



A neural model of retrospective attention in visual working memory

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ARTICLE INFO

Keywords:

Working memory
Retrospective cueing
Attention
Neural coding
Resource model

ABSTRACT

An informative cue that directs attention to one of several items in working memory improves subsequent recall of that item. Here we examine the mechanism of this retro-cue effect using a model of short-term memory based on neural population coding. Our model describes recalled feature values as the output of an optimal decoding of spikes generated by a tuned population of neurons. This neural model provides a better account of human recall data than an influential model that assumes errors can be described as a mixture of normally distributed noise and random guesses. The retro-cue benefit is revealed to be consistent with a higher firing rate of the population encoding the cued versus uncued items, with no difference in tuning specificity. Additionally, a retro-cued item is less likely to be swapped with another item in memory, an effect that can also be explained by greater activity of the underlying population. These results provide a parsimonious account of the effects of retrospective attention on recall and demonstrate a principled method for investigating neural representations with behavioral tasks.

1. Introduction

Recall of sensory information from short-term memory storage is imperfect; however, not all memory representations are alike: cueing paradigms have revealed that memory resources can be allocated under voluntary control. Surprisingly, benefits are observed not only for items cued at the time of presentation (Gorgoraptis, Catalao, Bays, & Husain, 2011; Sperling, 1960), but also for items cued retrospectively (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; Pertzov, Bays, Joseph, & Husain, 2013; Souza, Rerko, Lin, & Oberauer, 2014). In such retro-cueing experiments, one item from a visual memory array is indicated during the retention interval by, e.g., a spatial cue. This cue picks out an item that is more likely to be probed in the subsequent test display. Even though the items are no longer visible at the time of the cue, significant advantages in recall are observed for retro-cued items over other items in the array.

The mechanism by which retro-cue benefits arise has not yet been clearly delineated. Proposals include the removal from memory of redundant information related to uncued items (Souza & Oberauer, 2016), a strengthening of the cued item's memory representation over and above its original encoding strength (Rerko, Souza, & Oberauer, 2014; Souza et al., 2014; Souza, Rerko, & Oberauer, 2015), protection of the cued item from temporal decay or interference from other items (Pertzov et al., 2013; Pertzov, Manohar, & Husain, 2016), and protection from interference that arises from subsequent visual input (Makovski, Watson, Koutstaal, & Jiang, 2010; Souza & Oberauer, 2016; Souza, Rerko, & Oberauer, 2016).

In recent retro-cue studies, the fidelity of recall has been investigated using the method of reproduction (e.g. Wilken & Ma, 2004) whereby participants report a probed feature from a memory array using an analogue (frequently circular) scale, such as a color

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<https://doi.org/10.1016/j.cogpsych.2017.12.001>

Accepted 13 December 2017

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wheel. Variability in feature reports produces a distribution around the true target value which typically differs from the circular normal (von Mises) distribution, having sharper peaks and longer tails. It has become common to analyse these responses using mixture models that describe errors as coming from one of several source distributions. In particular, response errors are often fit with a mixture of a normal distribution centered on the correct (target) feature value and a uniform distribution corresponding to random guesses (normal + uniform model; Zhang & Luck, 2008). A better fit is usually obtained if a further proportion of responses are drawn from normal distributions centered on non-target (unprobed) feature values, capturing “swap” errors (Bays, Catalao, & Husain, 2009; van den Berg, Awh, & Ma, 2014).

Crucially, results from mixture modelling analyses have proven largely uninformative about the retro-cue benefit, with the majority of studies that have looked for them finding changes in all three mixture components: an increase in precision, a decrease in random responses, and a decrease in swap errors (Gunseli, van Moorselaar, Meeter, & Olivers, 2015; Makovski & Pertzov, 2015; Murray, Nobre, Clark, Cravo, & Stokes, 2013; Souza et al., 2014, 2016; van Moorselaar et al., 2015; Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015; Williams, Hong, Kang, Carlisle, & Woodman, 2013). The meaningfulness of model parameters is critically dependent on the correctness of the model, however previous retro-cue studies typically have not considered alternatives to the normal + uniform model.

Here, we consider a different perspective on visual working memory based on the principles of neural population coding (Bays, 2014, 2015; Schneegans & Bays, 2017). The population coding model accounts for recall errors by encoding stimulus features in the activation of a population of tuned neurons. Because neural firing is stochastic, decoding of the population rarely recovers stimulus information veridically, leading to errors of varying magnitude. Bays (2014) showed that this simple model accurately predicts the non-normality of error distributions observed in continuous report tasks. Additionally, by incorporating normalization of the population activity into the model, one can predict how error distributions will change with set size (the number of items in the memory array). This neural resource model provides a better fit to empirical data than the slot + averaging model of Zhang and Luck (2008), which extended the normal + uniform model to multiple set sizes.

Population coding is thought to be a fundamental mechanism of sensory representation found for different feature dimensions throughout cortex (Pouget, Dayan, & Zemel, 2000; Zemel, Dayan, & Pouget, 1998), and is therefore a strong candidate mechanism for storing working memories. For the sake of example, we will consider sensory responses of a typical orientation-selective neuron in primary visual cortex (Hubel & Wiesel, 1962). An oriented stimulus falling within this neuron’s retinotopic receptive field can elicit varying degrees of spiking. The primary factor driving cellular activity is where the orientation of the stimulus falls relative to the preferred orientation of the neuron. Feature values that coincide with the preferred value evoke a much larger response than do more distal feature values. The neuron’s tuning curve, then, is a function that describes how its activity changes with distance from the preferred orientation. Electrophysiological observations indicate that tuning curves are typically well-described by a bell-shaped function, scaled by a peak firing rate reflecting the response to the preferred stimulus value. The extent to which distal features evoke a response in any given neuron is determined by the tuning curve width, quantified as the full-width at half-maximum (FWHM). Narrow curves localize activity to features that are very close to the preferred value; broader curves spread activity across a wider range of features.

When fitting the neural model to data both the peak firing rate and tuning width are treated as free parameters; to simplify modeling, it is assumed that all neurons share these parameters, varying only in their preferred stimulus value (although it has been shown that the model predictions are not strongly dependent on this assumption; Bays, 2014).

Here we examine which parameters of the population coding model are affected by the retro-cue. In order to do so, we collated data from numerous previous studies so that we could maximize statistical power for the purpose of model fitting, and so as to ensure the generality of our results. We find that the tuning characteristics of the population coding model are uniquely affected by the retro-cue. Specifically, behavioral performance is consistent with higher overall firing rate of the population encoding the cued stimulus, while the tuning curve width is unaffected.

2. Method

2.1. Task and data

This study focuses on results from delayed estimation (continuous report) tasks, in which observers are required to report or reproduce a remembered stimulus on an analogue scale. These tasks involve three stages: a sample display, consisting of an array of items to be remembered, is followed by a blank delay period, during which the items must be held in memory, which is succeeded by a probe display, indicating which one of the items in memory is to be reported and typically providing the means of reporting it. A retro-cue (Fig. 1a) is a stimulus appearing during the delay period that indicates one of the items in memory that is more likely than the others to be subsequently probed.

We sent out requests for data to authors of every published study, to our knowledge, that has combined a delayed estimation task with a retro-cue condition. From the replies we obtained data from eight experiments from five different laboratories, comprising 188 participants and 65,492 trials (see Table 1). Experiments differed in a number of aspects, including the feature dimension reported, the number of memory items, the presentation timings of the memory items and cues, and the validity of the cue (the frequency with which it correctly indicated the item that would be probed). Only valid retro-cue trials were used for the analysis. As effects of set size were not the focus of the present study, where more than one set size was tested we treated each as an independent data set.

In addition to the retro-cue condition, one condition in each experiment was assigned as the control condition for purposes of our analysis. Three different types of condition could be designated as the control, to account for differences in methodology across

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