

27. Henson, S. A. & Warner, R. R. Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. *Annu. Rev. Ecol. Syst.* **28**, 571–592 (1997).
28. Giraldeau, L. A. & Caraco, T. *Social Foraging Theory* (Princeton Univ. Press, Princeton, 2000).
29. Sober, E. & Wilson, D. S. *Unto Others* (Harvard Univ. Press, Cambridge, Massachusetts, 1998).
30. Boyd, R. & Richerson, P. J. Group selection among alternative evolutionarily stable strategies. *J. Theor. Biol.* **145**, 331–342 (1990).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank A. Dornhaus, M. Enquist, E. Fehr and L.-A. Giraldeau for comments on a previous version of this Letter.

Authors' contributions J.M.M. formulated the main ideas as a result of conversations with A.I.H.; J.M.M. also formulated the model, and was responsible for the material in Box 1; Z.B. carried out the computations, and prepared the figures; A.I.H. surveyed the literature, and had the main responsibility for writing the Letter.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.M.M. (john.mcnamara@bristol.ac.uk).

Neural activity predicts individual differences in visual working memory capacity

Edward K. Vogel & Maro G. Machizawa

Department of Psychology, University of Oregon, Eugene, Oregon 97403-1227, USA

Contrary to our rich phenomenological visual experience, our visual short-term memory system can maintain representations of only three to four objects at any given moment^{1,2}. For over a century, the capacity of visual memory has been shown to vary substantially across individuals, ranging from 1.5 to about 5 objects^{3–7}. Although numerous studies have recently begun to characterize the neural substrates of visual memory processes^{8–12}, a neurophysiological index of storage capacity limitations has not yet been established. Here, we provide electrophysiological evidence for lateralized activity in humans that reflects the encoding and maintenance of items in visual memory. The amplitude of this activity is strongly modulated by the number of objects being held in the memory at the time, but approaches a limit asymptotically for arrays that meet or exceed storage capacity. Indeed, the precise limit is determined by each individual's memory capacity, such that the activity from low-capacity individuals reaches this plateau much sooner than that from high-capacity individuals. Consequently, this measure provides a strong neurophysiological predictor of an individual's capacity, allowing the demonstration of a direct relationship between neural activity and memory capacity.

To measure the neural correlates of visual memory capacity, we recorded event-related potentials (ERPs) from normal young adults while they performed a visual memory task. On each trial they were presented with a brief bilateral array of coloured squares and were asked to remember the items in only one hemifield, which was indicated with an arrow (Fig. 1a). Memory was tested one second later with the presentation of a test array that was either identical to the memory array or differed by one colour. Subjects pressed one of two buttons to indicate whether the two arrays were identical or different. We have used variations of this paradigm previously and have found that observers are accurate for array sizes of up to three

to four items, and that performance is not significantly influenced by perceptual or verbal processes^{1,3}.

In the first experiment, we recorded ERPs to the onset of a four-item memory array so that we could observe the sustained electrophysiological response during the memory retention interval. A few previous ERP studies have observed a sustained response during working memory tasks for foveally presented stimuli, but did not examine lateralized effects^{13,14}. In contrast, we took advantage of the primarily contralateral organization of the visual system by presenting lateralized stimuli in each hemifield so that we could measure the spatially specific hemispheric responses to memory arrays that were either contralateral or ipsilateral with respect to electrode position^{15,16}. Approximately 200 ms after the onset of the memory array, we found a large negative-going voltage over the hemisphere that was contralateral to the memorized hemifield, and this response persisted throughout the duration of the memory retention interval (Fig. 1b). This response was focused primarily over the posterior parietal and lateral occipital electrode sites and strongly resembled delay activity recorded from individual neurons in monkey visual cortex^{12,17}.

Numerous processes contribute to visual memory performance, and we sought to determine which aspects of processing are reflected by the contralateral delay activity. Although this effect seems to reflect the maintenance of object representations from the memory array, it is necessary to rule out the possibility that it reflects executive processes¹⁸ involved in performing the task, or even more general processes such as increased effort or arousal^{19–21}. In the second experiment, we tested this by varying the number of items in the memory array to establish whether the amplitude is sensitive to the number of representations that are being held in visual memory. Memory arrays in this experiment varied from one to four items in each hemifield (average capacity in this task is normally around three items^{3,7}). To compare directly the magnitude of activity across array sizes, we constructed 'difference waves' in which the ipsilateral activity was subtracted from the contralateral activity for each array size, which removes the contribution of any nonspecific, bilateral ERP activity.

As shown in Fig. 2a, the amplitude was highly sensitive to the number of items in the memory array. Indeed, increasing an array

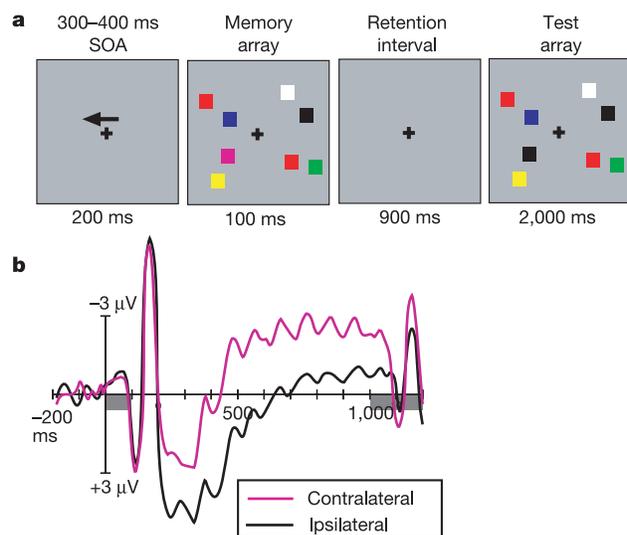


Figure 1 Stimuli and results from experiment one. **a**, Example of a visual memory trial for the left hemifield. SOA, stimulus onset asynchrony. **b**, Grand averaged ERP waveforms time-locked to the memory array averaged across the lateral occipital and posterior parietal electrode sites in experiment one. The two grey rectangles reflect the time periods for the memory and test arrays, respectively. Note that, by convention, negative voltage is plotted upwards.

from one to two squares or from two to three squares resulted in a substantial increase in amplitude. Moreover, because memory performance for near-capacity arrays can fluctuate over time, leading to occasional incorrect responses, we compared the amplitude of the delay activity for correct and incorrect trials. The amplitude for incorrect trials was considerably smaller than that for correct trials ($P < 0.01$), further suggesting that the delay activity specifically reflects the maintenance of successful representations in visual memory. Nevertheless, it is possible that the extent of executive processes also increases with additional memory items. Moreover, there are small but reliable differences in accuracy across array sizes, which leaves open the possibility that increases in arousal or effort for larger arrays may have produced the increase in amplitude.

The amplitude of the contralateral delay activity may have increased as the result of increasing the number of representations, more executive processing, or higher difficulty; however, these alternatives make different predictions for array sizes that exceed visual memory capacity. For example, when comparing a trial containing four memory items to a trial containing eight, the number of active memory representations should be approximately identical, because both trials exceed a typical individual's memory capacity. That is, the subject can maintain only three to four items whether the attended side of the array contains four or eight items. In contrast, the difficulty and extent of executive processing increases substantially for eight-item arrays compared with four-item arrays²². Indeed, this has been a significant limitation of previous neurophysiological studies that have reported memory load effects, because the amount of activity continues to increase for loads that exceed capacity, indicating that these measures are not directly measuring memory capacity^{10,21,23}. Therefore, in the third and fourth experiments, we compared the delay activity for supra-capacity arrays with memory arrays at or near capacity. If it reflects the active representations held in visual memory, we would expect no difference in amplitude between supra-capacity arrays and

capacity arrays. However, if it reflects executive processes or the amount of general effort, we would expect that amplitude should continue to increase for supra-capacity arrays.

The results of the third experiment show that although there was a significant increase in amplitude from arrays of two items per side to arrays of four items per side, there was no increase from four items to six items (Fig. 2b). That is, the amplitude reached a limit with arrays of approximately four items per side. We tested this further in the fourth experiment by following the same experimental design but with larger array sizes (Fig. 2c). Again we found a significant amplitude increase from two to four items per side, but no increase from four items to either eight or ten items per side. These results strongly support the hypothesis that the delay activity reflects the specific maintenance of representations in visual memory because its amplitude is sensitive to the number of successful representations that are active in memory at the time. In addition, the absence of continued amplitude increase beyond capacity also minimizes the possibility that the sub-capacity amplitude effects in

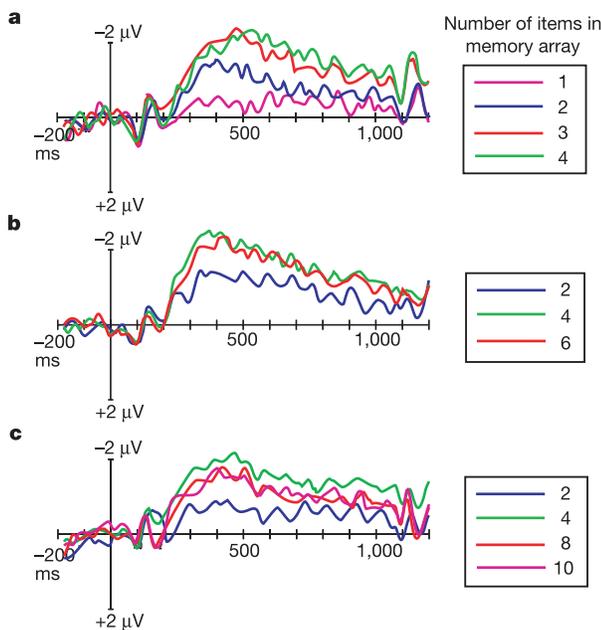


Figure 2 ERP difference waves at lateral occipital and posterior parietal electrode sites for experiments two, three and four, respectively. **a**, Pairwise comparisons yielded significant differences in amplitude between array sizes of one, two and three ($P < 0.001$), but no difference between three and four items ($P > 0.20$) in experiment two. **b, c**, No significant differences in amplitude were observed between arrays of four, six, eight or ten items ($P > 0.25$ in all cases) in experiments three and four.

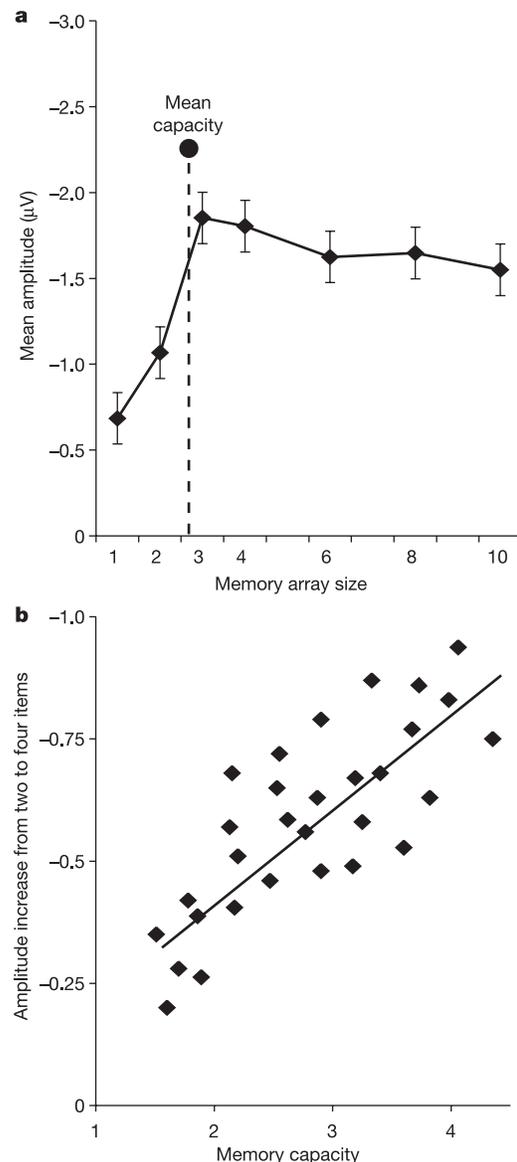


Figure 3 Mean amplitude and visual memory capacity. **a**, Mean amplitude and visual memory capacity across experiments two, three and four. Error bars reflect 95% confidence intervals. **b**, The correlation between an individual subject's memory capacity and the increase in amplitude of delay activity between two- and four-item arrays.

the second experiment were because of increases in the size of the 'attentional spotlight'²⁴, because supra-capacity arrays require a larger spotlight than at- or below-capacity arrays, but show no increases in amplitude.

The supra-capacity array sizes in these experiments provided substantial increases in both the extent of executive processes and the difficulty in performing the task. For example, there was a 32% reduction in accuracy between arrays of four and ten items, yet there was no increase in the amplitude of the contralateral delay activity. Furthermore, we also observed a more centrally distributed bilateral wave during the task that was modulated by the number of items in the memory array. However, in sharp contrast to the contralateral activity, the amplitude of this bilateral wave continued to increase significantly for arrays that exceeded memory capacity, suggesting that it is sensitive to the amount of general effort involved in performing the task²¹.

These results suggest that the contralateral delay activity indexes the currently active representations maintained in visual memory; that is, increasing in magnitude as the number of items increases, but reaching a limit once visual memory capacity is exhausted. To demonstrate this effect further, we quantified the mean amplitudes for each array size for experiments two to four. As shown in Fig. 3a, amplitude increased monotonically from one to three items, but this increase levelled off at three items. We also computed visual memory capacity estimates for each subject, using a standard formula^{7,25}. The mean capacity of the group was 2.8 items, which is approximately when the memory delay activity reaches a limit. This further supports the proposal that the specific limitation in visual memory capacity determines when this delay activity reaches a limit.

To gauge this relationship more finely, we examined the variability across individuals for each measure. That is, we assessed whether a given individual's memory capacity specifically dictates when his or her delay activity reaches a limit. If so, one would expect low-capacity subjects to reach the limit for smaller array sizes than would high-capacity subjects. Unfortunately, it is difficult to determine precisely the limit with a categorical data set such as array size (for example, there is no array size of 2.6). Instead, we computed the amplitude increase between two items and four items per side for each subject across all experiments, the logic being that the amount of amplitude increase between these two array sizes should be specifically determined by memory capacity. For example, when a subject with a low capacity of 1.8 items is shown a two-item array, capacity should be completely consumed with the amplitude reaching a limit, resulting in little or no amplitude increase from two to four items. In contrast, a subject with a high capacity of 4.5 items would be expected to be well below the limit for a two-item array, and should therefore show a large increase in amplitude for a four-item array.

The magnitude of the amplitude increase between two and four items was plotted as a function of each subject's memory capacity in Fig. 3b. These two measures were very strongly correlated ($r = 0.78$; $P < 0.0001$), with low-capacity subjects producing very little amplitude increase and high-capacity subjects showing larger amplitude increases. Importantly, an individual's memory capacity was not significantly correlated with either the amplitude increase between arrays of four and six items or the absolute amplitude of activity for a given array size.

These results show that the observed memory delay activity indexes the maintenance of active representations in visual memory. Moreover, they demonstrate a strong neurophysiological predictor of visual memory capacity. That is, simply by measuring the amplitude increase across memory array sizes, we could accurately predict an individual's memory capacity. Visual working memory is thought to have a central role within cognition because it maintains representations from the environment so that they may be acted on or manipulated^{3,26}. Indeed, an individual's ability to perform many

high-level cognitive functions has been shown to be directly influenced by his or her memory capacity^{5,27–29}. These results provide the first link between this important cognitive limitation and neural activity. □

Methods

Twelve neurologically normal college students participated in each experiment (age range of 21–33) and gave informed consent according to procedures approved by the University of Oregon. Each of these observers performed 240 trials per condition in each experiment. All stimulus arrays were presented within two $4^\circ \times 7.3^\circ$ rectangular regions that were centred 3° to the left and right of a central fixation cross on a grey background (8.2 cm^{-2}). Each memory array consisted of 1–10 coloured squares ($0.65^\circ \times 0.65^\circ$) in each hemifield. Each square was selected at random from a set of seven highly discriminable colours (red, blue, violet, green, yellow, black and white), and a given colour could appear no more than twice within an array. Stimulus positions were randomized on each trial, with the constraint that the distance between squares within a hemifield was at least 2° (centre to centre). The colour of one square in the test array was different from the corresponding item in the memory array in 50% of trials; the colours of the two arrays were identical on the remaining trials. At the beginning of each trial, a central arrow cue instructed the subjects to remember the items in either the left or the right hemifield.

We computed visual memory capacity using a formula developed by Pashler²³ and refined by Cowan⁷. Essentially, this approach assumes that if an observer can hold K items in memory from an array of S items, then the item that changed should be one of the items being held in memory on K/S trials, leading to correct performance on K/S of the trials on which an item changed. To correct for guessing, this procedure also takes into account the false alarm rate. The formula is $K = S \times (H - F)$, where K is the memory capacity, S is the size of the array, H is the observed hit rate and F is the false alarm rate.

ERPs were recorded in each experiment using our standard recording and analysis procedures³⁰, including rejection of trials contaminated by blinks or large ($>1^\circ$) eye movements. We recorded from 22 standard electrode sites (international 10/20 system) spanning the scalp. We computed contralateral waveforms by averaging the activity recorded at right hemisphere electrode sites when subjects were cued to remember the left side of the memory array with the activity recorded from the left hemisphere electrode sites when they were cued to remember the right side. Contralateral delay activity was measured at posterior parietal, lateral occipital and posterior temporal electrode sites as the difference in mean amplitude between the ipsilateral and contralateral waveforms, with a measurement window of 300–900 ms after the onset of the memory array.

Received 23 December 2003; accepted 26 February 2004; doi:10.1038/nature02447.

- Luck, S. J. & Vogel, E. K. The capacity of visual working memory for features and conjunctions. *Nature* **390**, 279–281 (1997).
- Sperling, G. The information available in brief visual presentations. *Psychol. Monogr.* **74**, Whole No. 498 (1960).
- Vogel, E. K., Woodman, G. F. & Luck, S. J. Storage of features, conjunctions, and objects in visual working memory. *J. Exp. Psychol. Hum. Percept. Perform.* **27**, 92–114 (2001).
- Jevons, W. S. The power of numerical discrimination. *Nature* **3**, 281–282 (1871).
- Engle, R. W., Kane, M. J. & Tuholski, S. W. in *Models of Working Memory: Mechanisms of Active Maintenance and Executive Control* (eds Miyake, A. & Shah, P.) 102–134 (Cambridge Univ. Press, New York, 1999).
- Miller, G. A. The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychol. Rev.* **63**, 81–97 (1956).
- Cowan, N. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behav. Brain Sci.* **24**, 87–185 (2001).
- Jonides, J. et al. Spatial working memory in humans as revealed by PET. *Nature* **363**, 623–625 (1993).
- Courtney, S. M., Ungerleider, L. G., Keil, K. & Haxby, J. V. Transient and sustained activity in a distributed neural system for human working memory. *Nature* **386**, 608–611 (1997).
- Cohen, J. D. et al. Temporal dynamics of brain activation during a working memory task. *Nature* **386**, 604–608 (1997).
- Miller, E. K., Erickson, C. A. & Desimone, R. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J. Neurosci.* **16**, 5154–5167 (1996).
- Fuster, J. M. & Jervey, J. P. Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. *J. Neurosci.* **2**, 361–375 (1982).
- Ruchkin, D., Johnson, R., Grafman, J., Canoune, H. & Ritter, W. Multiple visuospatial working memory buffers: Evidence from spatiotemporal patterns of brain activity. *Neuropsychologia* **35**, 195–209 (1997).
- Ruchkin, D., Johnson, R., Canoune, H. & Ritter, W. Short-term memory storage and retention: An event-related brain potential study. *Electroencephalogr. Clin. Neurophysiol.* **76**, 419–439 (1990).
- Gratton, G. The contralateral organization of visual processing: A theoretical concept and a research tool. *Psychophysiology* **35**, 638–647 (1998).
- Woodman, G. F. & Luck, S. J. Electrophysiological measurement of rapid shifts of attention during visual search. *Nature* **400**, 867–869 (1999).
- Miller, E. K., Li, L. & Desimone, R. Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *J. Neurosci.* **13**, 1460–1478 (1993).
- Baddeley, A. Exploring the central executive. *Q. J. Exp. Psychol. A* **49**, 5–28 (1996).
- Hillyard, S. A., Vogel, E. K. & Luck, S. J. Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Phil. Trans. R. Soc. Lond. B* **353**, 1257–1270 (1998).
- Rypma, B. & D'Esposito, M. D. The roles of prefrontal brain regions in components of working memory. *Proc. Natl. Acad. Sci. USA* **96**, 6558–6563 (1999).
- Ruchkin, D., Canoune, H., Johnson, R. & Ritter, W. Working memory and preparation elicit different patterns of slow wave event-related brain potentials. *Psychophysiology* **32**, 399–410 (1995).

22. Rypma, B. & D'Esposito, M. D. A subsequent-memory effect in dorsolateral prefrontal cortex. *Cogn. Brain Res.* **16**, 162–166 (2003).
23. Rypma, B., Prabhakaran, V., Desmond, J., Glover, G. H. & Gabrieli, J. D. Load-dependent roles of frontal brain regions in the maintenance of working memory. *Neuroimage* **9**, 216–226 (1999).
24. Eriksen, C. W. & St James, J. D. Visual attention within and around the field of focal attention: A zoom lens model. *Percept. Psychophys.* **40**, 225–240 (1986).
25. Pashler, H. Familiarity and visual change detection. *Percept. Psychophys.* **44**, 369–378 (1988).
26. Logie, R. H. *Visuo-Spatial Working Memory* (Erlbaum, Hove, UK, 1995).
27. Kane, M. J. & Engle, R. W. Working memory capacity and the control of attention: The contributions of goal neglect, response competition, and task set to Stroop interference. *J. Exp. Psychol. Gen.* **132**, 47–70 (2003).
28. Daneman, M. & Merikle, P. M. Working memory and language comprehension: A meta-analysis. *Psychon. Bull. Rev.* **3**, 422–433 (1996).
29. Kyllonen, P. C. & Christal, R. E. Reasoning ability is (little more than) working memory capacity. *Intelligence* **14**, 398–433 (1990).
30. Vogel, E. K., Luck, S. J. & Shapiro, K. L. Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *J. Exp. Psychol. Hum. Percept. Perform.* **24**, 1656–1674 (1998).

Acknowledgements The research reported here was supported by a grant from the US National Institute of Mental Health.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to E.K.V. (vogel@darkwing.uoregon.edu).

Capacity limit of visual short-term memory in human posterior parietal cortex

J. Jay Todd & René Marois

Vanderbilt Vision Research Center, Department of Psychology, Vanderbilt University, 530 Wilson Hall, Nashville, Tennessee 37203, USA

At any instant, our visual system allows us to perceive a rich and detailed visual world. Yet our internal, explicit representation of this visual world is extremely sparse: we can only hold in mind a minute fraction of the visual scene^{1,2}. These mental representations are stored in visual short-term memory (VSTM). Even though VSTM is essential for the execution of a wide array of perceptual and cognitive functions^{3–5}, and is supported by an extensive network of brain regions^{6–9}, its storage capacity is severely limited^{10–13}. With the use of functional magnetic resonance imaging, we show here that this capacity limit is neurally reflected in one node of this network: activity in the posterior parietal cortex is tightly correlated with the limited amount of scene information that can be stored in VSTM. These results suggest that the posterior parietal cortex is a key neural locus of our impoverished mental representation of the visual world.

To investigate the neural basis of VSTM's storage capacity limit, 17 subjects were scanned while performing a parametric load manipulation¹⁴ of a delayed visual matching-to-sample task (Fig. 1). On each trial, subjects were briefly presented with a sample display containing one to eight coloured discs and, after a 1,200-ms retention interval, decided whether a single probe disc matched one of the sample discs in location and colour. A 1,200-ms delay maximizes VSTM's capacity: with delays shorter than 1 s, VSTM capacity is inflated by sensory (iconic) representations of the display¹⁵, whereas long delays not only underestimate VSTM capacity owing to memory degradation¹⁵, but also favour the recruitment of rehearsal mechanisms and verbal/abstract recoding of the visual material¹⁶. To minimize verbal strategies further, a verbal working-

memory/articulatory suppression task was administered concurrently with the VSTM task: throughout the trial, subjects rehearsed two digits presented at trial onset and reported them at trial offset. Performance in this task was high and independent of VSTM set size (92–94% accuracy across set sizes; $F_{5,80} = 0.64$, $P = 0.67$), attesting to the absence of a trade-off between the verbal and visual tasks, as predicted from the independence of these two working-memory systems^{17,18}.

Accuracy in the VSTM task declined with increased set size (set size 1, 97.7%; set size 2, 94.2%; set size 3, 90.0%; set size 4, 86.2%; set size 6, 73.3%; set size 8, 68.5%). The number of objects encoded at each set size, estimated with Cowan's K formula¹¹, increased up to set size 3 or 4, and levelled off thereafter (Fig. 2; t -test between set sizes 4 and 8, $P > 0.05$). This behavioural function is fitted significantly better by a quadratic function than by a linear function ($P = 0.01$)¹⁹. Thus, VSTM storage capacity is about three or four items, which is consistent with previous studies^{11,13}. Importantly, this capacity limit is not due to insufficient time to encode items in VSTM⁴. Tripling the sample presentation time from 150 to 450 ms in a separate experiment did not affect the K function ($n = 16$, $P = 0.28$), an observation consistent with previous findings^{12,13}. The VSTM task therefore expresses the capacity limit of VSTM storage as opposed to a limitation in spatially attending to the display or encoding items in VSTM.

The brain substrates mediating VSTM's storage capacity limit should demonstrate a response profile paralleling the behavioural K function: activation should increase until set size 3 or 4 and level off thereafter. To isolate such regions, a voxel-based multiple regression analysis with K -weighted set size coefficients was performed. The resulting statistical parametric maps revealed a single bilaterally symmetric area in the intraparietal and intraoccipital sulci (IPS/IOS; $P < 0.05$ corrected). Time-course analysis (Fig. 3a) confirmed a strong correlation between the IPS/IOS peak response amplitude and the number of objects encoded ($r = 0.54$, $P < 0.001$; Fig. 2). The peak blood oxygenation level-dependent (BOLD) response function reached a plateau by set size 4 (t -test between 4 and 8, $P < 0.05$) and was better described by a quadratic function than by a linear function ($P < 0.01$). This parietal activation is not simply related to task difficulty: accuracy decreased and reaction

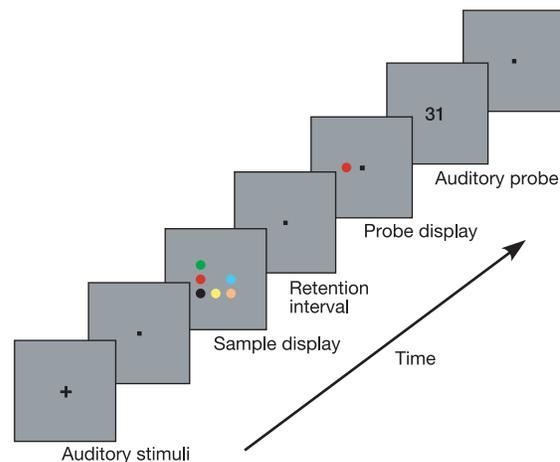


Figure 1 Trial design. Each trial began with the auditory presentation of two digits to be rehearsed throughout the trial. A sample display containing a variable number of coloured discs was then presented for 150 ms, followed by a 1,200-ms retention period, and then by a single coloured probe disc. Subjects judged whether the colour of the probe matched the colour of the disc shown at the same position in the sample display. Afterwards, two digits appeared and subjects indicated whether these were the same as those presented at trial onset.