## Response to Comment on "Dynamic Shifts of Limited Working Memory Resources in Human Vision"

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Cowan and Rouder suggest that a modification to the four-slot model of visual working memory fits the available data better than our distributed resource model. However, their comparisons of statistical fit are biased in favor of the slot model. Here, we compare the predictions of the two models and present further evidence against the division of visual memory into slots.

long-standing and influential model of visual working memory proposes a fixed number of discrete memory slots, each storing one visual item (1-3). Recently, this "item-limit" model has been challenged by studies showing that the resolution with which items are held in memory depends on the number of items stored, even when this number is below the proposed limit (4-7). Rather than being stored in separate slots, these results suggest that discrete visual items share a common memory resource that must be distributed between them (Fig. 1, left). We have demonstrated (7) that performance on memory tasks can be captured by a power law describing how the proportion of resources allocated to an item determines the precision with which it is stored. Crucially, we have shown that this "resource" model also predicts the apparent discontinuity in change detection performance that provided the original incentive for dividing memory into slots.

Several attempts have been made to modify the item-limit model to see if it too can be made to account for changes in precision (5, 6, 8). One proposal by Zhang and Luck (8) allows slots to "double up" and store the same item, combined with an averaging process to obtain a single estimate per item. By taking a quote from our article out of context, Cowan and Rouder (9)might be misunderstood to suggest that we overlooked this hypothesis; in fact, we addressed this proposal in our supplementary text (7). Nonetheless, it is worth examining in more detail.

By allowing multiple slots to combine and thereby represent items with greater precision, this "slots + averaging" model behaves like a quantized version of the resource model, and so is almost indistinguishable from the resource model for small numbers of items (Fig. 1, right). Exceptions occur only when the number of slots is not divisible by the number of items, in which case some items must be allocated more slots than others. No evidence for such unequal allocation has been reported, and indeed this consideration appears to have been overlooked by both (8) and (9).

Once the number of items equals the number of slots, Zhang and Luck's model makes the strong prediction that any further increases in set size cannot affect the precision with which items are stored, only the probability that an item enters memory. In comparison, the resource model does not predict a "hard limit" on the number of items stored (although neither do we claim that resources will always be distributed equally among all items: outside of the laboratory, this will rarely be an optimal strategy).

If we accept Zhang and Luck's model, their results indicate that working memory capacity is limited to about two items (0.38 probability of storing any individual item in a six-item array) [figure 2A and supplementary figure 3 in (8)]. This claim is inconsistent with our previous finding that precision continues to decrease with set size up to at least six items, even when we allow for the possibility that some items are not stored [supplementary text and figure S3 in (7)]. Cowan and Rouder now present a reanalysis of our data, which they claim shows that the Zhang and Luck model fits the data slightly better than our resource model. However, their formulation of the slot model [equations 2 and 3 in (9)] has more free parameters than the resource model [equation 1 in (9)], rendering this comparison invalid (10). Indeed, their equation 1 provides a more than adequate fit to our full data set, as shown in Fig. 2A.

Nonetheless, Cowan and Rouder are correct to point out that the two models make the most divergent predictions when larger changes to stimuli are used. We have therefore repeated our experiment with a wider range of stimulus displacements (Fig. 2B). The "slots + averaging" model predicts that the response function will asymptote to a nonmaximal value once the number of slots is exceeded (blue dashed line). However, we find no evidence of this even for six items (blue symbols). As discussed previously [supplementary text in (7)], the true error distribution for a feature such as color or shape will be observed only if the tested parameter space corresponds to the parameter space in which the feature is stored in the brain. This may explain why Zhang and Luck (8), testing in an arbitrary color space, did not observe a Gaussian distribution at extreme values.

Cowan and Rouder also present an analysis from a previous study (11), in which the authors attempted to differentiate between item-limit and resource models without examining precision. Instead, they constructed mathematical models of performance in a change-detection task based on the competing theories and attempted to fit them to experimental data. The authors again claim that the item-limit model provides a better fit than the resource model. In fact, the item-limit model



Fig. 1. Allocation of visual working memory under the resource model (7) and the slots + averaging model (8). In the resource model (left), a common memory resource (yellow) is shared out between multiple visual items (black symbols). Larger circles indicate greater resources dedicated to representing an item in memory, and so greater precision on subsequent recall. In the slots + averaging model (right), memory is divided into discrete slots (here, four) of equal resolution (yellow circles), and multiple slots can combine to represent an item with increased precision. The two models make equivalent predictions for one, two, and four items. For three items, slots must be allocated unevenly in the slots + averaging model, so that one item is stored with greater precision than the others. When the number of items exceeds the number of slots, the slots + averaging model predicts that no information will be stored about items without a slot.

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**Fig. 2.** (**A**) Combined performance on location and orientation memory tasks as reported in (7). On each trial, *N* items were presented, then briefly blanked; one item reappeared, changed in either location or orientation, and subjects had to indicate the direction of change. Gaze was monitored to ensure that fixation was maintained. Stimulus change is plotted relative to the standard deviation of the N = 1 response function  $[\sigma_0 \text{ in } (9)]$ . Curves represent the maximum-likelihood fit of the resource

В 1.0 Probability of reporting +ve change 0.8 0.6 0.4 0.2 N = 4N = 6 (4-slot model) -⊶ N = 6 (actual data) 0 -12 -8 0 12 4 8 -4 Change to stimulus

model defined by equation 1 in (9). (B) New data from four subjects on the location memory task with an extended range of displacements (up to 10° of visual angle, corresponding to >11  $\sigma_0$ ). The green line indicates the slope of the mean response function for four items. The blue dashed line represents the N = 6 response function predicted by an item-limit model with four slots. Blue solid line and symbols indicate the actual N = 6 response function (error bars, ±1 SE).

fits their experimental data poorly (11), but rather than accepting this as evidence against the theory, the authors introduce an additional component: an attention parameter (*a*) intended to account for trials when subjects do not pay attention [see equations 4 and 5 in (9)]. Their comparison of statistical fit is clearly biased in favor of this extended slot model, because no attention component is included in their formulation of the resource model [equations 6 and 7 in (9)].

In conclusion, the item-limit model of visual memory cannot be brought into agreement with current results except by introducing new mechanisms, such as combining and averaging of memory slots, for which there is no behavioral evidence or known neurophysiological basis. In contrast, a resource model represents a highly parsimonious account of visual memory, able to explain both old and new results, and with a plausible neural basis in population coding (12).

## **References and Notes**

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