



Figure 7. Proportion Yes Responses as a Function of Difference between Probe and To-Be-Remembered Item (in Units of JND)

Twelve participants' data are shown in thin lines, with the average in thick red. These curves are well described by the exponential function of Equation 4. This function relates actual stimulus values to their mental representations. $P(\text{yes})$ responses indicate proportion of Yes responses. doi:10.1371/journal.pbio.0050056.g007

individual participants as well, and the parameters are similar in the individual participant fits and the fits to the average. The τ and σ parameters showed most variability across participants. Models in which the τ parameter was estimated from an independent dataset in which study lists comprised just one item are indicated. The value for A calculated from data with list length 1 was 0.93 for the data averaged over participants, with individual participant values ranging from 0.88 to 1.02. The value for τ calculated from data with list length 1 ranged from 0.43 to 1.41 across participants. When τ was allowed to vary in the five-parameter model, the value ranged from 0.97 to 3 (the maximum of the allowed range) across participants. The parameter τ and the criterion C have somewhat of a reciprocal relationship mathematically, and so their values depend on one another: as C decreases, τ increases.

Interestingly, the α parameter was not significantly less than 1, indicating that in this experiment, when participants had to remember only two stimuli, both stimuli were remembered equally well. When participants must maintain more stimuli in memory, however, they are more likely to forget stimuli presented earlier in the list, as is shown in Figure 4.

Note that the β parameter remained negative and with a similar value regardless of model. Note that in both the four- and five-parameter models, $\beta \sim -1$. This result is similar to that found by Kahana and Sekuler [1].

Results indicated that models must incorporate inter-item homogeneity in order to fit the data well. The three-parameter model that did not incorporate inter-item homogeneity (as shown in Figure 8A) accounted for only 51% of the variance (r^2), and had an Akaike information criterion (AIC) value (see Methods) of 1,010 (higher AIC values indicate worse fit [27]). On the other hand, the four-parameter model accounted for 78% of the variance (r^2), and

Table 1. Parameter Values for Models with Three, Four, or Five Free Parameters

| Model | Parameter | | | | |
|------------------|-----------|-------------------|----------|---------|------|
| | σ | τ | α | β | C |
| Three parameters | 1.11 | 0.67 ^a | 1 | — | 0.57 |
| Four parameters | 0.99 | 0.67 ^a | 1 | −1.12 | 0.43 |
| Five parameters | 1.04 | 1.69 | 1 | −1.10 | 0.12 |

^aModel in which the τ parameter was estimated from an independent dataset in which study lists comprised just one item.
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had a considerably lower AIC value of 652. The five-parameter model, allowing τ to vary according to the list length 2 data, accounted for 81% of the variance (r^2) and had a slightly higher AIC value of 696, indicating that the addition of this extra parameter does not make the model more generalizable.

Discussion

The ripple stimuli used here share many similarities with visual grating stimuli. Grating stimuli have long been a fixture of psychophysical experiments because they can be used to explore some properties of vision that are thought to be fundamental: spatial location, luminance, orientation, and spatial frequency. Similarly, the ripple sounds used in the present study can be used to examine some fundamental properties of hearing: frequency spectrum, sound level, and temporal frequency. The experiments presented here make use of the similarities to explore whether the fundamental information processing steps in vision and hearing are similar.

Moving ripple stimuli and visual gratings are processed by the nervous system in analogous ways, and therefore represent an important class of stimuli for comparing memory in the visual and auditory domains. Both auditory and visual cortical receptive fields have characteristic center-surround properties [7,9,15]. Further, edge detection in visual cortex appears to have an analog in auditory cortex [28]. Relatedly, both auditory and visual systems appear to exploit “sparse” coding [29]: when presented with stimuli of the appropriate type, individual cells respond very strongly to one example of the stimulus type and less strongly to other examples. In the visual modality, single primary visual cortical cells show large responses and specific tuning for oriented sine-wave gratings, or Gabor patches [9,30]. In the auditory modality, single primary auditory cortical cells show large responses and specific tuning for moving ripple stimuli [7,9,15].

Thus, early stages of cortical processing seem to treat Gabor patches and moving auditory ripples in an analogous fashion. Although a number of studies have examined recognition memory for Gabor patches [1,3], comparable tests of memory for auditory ripple stimuli have been lacking until now.

Parametrically manipulable stimuli were used in order to explore how memory alters the representation of stimuli. By using an auditory stimulus set for which early processing is