After this time, the probability that an item remains in memory declines, but the remaining representations exhibit little or no change in strength or precision. These findings dovetail with observations of all-or-none transitions in working memory encoding (Zhang & Luck, 2008), in attentional selection (Sergent & Dehaene, 2004), and in recognition memory (Quiroga, Mukamel, Isham, Malach, & Fried, 2008; Yonelinas, 1994). This convergence suggests that many higher-level brain processes may operate in a thresholded fashion, an important characteristic of dynamic, feedback-driven biophysical systems (Ferrell & Machleder, 1998; Lau & Bi, 2005). This may be important for providing stable representations that can serve as symbols in high-level processes (Hummel & Holyoak, 1997).

We are not, however, assuming that the representations themselves are “all or none.” When an item is represented in working memory, our model proposes that it is a noisy, metric representation. However, these representations are actively maintained via recurrent feedback, forming attractors in a dynamic state space (see Simmering, Schutte, & Spencer, 2008), and these attractors can suddenly terminate. Thus, we are proposing *some-or-none* representations (as in Sherman, Atri, Hasselmo, Stern, & Howard, 2003). It is possible that some aspect of the memory representation declines gradually over time, leading to sudden termination when a threshold has been reached (just as a gradual increase in temperature may eventually cause a computer to suddenly shut down). If there is some kind of gradual decline, however, it does not greatly impact the precision of the representation.

Most psychophysical studies of working memory have addressed decay by asking whether discrimination thresholds increase over time (Cornelissen & Greenlee, 2000; Fahle & Harris, 1992; Lee & Harris, 1996; Magnussen & Greenlee, 1999)}. In these studies, observers must decide whether two stimuli separated by a delay are the same or different. As the delay increases, a progressively larger difference between sample and test is necessary to achieve a given performance level, which has been taken as evidence for gradual decay. However, this pattern could also result from an increase in the *lapsing rate*, an important but often-ignored parameter that reflects lapses of attention, eye blinks, mistakes in response execution, etc. The lapsing rate is functionally equivalent to p(failure), because both reflect trials on which the observer has no information at all (as opposed to noisy information). Assuming a near-zero lapsing rate is equivalent to assuming that sudden death never occurs. This assumption can create a significant bias in threshold measurement (e.g., Green, 1995) so that an increase in p(failure) will lead to an artifactual increase in the estimated discrimination threshold. The same problem arises in previous decay studies using other psychophysical variables (e.g., Cornelissen & Greenlee, 2000; Paivio & Bleasdale, 1974).

The present results are consistent with the possibility that observers do not lose the color or shape from memory, but instead lose feature-location bindings so that they do not know which item to report. However, we obtained the same pattern of results in a follow-up experiment with a single color on each trial, which eliminated the need to bind color and location. It is also possible that observers lose the ability to distinguish between the stimuli presented on the current trial and those presented on previous trials (i.e., loss of distinctiveness; see Winkler, Schroger, & Cowan, 2001). Even if true, however, this would still reflect a sudden death of information in working memory (i.e., bindings of features with time of occurrence).

Sudden death may not be the only way in which information is lost from working memory. Indeed, working memory for location appears to drift over time (Simmering, Peterson, Darling, & Spencer, 2008). Moreover, because each part of a complex object appears to be stored in a separate “slot” in working memory (Sakai & Inui, 2002), the sudden death of individual part representations could lead to a progressive decrease in the quality of the overall object representation (Bower, 1967). In addition, we observed a small (and nonsignificant) decrease in precision between delays of 1 and 10 seconds. However, the present results demonstrate that complete forgetting can occur with a relatively high probability over a relatively brief delay, and this may be the main means of information loss from visual working memory in daily life.

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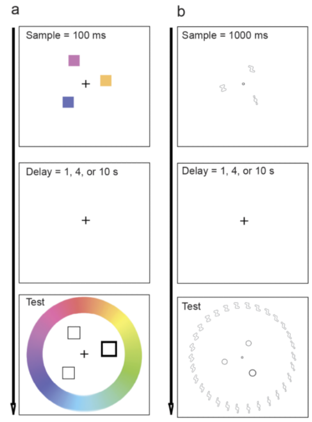

Figure 1.
(a) Stimuli from the color experiment. Each sample square subtended 2° × 2° of visual angle at a viewing distance of 57 cm, and each was centered at one of eight equally spaced locations on an invisible circle (4.5° radius). The color wheel consisted of 180 colors that were evenly distributed (in terms of perceptual similarity) along a color circle in the L*a*b color space of the 1976 Commission Internationale de l'Eclairage. This color circle was centered at (L=70, A=20, B=38) with a radius of 60 units. All colors had equal luminance. The color wheel was 2.2° thick and was centered on the monitor with a radius of 8.2° of visual angle. The sample array colors were randomly selected from this color set, with a minimum distance of 24 degrees in color space. (b) Stimuli from the shape experiment. Each shape subtended approximately 1.6° × 1.6° of visual angle and was defined by two sinusoidal components: one with a frequency of 2 cycles per perimeter (cpp), an amplitude of 0.5, and a phase of 0°; and one with a frequency of 4 cpp, an amplitude of 0.5, and a phase that varied between 0 and 360° in steps of 2°.

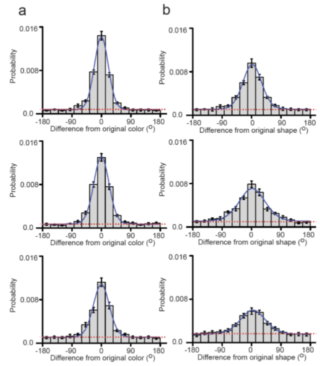

Figure 2.
Results from the color (a) and shape (b) experiments, showing the probability distribution of the difference between the tested value and the reported value (bars, error bars represents standard error), along with the fit of the Zhang & Luck (2008) model (solid line). The width of the central peak is inversely related to the precision of the representations, and the vertical offset (indicated by the broken lines) reflects the probability that no information about the color was available at the time of report.

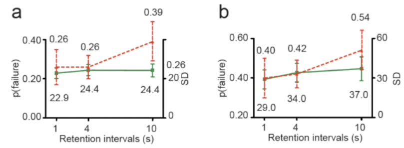

Figure 3.

Estimates of memory precision (SD, solid line, right y-axis) and probability of memory failure (p(failure), dashed line, left y-axis) for each retention interval from the color (a) and shape (b) experiments. Error bars show within-subjects 95% confidence intervals (Cousineau, 2007).