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The capacity of visual working memory for features and conjunctions

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Short-term memory storage can be divided into separate sub-systems for verbal information and visual information[1], and recent studies have begun to delineate the neural substrates of these working-memory systems[2–6]. Although the verbal storage system has been well characterized, the storage capacity of visual working memory has not yet been established for simple, supra-threshold features or for conjunctions of features. Here we demonstrate that it is possible to retain information about only four colours or orientations in visual working memory at one time. However, it is also possible to retain both the colour and the orientation of four objects, indicating that visual working memory stores integrated objects rather than individual features. Indeed, objects defined by a conjunction of four features can be retained in working memory just as well as single-feature objects, allowing sixteen individual features to be retained when distributed across four objects. Thus, the capacity of visual working memory must be understood in terms of integrated objects rather than individual features, which places significant constraints on cognitive and neurobiological models of the temporary storage of visual information[7].

To measure the capacity of working memory for simple features, we used a variant of the sequential comparison procedure developed by Phillips[8]. Subjects viewed a sample array and a test array on each trial, separated by a brief delay, and then indicated whether the two arrays were identical or differed in terms of a single feature. The accuracy of this discrimination was assessed as a function of the number of items in the stimulus array (the set size) to determine how many items could be accurately retained in working memory. In addition, control experiments were conducted to ensure that performance truly reflected the capacity of visual working memory and was not influenced by verbal working memory or by limitations in perception, memory encoding, or decision processes.

The first set of experiments examined working memory capacity for simple colours (Fig. 1a). The sample array consisted of 1–12 coloured squares and was presented for 100 ms. This was followed by a 900-ms blank delay interval and then a 2,000-ms presentation of the test array, which was either identical to the sample array or differed in the colour of one of the squares. Performance was nearly perfect for arrays of 1–3 items and then declined systematically as the set size increased from 4 to 12 items. According to the method for estimating memory capacity described by Pashler[9], these data indicate that the observers were able to retain the colours of roughly four items in working memory, which is similar to previous estimates for alphanumeric characters[21].

To demonstrate that this estimate of capacity accurately reflects limitations in visual working memory with no significant contribution from verbal working memory, we tested the effects of adding a verbal memory load. In half of the trial blocks, the observers were presented with two digits before each sample array and were required to hold these digits in memory and then say them aloud at the end of the trial. Adding a verbal load did not significantly alter performance on the colour task (Fig. 1a), indicating that our capacity estimate was not influenced by verbal working memory.

It was also necessary to demonstrate that the relatively small memory capacity observed in this experiment was not a result of limitations in processes other than working-memory storage. To rule out limitations in perceiving the stimuli and encoding them in working memory, we varied the duration of the sample stimulus, comparing the original 100-ms duration with a 500-ms duration. This allowed substantially more time for perceiving the stimuli and encoding them in memory, which should have led to improved performance if these were limiting factors. However, performance was not significantly influenced by variations in sample duration (Fig. 1b), indicating that the errors at set sizes of 4–12 reflected limitations in storage capacity rather than limitations in perceiving or encoding the stimuli.

We next examined the possibility that performance was limited by decision factors. At larger set sizes, more decisions must be made, and this can lead to an increase in errors even in the absence of any capacity limitations[10,11]. To rule out this explanation, we conducted an experiment in which the memory requirements were the same as in the original experiment but only a single decision was necessary, regardless of the set size. Specifically, we used a partial report procedure in which we cued the observers to make a decision about only one of the items in the test array by presenting an outline box around the one item that might have been different from the sample array. This required them to retain information from all of the items in the sample array, but allowed them to restrict decision processes to a single item in the test array. As shown in Fig. 1b, this manipulation did not significantly alter performance, indicating that accuracy was not limited by decision factors (or, alternatively, that the subjects were unable to use the cue box effectively, which seems unlikely given that previous studies have found similar cues to be very effective in improving performance in decision-limited tasks[12,13]).

To determine whether capacity is different for different feature dimensions, memory for orientation was compared with memory for colour using 4, 8 or 12 bars that varied both in colour and in orientation. The observers were instructed to detect either colour changes or orientation changes (in different trial blocks), and a verbal load was used in both cases. The effects of set size on accuracy were nearly identical for colour and orientation, with a capacity of about four items for both feature types.

We then assessed whether visual information is stored in working memory as individual features or as integrated objects. This was tested by comparing memory for simple features with memory for objects defined by a conjunction of features. Observers performed the same sequential comparison task used above (while performing a concurrent verbal load task) with arrays of 2, 4 or 6 coloured bars of varying orientations. Relatively small set sizes were used so that the objects could be widely spaced, which was necessary to avoid 'illusory conjunctions' in the perception of the bars[14]. In one condition, only colour could vary between the sample array and the test array, and the observers were instructed to look for a colour change. In a second condition, only orientation could vary, and the

observers were instructed to look for an orientation change. In the third and critical condition, either colour or orientation could vary, and the observers were required to remember both features of each object. In this last condition, accurate performance with a set size of four objects would require the observer to retain eight features (four colours and four orientations), whereas only four features would be required for accurate performance in the simple feature conditions. Performance was essentially identical for the feature and conjunction conditions despite the greater total number of features that had to be retained in the conjunction condition (Fig. 1c). This indicates that visual working memory stores integrated object percepts rather than individual features, just as verbal working memory can store higher-order 'chunks'[15]. This is also analogous to findings from visual attention experiments, which have shown that attention is directed to entire objects rather than to individual features and that, consequently, two features of a given object can be reported as accurately as a single feature[16].

Because the stimulus arrays shown in Fig. 1c always varied in both colour and orientation, it is possible that the subjects were unable to avoid encoding both features even when only one feature was relevant. To rule out this potential explanation of the similar results obtained for the feature and conjunction conditions, a second version of this experiment was conducted in which the irrelevant feature dimension was held constant in the single-feature conditions (all of the rectangles were black when the subjects were required to remember orientation and all were vertical when the subjects were required to remember colour). The results were virtually identical to those shown in Fig. 1c, with statistically indistinguishable performance in the feature and conjunction conditions.

To extend these findings, we conducted an experiment in which the objects were defined by a conjunction of four features: colour, orientation, size and the presence or absence of a gap. Performance was just as good in this quadruple conjunction condition as it was in the individual feature conditions (Fig. 1d), indicating that 16 features distributed across 4 objects can be retained as accurately as 4 features distributed across 4 objects.

The surprisingly good performance for conjunctions could be explained by the use of separate, independent memory systems for each feature type rather than the storage of integrated object representations. To rule out this possibility, we examined colour–colour conjunctions in which each object consisted of a large square of one colour and a small inner square of a different colour. Observers were just as accurate with these colour–colour conjunctions as they were with either the large outer squares or the small inner squares presented alone (Fig. 1e). Thus, eight colours distributed across four objects can be retained as accurately as four colours distributed across four objects. Because both features of each object consisted of colours, the high accuracy observed in the conjunction condition cannot be explained by the existence of independent memory systems for different features.

These results indicate that integrated object percepts are stored in visual working memory, leading to a large capacity for retaining individual features as long as the features are confined to a small number of objects. Although there may be limits on the number of features that can be linked together in a single object representation, our results indicate that at least four features can be joined in this manner with no cost in terms of storage capacity.

The present findings have important implications for both the nature of the input to, as well as the contents of, visual working memory. Specifically, studies of selective attention indicate that attentional processes are used to combine the features of an object
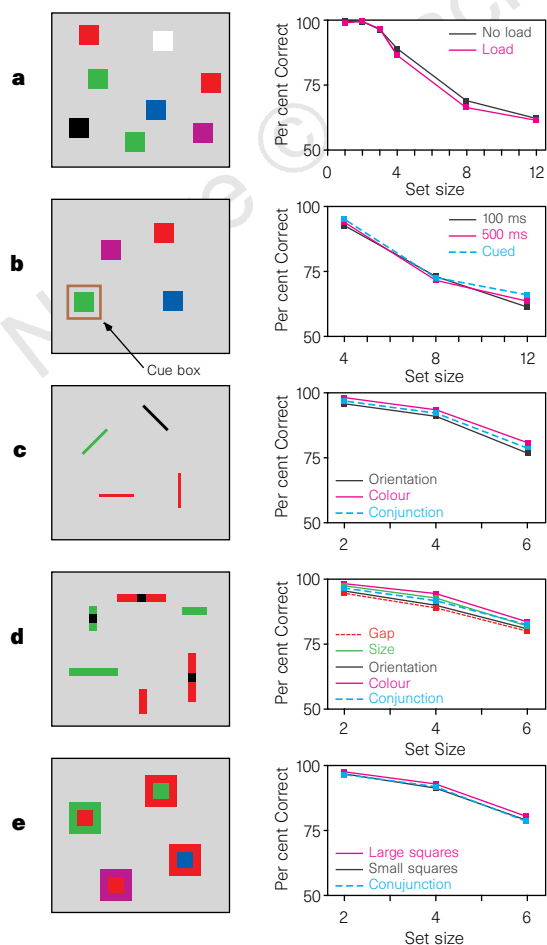

Figure 1 Example stimulus arrays (not drawn to scale) and performance on the sequential comparison task. All set size effects shown here were statistically significant at the $P < 0.001$ level (ANOVA). No other effects approached the $P < 0.05$ level of significance. **a**, Performance with and without a verbal load for simple colour stimuli. **b**, Comparison of 100-ms and 500-ms sample durations for simple colour stimuli (with a verbal load and no cue box). Also shown is the performance in a similar experiment with a cue box that indicated the one item that might have changed colour (100-ms sample duration and no verbal load). **c**, Comparison of performance when the observers were instructed to detect a colour change, an orientation change or a change in either feature (conjunction task). **d**, Comparison of performance for each of four simple features and the conjunction of all four features. **e**, Comparison of performance for colour–colour conjunctions versus the individual large and small squares.

into an integrated percept[17], and it is these integrated object percepts that appear to be stored in visual working memory. Neurobiological accounts of working memory must therefore include a mechanism for keeping the features of an object bound together during the retention interval. A leading candidate mechanism is the use of oscillatory or temporally correlated firing patterns among the neurons that code the features of an object[18–20]. Such a mechanism can also readily explain the relatively small number of objects that can be held in working memory concurrently: as the number of concurrent objects increases, the possibility of accidental correlations between neurons that code different objects also increases[7]. However, this would not necessarily place any limits on the number of features that can be bound together into a single object representation, which is consistent with our findings. □

Methods

Ten neurologically normal college students participated in each experiment. Each of these observers received 32–40 trials in each condition, where a condition consisted of a combination of set size and some other variable, such as the presence or absence of a verbal load.

All stimulus arrays were presented within a $9.8° \times 7.3°$ region on a video monitor with a grey background ($8.2\,cd\,m^{-2}$), and the items in a given array were separated by at least $2.0°$ (centre to centre). One feature of one item in the test array was different from the corresponding item in the sample array on 50% of trials; the sample and test arrays were otherwise identical.

The experiments shown in Fig. 1a used sample arrays consisting of 1, 2, 3, 4, 8 or 12 coloured squares ($0.65° \times 0.65°$), each of which was selected at random from a set of 7 highly discriminable colours (red, blue, violet, green, yellow, black and white). The experiments shown in Fig. 1b used the same stimuli, but set size was limited to 4, 8 or 12 items.

The experiments testing combinations of colour and orientation (Fig. 1c) used arrays of $0.03° \times 1.15°$ rectangles, each of which was constructed by combining one of four orientations (vertical, horizontal, $-45°$ and $+45°$) with one of four colours (red, green, blue and black). The stimuli used in the experiment shown in Fig. 1d were combinations of horizontal or vertical, red or green, small or large ($0.13° \times 1.0°$ or $0.13° \times 2.0°$) and continuous or broken (broken by a $0.26°$ black gap).

The colour–colour conjunction stimuli shown in Fig. 1e consisted of a small square ($0.65° \times 0.65°$) embedded in a large square ($1.3° \times 1.3°$). The inner and outer colours for a given object were selected from the set of red, green, violet and blue with the constraint that the inner and outer colours were always different from each other. The simple feature conditions of this experiment used either the large squares presented alone or the small squares presented alone.

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A role for the Ras signalling pathway in synaptic transmission and long-term memory

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Members of the Ras subfamily of small guanine-nucleotide-binding proteins are essential for controlling normal and malignant cell proliferation as well as cell differentiation[1]. The neuronal-specific guanine-nucleotide-exchange factor, Ras-GRF/CDC25Mm (refs 2–4), induces Ras signalling in response to Ca^{2+} influx[5] and activation of G-protein-coupled receptors *in vitro*[6], suggesting that it plays a role in neurotransmission and plasticity *in vivo*[7]. Here we report that mice lacking Ras-GRF are impaired in the process of memory consolidation, as revealed by emotional conditioning tasks that require the function of the amygdala; learning and short-term memory are intact. Electrophysiological measurements in the basolateral amygdala reveal that long-term plasticity is abnormal in mutant mice. In contrast, Ras-GRF mutants do not reveal major deficits in spatial learning tasks such as the Morris water maze, a test that requires hippocampal function. Consistent with apparently normal hippocampal functions, Ras-GRF mutants show normal NMDA (*N*-methyl-D-aspartate) receptor-dependent long-term potentiation in this structure. These results implicate Ras-GRF signalling via the Ras/MAP kinase pathway in synaptic events leading to formation of long-term memories.

Several distinct mechanisms leading to Ras activation and initiation of the MAP kinase (MAPK) cascade have been elucidated[8]. Growth-factor receptors of the tyrosine kinase family activate Ras proteins by recruiting the ubiquitously expressed Sos exchange