

intermixed. On each trial, a fixation cross appeared for 200 ms, followed by a stimulus member in the centre of the screen. For respond trials, the stimulus was presented for up to 4 s, or until the subject responded, and subjects had to report the response as quickly as possible. For suppression trials, the stimulus remained on the screen for 4 s. If a subject responded, a loud error beep sounded. Trials were separated by a 400-ms intertrial interval. Suppression and respond trials were conducted on different word pairs, with five pairs participating in each of the 0 (baseline), 1, 8 and 16-repetition conditions for both the respond and suppression conditions. Respond trials on filler pairs were also included so that 67% of the trials in the think/no-think phase required a response, encouraging a strong mental set to respond that had to be overridden, as in go/no-go tasks.

After the think/no-think phase, we tested the subjects' memory for all of the word pairs in two ways. In both tests, a cue for each word pair was presented in the centre of the screen for up to 4 s, or until subjects spoke the response. Pairs for the different respond and suppress conditions were intermixed pseudo-randomly, with the constraint that the average test position for each condition was equated. In the same-probe test, subjects' recall for each pair was cued with the stimulus member that was paired with the response throughout the experiment. In the independent probe test, subjects were cued with the category name for each exemplar along with its first letter. In each case, subjects were asked to recall the studied item that fit the cues and not to withhold any items. Half of the subjects in each experiment got the same-probe test first, and half were given the independent probe test first.

Subjects in experiment 2 were given 25 cents for each correct answer, up to a maximum of \$4. Subjects in experiment 3 were given a questionnaire after the experiment in which they were asked about their impressions of our (false) hypothesis that memory would improve with attempts to suppress an item.

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Masking unveils pre-amodal completion representation in visual search

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When one object is partly occluded by another, its occluded parts are perceptually 'filled in', that is, the occluded object appears to continue behind its occluder. This process is known as amodal completion¹. The completion of a partially occluded object takes about 200 ms (ref. 2), and pre-completion information (that is, information from before amodal completion has occurred) exists in the visual system for that duration^{2,3}. It has been suggested, however, that observers cannot make use of this information, even when it is beneficial to do so: visual search for a target that appears to be partly occluded, for example, is slower than for a target that does not undergo occlusion, despite both targets being physically identical^{4–6}. Here we show that visual search does have access to pre-completion representations, but only for a limited time that depends on the size of the occluded region.

Early investigations of visual search focused on discovering the elementary features available in early vision^{7–12}, whereas more recent work has demonstrated that the input to visual search is much more complex than previously assumed^{13,14}. Although it seems that the entry level for vision (that is, entire objects or individual features) can be quite high in many cases, questions remain about the nature of the information available at earlier stages of processing. In the case of amodal completion, for example, it seems that visual search relies on a post-completion representation even when this impairs search^{4–6}. This finding can be interpreted in at least three ways. First, it could be that there is no pre-amodal completion stage in processing. This is unlikely because other studies have shown that pre-completion information is available for certain perceptual judgements^{2,3}. Second, it is possible that pre-completion information exists only implicitly, as an 'ingredient' in the computation of a completed representation, and is not explicitly available for all perceptual judgements. Examples of this include monocular information during binocular rivalry¹⁵, and very high spatial frequency information¹⁶, both of which are present in

Table 1 Percentage of mean target-absent error rates

Experiment	Number of items in display			
	2	4	6	8
Medium notch (100-ms SOA)	11.4	17.7	20.3	12.3
Medium notch (250-ms SOA)	3.5	4.6	5.5	3.0
Small notch	18.7	19.8	22.5	15.6
Large notch	2.0	4.0	3.0	1.9

early vision but are apparently barred from awareness. The third possibility is that an explicit pre-completion representation is at least momentarily available, but a later amodally completed representation pre-empts the pre-completion representation in visual search¹⁴.

The third interpretation predicts that it should be possible to reveal the presence of the pre-completion representation by interrupting processing before amodal completion has been fully achieved. Such an interruption can be achieved by the use of a mask^{17,18}. In our experiments, participants searched for a notched disk target among complete disks and squares (Fig. 1). With unlimited exposure duration, when the notched target disk abuts a square (adjacent condition), search is inefficient because the notched target is rendered similar to the complete distractor disks by amodal completion; however, search is efficient when the target stands separate from the square (separate condition) and completion is not possible⁵. This result suggests that visual search mechanisms do not have access to the pre-completion representation. The same result should be obtained if a mask interrupts processing of the display after amodal completion has had time to occur (> 200 ms (ref. 2)). If, however, a mask terminates the display before amodal completion finishes (< 200 ms), search should be equally efficient in the separate and adjacent conditions because the representation of the target in the adjacent condition remains notched, and therefore is easily discriminated from the distractor disks. We used two different stimulus-onset asynchronies (SOAs) for the mask: 100 ms (intended to prevent amodal completion) and 250 ms (long enough to permit completion). All conditions were presented in mixed blocks to prevent the use of a stimulus- or SOA-dependent strategy.

The results are shown in Fig. 2; target-absent data for this and all subsequent experiments are summarized in Table 1—our analyses will centre on the target-present trials because the target-absent trials do not contain any candidates for amodal completion. Our statistical analyses focus on error rate. The interpretation of response times is problematic when error rates vary systematically across conditions. Search efficiency (as indexed by the slope of the search function) was greater in the separate condition than in the

adjacent condition for the 250-ms SOA (Fig. 2b; analysis of variance (ANOVA), $F(3, 33) = 4.84, P < 0.01$), which replicates previous findings⁵. In the 100 ms condition, there was no difference in search efficiency (Fig. 2a; $F(3, 33) = 1.03$, not significant). The absence of a difference in search efficiency in the 100 ms condition was not due to a decrease in search efficiency for the more efficient separate condition ($F < 1$). This result is paradoxical: a manipulation that increased task difficulty (that is, reducing the target-mask SOA) yielded increased search efficiency.

Although there was no difference in search efficiency in the 100-ms SOA condition, there was a main effect of target type (adjacent versus separate) ($F(1, 11) = 8.72, P < 0.05$). We attribute this effect, which has been reported elsewhere⁵, to differences between the two target types that are unrelated to amodal completion. Amodal completion affects the slopes of the search functions because it renders the target more similar to the distractors, incurring an additional cost with every additional distractor item in the display. The greater intercept in the adjacent condition, on the other hand, indicates factors affecting the target irrespective of the number of distractors. Such factors may include the greater spatial proximity of the target disk to its neighbouring square in the adjacent condition than in the separate condition, and hence its greater vulnerability to

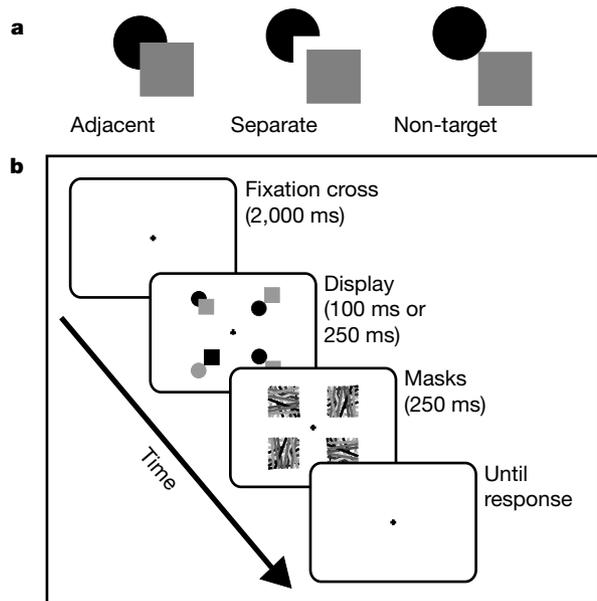


Figure 1 Visual search task. **a**, The target is either a notched disk abutting a square (adjacent condition) or standing separate from the square (separate condition); distractors are complete disks and squares. **b**, Sequence of events on each trial (see Methods for details).

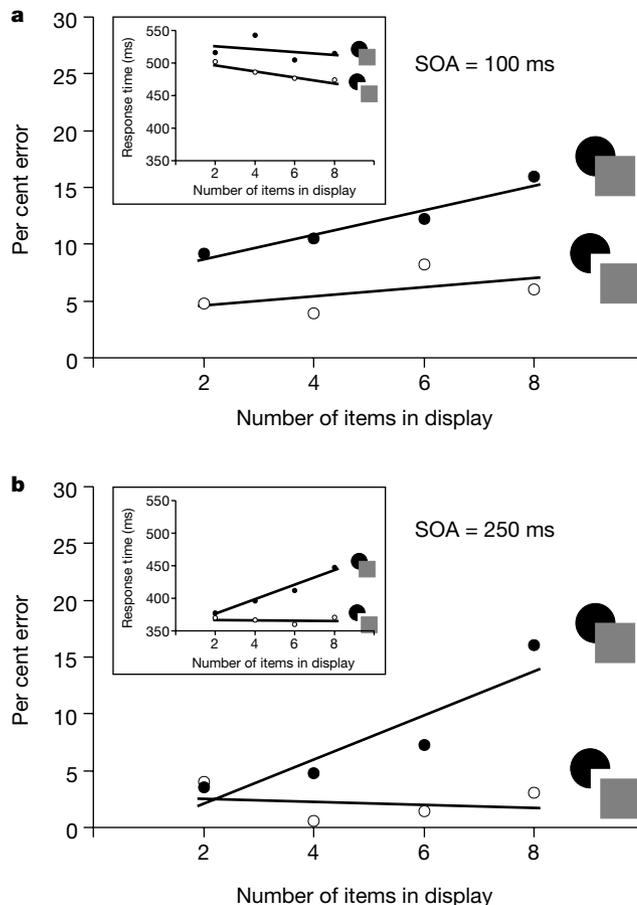


Figure 2 Participants' performance as a function of SOA, target type (adjacent or separate), and number of items in the display. Closed symbols represent the adjacent condition, open symbols the separate condition (also for Figs 3 and 4). The insets show the response-time data for each condition. **a**, 100-ms SOA. The adjacent and separate conditions yielded equivalent search efficiencies. **b**, 250-ms SOA. Search was less efficient in the adjacent than in the separate condition. The response-time data show the same pattern of results, with equally efficient search in the 100 ms condition and a pronounced slope difference in the 250 ms condition.

lateral masking or related effects.

Our use of error rates as a measure of search efficiency is validated by the congruence of the response-time data with the error data (see Fig. 2, insets), and by the fact that the 250-ms condition error data replicate previous findings⁵. As a further check on the reliability and validity of our results, we replicated the new finding from the first experiment (the equality of search efficiency for adjacent and separate targets at the 100-ms SOA) using response time as a dependent measure. The design of the experiment was the same as in the previous experiment, with the exception that the target and mask displays were cycled continuously until a response was issued, and that participants made a speeded response with accuracy being stressed. We assumed that the mask would prevent completion on each cycle. We recorded response time as a

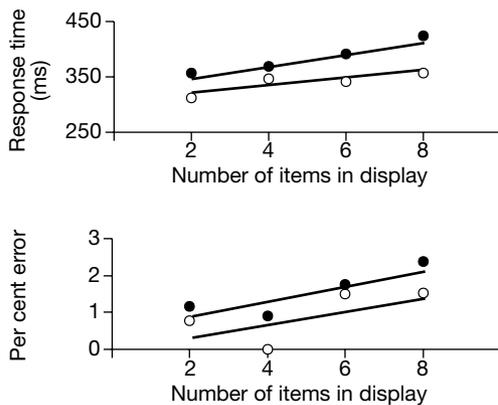


Figure 3 Participants' performance as a function of target type (adjacent or separate) and number of items in the display. A replication of the 100 ms condition using response time as a dependent measure confirmed the results of the first experiment.

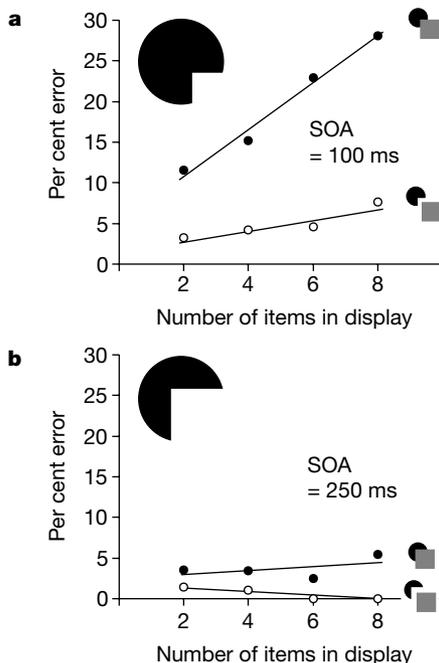


Figure 4 Participants' performance as a function of target type (adjacent or separate) and number of items in the display. **a**, Small-notched target disk. When a target disk with a small notch is used, there is a difference in search efficiency between the adjacent and separate conditions even at the 100-ms SOA. **b**, Large-notched target disk. When a target disk with a large notch is used, both target types yield equivalent search efficiencies even at the 250-ms SOA.

function of display exposure time, and excluding mask presentation time. The results are shown in Fig. 3. As before, the slopes for the adjacent and separate targets are comparable (7.5 versus 11.1 ms per item) and statistically indistinguishable ($t(14) = 1.53$, not significant; Student's t -test). This finding stands in marked contrast to the pattern of results observed with much longer display durations⁴⁻⁶.

We extended the result obtained in the first experiment by manipulating the size of the occluded region, which is known to affect the time required for amodal completion, with large regions requiring more time than smaller regions¹⁹. If the size of the notch in the target is reduced substantially (from 25 to 9% of the entire disk), and amodal completion can thus be achieved even before the onset of the mask at the 100-ms SOA¹⁹, we should observe a difference in search efficiency between the adjacent and separate conditions, even at this short SOA. If, conversely, the size of the notch is increased substantially (from 25 to 37%), amodal completion should be slowed to such an extent that even the 250-ms SOA will interrupt processing before the pre-completion representation is pre-empted. In this case, one would predict no difference in search efficiency at the long SOA.

As shown in Fig. 4, these predictions were borne out. The target with the small notch yielded a difference in search efficiency even at the 100-ms SOA ($F(3, 33) = 2.90$, $P < 0.05$). The target with the large notch, by contrast, produced no difference in search efficiency even at the 250-ms mask SOA ($F(2, 22) = 1.42$, not significant). The results for the target with the small notch (Fig. 4a) were qualitatively similar to those obtained in the first experiment in the 250 ms condition, as one would expect if amodal completion had occurred too quickly even for the 100-ms SOA. An ANOVA test comparing the two conditions across experiments confirmed that the results were statistically indistinguishable ($F < 1$). Similarly, the large-notch target yielded a pattern of results similar to that observed in the 100 ms condition of the first experiment (see Fig. 4b). Again, statistical analysis confirmed that the results were comparable ($F < 1$).

Our findings indicate not only that pre-amodal completion information is present in the visual system along the path to a final, completed representation, but that, at least briefly, its representation is sufficiently explicit to subserve overt, conscious behaviour. The assertion that visual search has no access to low-level information^{4-6,20} should be tempered by the finding that it can, under some conditions, gain access to this information. Of course, obligatory use of a post-completion representation under normal circumstances makes adaptive sense because search would otherwise be routinely inefficient in a world that abounds with occlusions. □

Methods

Participants performed visual search for a target that was either a notched disk abutting a square (adjacent condition), or a notched disk standing separate from the square (separate condition); distractors were complete disks and squares (see Fig. 1a). In the first case, the target was a candidate for amodal completion; in the second case, it was not. Displays consisted of 2, 4, 6 or 8 disk-square combination pairs arranged around a central fixation cross; on half the trials one of these was a target pair. The diameter of the disk subtended 1.2° of visual angle, and one side of the square subtended the same angle. The entire display measured 8.0° across.

Each trial began with a fixation cross at the centre of the screen, followed by the search display (see Fig. 1b). The search display was replaced by a mask display after either 100 or 250 ms; the duration of the mask display was 250 ms. The mask display was followed by a blank screen with a fixation cross. Participants reported whether the notched disk target was present or absent by pressing one of two keys. We stressed the need for accuracy over speed. Participants completed one practice block with a long mask-onset time (950 ms) and another with the actual parameters used in the subsequent experimental blocks (100 and 250 ms). All conditions were presented in fully mixed blocks. Participants completed a total of 512 experimental trials. A new set of 12 undergraduate students naive to the purposes of the study participated in each experiment. Fifteen observers participated in the response time replication of the new finding of the first experiment. In this experiment, the target and mask displays were cycled repeatedly, without inter-stimulus interval, until a response was made.

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Neurogenesis in the adult is involved in the formation of trace memories

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The vertebrate brain continues to produce new neurons throughout life^{1–12}. In the rat hippocampus, several thousand are produced each day, many of which die within weeks¹³. Associative learning can enhance their survival^{13,14}; however, until now it was unknown whether new neurons are involved in memory formation. Here we show that a substantial reduction in the number of newly generated neurons in the adult rat impairs hippocampal-dependent trace conditioning, a task in which an animal must associate stimuli that are separated in time¹⁵. A similar reduction did not affect learning when the same stimuli are not separated in time, a task that is hippocampal-independent^{16,17}. The reduction in neurogenesis did not induce death of mature hippocampal neurons or permanently alter neurophysiological properties of

the CA1 region, such as long-term potentiation. Moreover, recovery of cell production was associated with the ability to acquire trace memories. These results indicate that newly generated neurons in the adult are not only affected by the formation of a hippocampal-dependent memory¹³, but also participate in it.

We used a toxin for proliferating cells, the DNA methylating agent methylazoxymethanol acetate (MAM)^{18–20}, to diminish the number of adult-generated cells in the dentate gyrus of rats. First, we identified a dose that would deplete the new cells without impairing overall health. Adult male Sprague–Dawley rats ($n = 18$, 3 per dose) were injected subcutaneously with MAM at daily doses of 0, 3, 4, 5, 7 and 15 mg kg⁻¹ for 14 d. We chose this regime because numbers of newly generated cells increase up to 10 d after mitosis and decline thereafter²¹. Thus, 14 d of treatment should prevent their incorporation to the granule cell layer. Twelve hours after the last MAM injection, rats were injected with 5-bromodeoxyuridine (BrdU), a marker of dividing cells²², and perfused 2 h later (see Supplementary Information). Daily treatment for 14 d with 5 mg kg⁻¹ MAM decreased the number of granule cells labelled with BrdU and TUC-4, a marker of immature neurons²³, by roughly 80% ($P < 0.05$). Rats treated with 5 mg kg⁻¹ MAM continued to gain weight during treatment and were indistinguishable in general appearance from vehicle-treated rats. Liver cytology was normal. Doses lower than 5 mg kg⁻¹ had smaller effects on cell number, 7 mg kg⁻¹ was associated with weight loss, and 15 mg kg⁻¹ with weight loss and decline in overall health. Therefore, in the subsequent studies, rats were treated with 5 mg per kg per day, for 14 d.

In the first conditioning experiment, rats were fitted with headstages and electrodes to deliver periorbital stimulation to the eyelid and to record electromyographic (EMG) activity associated with eyelid closure. After 5 days of recovery, rats were injected subcutaneously with 5 mg kg⁻¹ MAM or saline daily, for 14 d. Rats received three injections of BrdU, on days 10, 12 and 14 (10, 8 and 6 d before perfusion) to label large numbers of immature cells. Rats were untreated for 2 d, then trained with delay or trace conditioning. In both tasks, a white noise conditioned stimulus predicts the occurrence of an unconditioned stimulus of periorbital eyelid stimulation. As the animal learns, it blinks in response to the conditioned

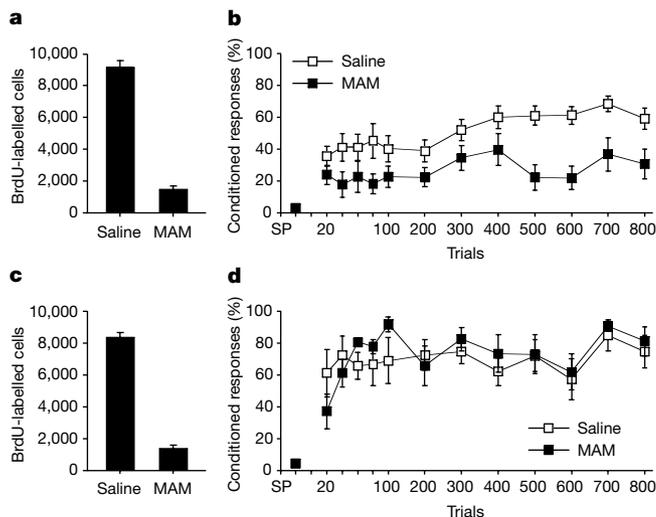


Figure 1 Adult-generated neurons are involved in trace but not in delay conditioning. **a**, Total numbers of BrdU-labelled cells in the dentate gyrus before trace conditioning. Bars represent mean \pm s.e.m. **b**, Spontaneous blink rate (SP) and the percentage of conditioned responses (mean \pm s.e.m.) across 800 trials of hippocampal-dependent trace conditioning in rats treated with MAM versus saline. **c**, Total numbers of BrdU-labelled cells in the dentate gyrus before delay conditioning. **d**, SP and percentage of conditioned responses across 800 trials of hippocampal-independent delay conditioning in rats treated with MAM versus saline.