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Supporting Online Material for

Dynamic Shifts of Limited Working Memory Resources in Human Vision

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Materials & Methods

Methods.

Subjects and apparatus. A total of 32 experimentally-naïve subjects participated in the study after giving informed consent (age 19–42; 15 male, 17 female; all with normal or corrected-to-normal vision). Stimuli were presented on a 21” CRT monitor viewed at a distance of 70 cm, with a refresh rate of 140 Hz (mean delay <4 ms, phosphor persistence <1 ms). Eye position was monitored online at 1000 Hz using a frame-mounted infra-red eye tracker.

General procedure. Subjects reported the direction of a change to a visual item’s *location* or *orientation* that occurred during a brief blanking of the display. Stimuli consisted of colored squares (location task, 0.8º x 0.8º) or randomly-oriented colored arrows (orientation task, 1.25º radius) presented against a grey background. Stimulus colors were randomly selected on each trial, without repetition, from a set of highly discriminable colors (white, black, red, green, blue, yellow, cyan). Each trial began with a sample display of between one and six items, followed by a blanking period, brief presentation of a probe display, then the subject’s response. The probe display consisted of the reappearance of a randomly-chosen item from the sample display, displaced horizontally from its original position (0.5º, 2º, or 5º, leftward or rightward) or rotated (5º, 20º, or 45º, clockwise or counter-clockwise).

Experimental conditions differed in the eye movements made by subjects between presentation of the sample display and the probe display. In the first experiment (Figs 1 & 2), subjects either maintained fixation on a cross 10º from the centre of the stimulus array (*fixation* condition), or after 1000 ms made a saccade from the fixation cross towards one of the display items (*saccade* condition). In two further conditions (Fig. 4A & B), a flash of one of the sample display items after 1000 ms acted either as a signal to saccade to the flashed item (*saccade-to-cue* condition) or as an attention-grabbing but task-irrelevant distractor (*fixation-with-cue* condition). In the saccade conditions, blanking of the sample display was triggered by the onset of the eye movement; in the fixation conditions, the sample display period was adjusted to match display time in the saccade conditions. In the second experiment (Fig. 4C), the sample display consisted of five items and subjects had to fixate each item in turn, without revisiting any item: the blanking period was triggered by the onset of a saccade towards the final item. Full details of each experiment are given below.

Experiment 1. 16 subjects participated in this experiment, 8 on the location task and 8 on the orientation task. Following a short practice session, each subject completed a block of 160 trials in each of four conditions (*saccade*, *fixation*, *saccade-to-cue*, *fixation-with-cue*) in a counterbalanced order. All trials began with the presentation of a fixation cross deviated 7º horizontally from the display centre (alternating left or right on each trial). Once the subject was fixating the cross, the sample display was presented. The number of items in the sample display was varied from trial to trial (1, 2, 4 or 6 items). Items were randomly arranged within an invisible square (9º x 9º) centred 10º horizontally from the fixation cross, with a minimum separation of 3º between items.

On trials in the *saccade* condition, at an auditory go-signal (1000 ms after onset of the sample display) subjects made an eye-movement to one of the display items, specified by color (each subject was randomly allocated a color prior to the experiment that would indicate the saccade target on each trial). The onset of the saccade, determined by the detection of a horizontal gaze position deviated 2º or more from the fixation cross, triggered the blanking period (500 ms), followed by the probe display (250 ms). Subjects then indicated with a button-press in which direction they judged the probe item to have moved/rotated. To ensure only genuine saccades were included, any trial in which eye velocity was less than 50º s^{-1} at the time the display was blanked were rejected during offline analysis.

The *fixation* condition was identical to the saccade condition except that subjects maintained fixation on the cross throughout. The sample display period on fixation trials was matched to that on saccade trials based on an estimate of saccadic reaction time obtained from previous saccade trials or the initial practice session. *Saccade-to-cue* and *fixation-with-cue* conditions were identical to the corresponding conditions described above, except that a randomly chosen item flashed off (100 ms) and back on, beginning 1000 ms after onset of the sample display. On saccade-to-cue trials, this acted as a signal to saccade to the flashed item. On fixation-with-cue trials, subjects were instructed that the flashed item was irrelevant to the task. The flashed item was not predictive of the item to be probed, nor was the saccade target on saccade trials.

Experiment 2. A separate group of 16 subjects took part in this experiment, 8 on the location task and 8 on the orientation task. The sample display comprised five items: four items, separated by a minimum of 6º, randomly arranged on the circumference of an invisible circle (8º radius) centred on a fifth item. Subjects made eye movements from an initial fixation location to each item in turn, finishing with the central item. Each fixation on an item (criteria: distance < 1.5º, duration > 150 ms) was rewarded with an audible click, indicating to the subject that the fixation had been registered. Re-fixation of an item, or fixation of the central item out of order, caused the trial to be aborted, and immediately repeated with new randomly-generated stimulus parameters. Detection of a saccade towards the final item triggered the blanking period (250 ms), followed by the probe display (250 ms) and collection of the subject's response. As before, trials were rejected if eye velocity was found to be less than 50º s^{-1} at the time the display was blanked.

Analysis.

Statistical analysis. A probit regression model was used to estimate parameters of the cumulative gaussian distribution that best fit the relationship between response probability and stimulus displacement/rotation in each experiment. Any discrimination bias was indicated by the mean of the fitted gaussian (μ), and precision was determined by the reciprocal of the standard deviation ($1/\sigma$). Experimental parameters were identified as influencing precision if they had a significant ($p < 0.05$) effect on the *slope term* of the fitted regression model (Ref. S1). Bonferroni correction was used to correct for multiple comparisons.

Modelling of precision data. We used the mean precision estimates obtained in Experiment 1 to quantify the relationship between the precision with which an item is remembered (P) and the memory resources available to encode it (R). For a display of N items, the proportion of resources available for each item $\frac{R}{R_{max}}$ equals $\frac{1}{N}$. This value was plotted against the relative precision $\frac{P}{P_{max}}$, obtained by normalizing the mean precision estimate for each condition and set-size by precision in the $N = 1$ case (i.e. the maximum precision obtained when all resources are allocated to a single item). We approximated the relationship between these two variables with a power law:

$$\frac{P}{P_{max}} = \left(\frac{R}{R_{max}}\right)^k \tag{1}$$

The maximum likelihood value of k obtained from the data was then used to extrapolate estimates of relative precision to all set-sizes in the range 1–12 (Fig. 3B, solid line). The response functions corresponding to these precision estimates (assuming no discrimination bias) were determined by cumulative gaussian distributions with mean of zero and standard deviation $1/P$ (plotted in Fig. 3C; abscissa shows change to the stimulus in multiples of $\sigma = 1/P_{max}$).

As in the empirical data shown in Fig. 2, the predicted response curves become flatter with increasing number of items, reflecting changes in the distributions of error in the stored representation of the stimulus (Fig. 3C, inset). This has consequences for the ability to discriminate different magnitudes of stimulus change, as highlighted by the vertical lines. The dotted vertical line indicates a small change to the stimulus similar to that used in the current study – the probability of correctly discriminating the change falls rapidly with increasing number of items. In contrast, the dashed vertical line indicates a much larger stimulus change – in this case performance would be close to 100% for 1–4 items but fall with further increases in the number of items.

Comparison with change detection studies. In order to compare the predictions of our model with the results of earlier change detection studies, the probability of correctly identifying different magnitudes of stimulus change was determined from the response functions calculated in the previous step (Fig. 3D, black lines). This permitted a direct comparison with performance data from previous tests of visual memory capacity (green lines). To demonstrate the validity of the model, example results from the current study were also re-plotted as proportion of responses correct (red lines). The full results for all sizes of stimulus change are shown in Fig. S2. Both our data and the results from previous studies are consistent with the power-law model, with any apparent discrepancies explained simply by differences in the magnitude of stimulus change tested.

Estimating resource allocation. In Experiment 2, all N items in a display were fixated sequentially, and separate precision estimates $\{P_1, P_2, \ldots P_N\}$ were obtained for each item in the sequence. Given that the total resource $R_{\max}$ is equal to the sum of the resources allocated to each item, $\sum_{j=1}^{N} R_j$, it follows from (1) that the proportion of resources allocated to item i is given by

$$\frac{R_i}{R_{\max}} = \frac{R_i}{\sum_{j=1}^{N} R_j} = \frac{P_i^{1/k}}{\sum_{j=1}^{N} P_j^{1/k}} \tag{2}$$

By substituting into this equation the value of k obtained in the analysis of Experiment 1, we calculated the proportion of memory resources allocated to each item as a function of its order in the fixation sequence.

Comparison with Zhang & Luck (2008). In this study (*36*), subjects were presented with a brief sample display consisting of N colored items and then instructed to report the color of the item at a probed location by selecting from a color wheel. The distribution of errors was fitted with a mixture model comprising a (circular) gaussian distribution and a uniform distribution (Fig. S3 A, top). The response distribution predicted by this model is an 'elevated' gaussian function that tends to a non-zero value for large errors (blue curve, Fig. S3 A, top). Consistent with our results, at small set sizes the width of the guassian increased with increasing *N*. However, no significant change in gaussian width was observed when the set size increased from 3 to 6 items. The decrease in performance was instead attributed to the uniform distribution, which the authors interpreted as representing the number of 'guess' responses, and hence took to indicate that an upper limit on storage had been exceeded.

To test whether such a mixture model could account for our results, we performed an equivalent analysis on subjects' responses in our fixation condition. As ours is a discrimination rather than a report task, the equivalent model (illustrated in Fig. S3 A, bottom) is a mixture of a cumulative gaussian function (corresponding to a gaussian-distributed limited-precision memory of the item) and a uniform response function with probability 0.5 (corresponding to random guesses). The response distribution predicted by this mixture model is a 'compressed' sigmoidal function that, unlike a cumulative gaussian, does not asymptote to 0 or 1 for large stimulus changes (blue curve, Fig. S3 A, bottom).

We first normalized the data by estimated precision in the $N = 1$ case, and shifted the data to remove any bias. We then used a non-linear optimization algorithm to obtain maximum likelihood estimates (Ref. S2) for the two parameters of the model: the standard deviation of the cumulative gaussian (σ) and the mixture parameter (α, equivalent to P_m in (*36*)). The resulting fitted response curves are shown in Fig. S3 B (blue; curves fitted with a cumulative gaussian alone are shown in green for comparison).

Contrary to the Zhang & Luck model, the width of the gaussian component (σ) increased significantly with every increase in *N* (likelihood ratio test: $\chi^2 > 5.5$; $p < 0.02$). Hence, even when guesses are 'filtered out' by the uniform distribution, precision ($1/\sigma$) still decreases significantly with each increase in the number of items, including between 4 and 6 items (Fig. S3 C). The mixture parameter (α) showed some variation with number of items for smaller *N*, but, again unlike (*36*), we observe no change in α, and hence no increase in guessing, between 4 and 6 items ($\chi^2 < 0.01$; $p > 0.9$). The results of this reanalysis are therefore fully consistent with those described in the main body of this paper, and, contrary to (*36*), do not indicate any upper limit on the number of items that can be stored in visual memory.

Why do our findings differ from those of Zhang & Luck? One key difference is that eye movements were not controlled in their study. We have shown that making a saccade to an item has a substantial effect on the allocation of visual memory resources, enhancing the precision of memory for the saccade target and reducing precision for non-target items. However, the mixture model used by Zhang & Luck to analyse their data assumes that all stored items are represented with the same precision. While this assumption may be appropriate when eye movements are suppressed (as in our fixation condition) it is not valid when subjects are free to move their eyes, as we have demonstrated.

A second important difference between the two studies is in the choice of visual features investigated. We chose to test memory for object positions and orientations on the grounds that the internal representation of these features by neuronal populations is tolerably well understood (*17*). Theory predicts a gaussian distribution of error in the stored representation of a stimulus, but this gaussian distribution will only be observed if the tested parameter space corresponds to the internal parameter space in which the item is stored. The internal representation of object position and orientation can be considered at least monotonically related to absolute differences in distance or angle (e.g. we can reasonably assume that an absolute error of 20° in remembering a probed item's orientation corresponds to a larger *internal* misrepresentation of the stimulus than if the error were only 10°). In contrast, Zhang & Luck chose to test memory for object color and, in a second experiment, shape. In these cases, the parameter space of the internal representation is unknown and so the tested parameter space was chosen more or less arbitrarily (e.g. when the probed stimulus was in fact blue, a click on the yellow section of the color wheel was considered a greater error than a click on the red section). If this specification of the parameter space does not correspond to the internal representation of the tested feature, we would not expect the full gaussian distribution to be observed, with the result that larger internal errors might appear randomly distributed.

Supporting References

S1. P. McCullagh, J. Nelder, *Generalized Linear Models* (Chapman and Hall, London, 1989).

S2. I. J. Myung, *J Math Psy.* **47**, 90-100 (2003)

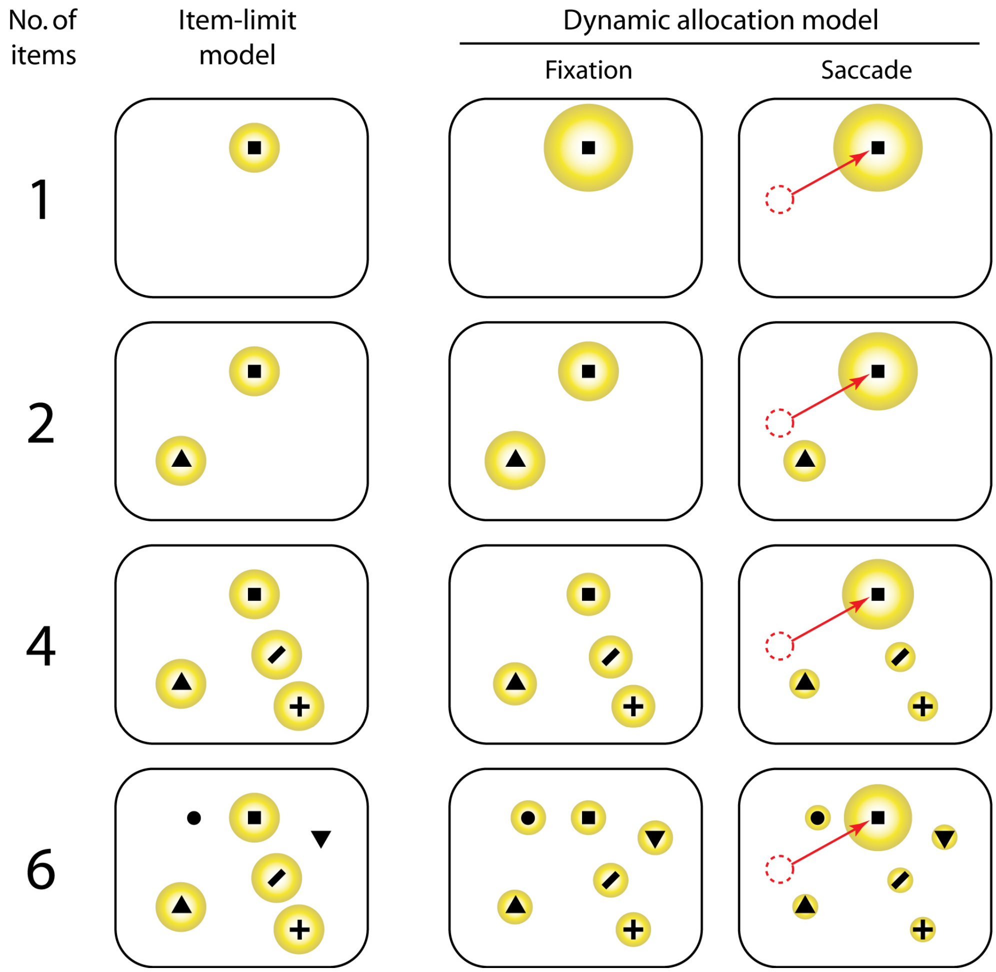

Fig. S1. Allocation of visual working memory.

The allocation of memory resources to multiple visual items (black symbols) is illustrated by the size of the yellow circles: larger circles indicate greater resources dedicated to representing an item in memory and so greater precision on subsequent recall. Red circles indicate gaze position. According to the item-limit model of memory capacity (left column), all items are remembered with equal precision up to the limit (here four), and no information is stored about items beyond this limit. In contrast, the dynamic allocation model proposes that limited memory resources must be shared out between items. In the absence of eye movements, resources may be shared equally (central column). Prior to a saccade (right column), the majority of resources are allocated to the saccade target, which is therefore remembered with greater precision than the other items after the saccade.

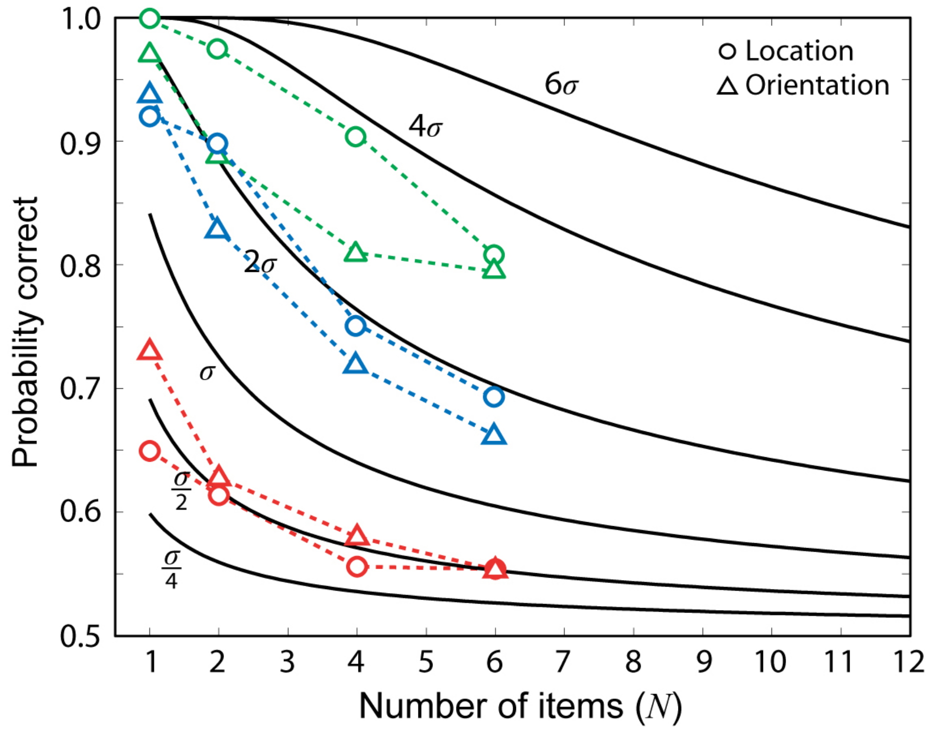

Fig. S2. Probability correct varies with the magnitude of change to be discriminated.

Probability correct for stimulus changes of different magnitudes (increasing *red-blue-green*). Data from Experiment 1, location task (circles): *red* 0.5°, *blue* 2°, *green* 5°; orientation task (triangles): *red* 5°, *blue* 20°, *green* 45°. Black lines indicate predictions of the power-law model, as in Fig. 3D. $\boldsymbol{\sigma}$ indicates one standard deviation of the N=1 response function.

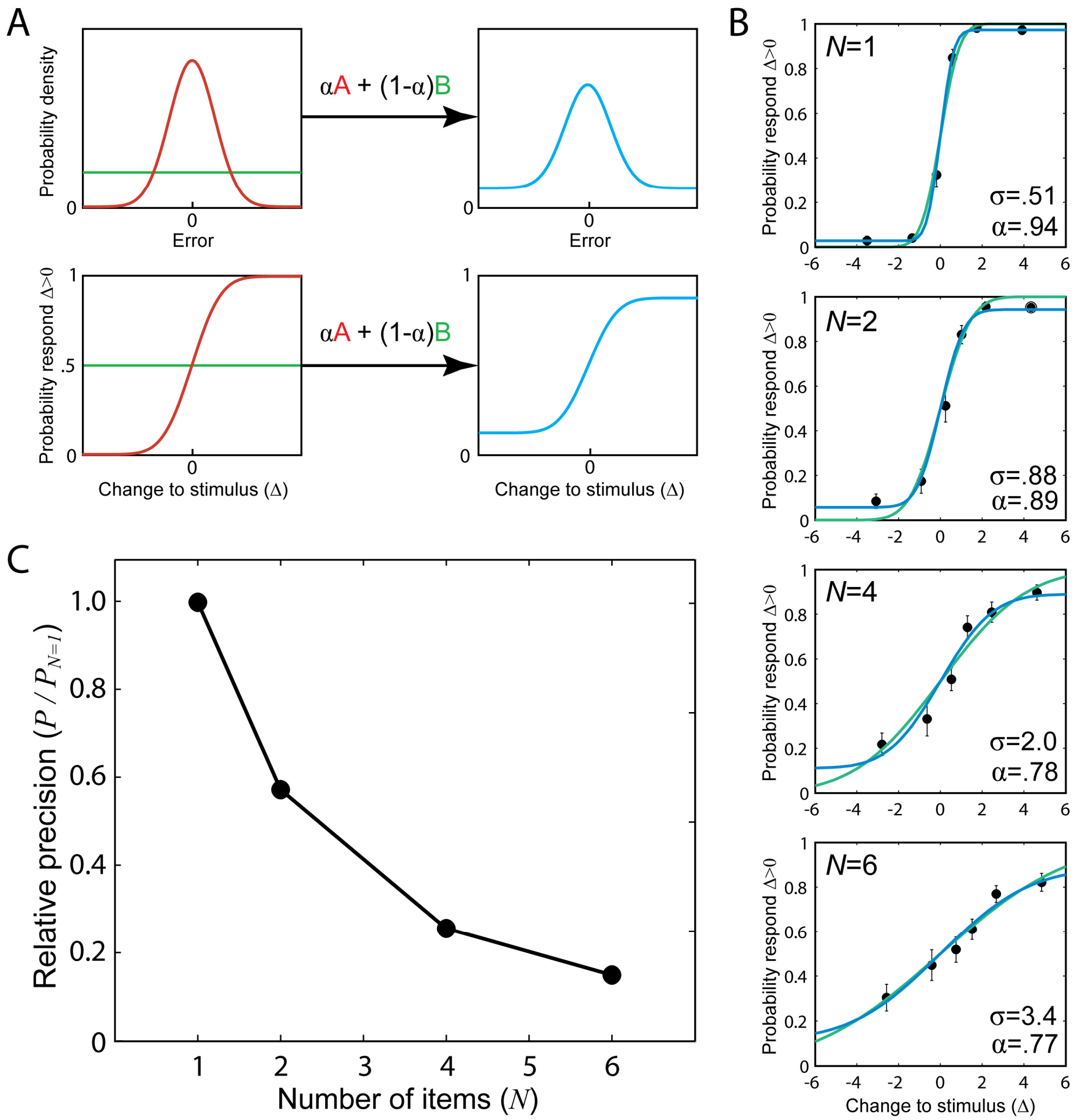

Fig. S3. Mixture model analysis.

(**A**) Illustration of the mixture model used in (*36*), top, and the equivalent model used in the reanalysis of our data, bottom. Subjects' responses are fitted with a mixture of two functions, one corresponding to a limited-precision memory of the probed item (red) and one corresponding to random guesses (green). Examples of the resulting combined distribution are shown in blue, for (*36*)'s report task (top) and our discrimination task (bottom).

(**B**) Response curves fitted to our data on the basis of a cumulative gaussian function alone (green) or the mixture model comprising cumulative gaussian and uniform components (blue). Note that the standard deviation of the gaussian component of the mixture model (σ) increases with each increment in the number of items (N). The mixture parameter (α) shows some variation with smaller N, but remains constant between 4 and 6 items.

(**C**) Relative precision calculated from the standard deviations of the cumulative gaussian component of the mixture model. Note that the monotonic dependence of precision on number of items is preserved, consistent with a limited resource model rather than a fixed number of items or 'slot' model.