or postsynaptic locus for the maintenance of LTP may be resolved by this data. Recent studies showing predominantly presynaptic LTP have used 2.5 mM Ca^{2+} for slice experiments[8,9,11], and some have reported a high proportion of failures[8,11], suggesting low initial release probabilities. Our e.p.s.ps recorded in 2.5 mM Ca^{2+} also showed low initial P and mainly presynaptic LTP. Other studies reporting postsynaptic LTP have used higher Ca^{2+} levels[17,18]. Our results in higher Ca^{2+} showed higher P values and larger v_1 changes. We expect that this clear correlation between initial release probability and the locus of change will be important for the further understanding of the mechanism of LTP at these synapses. □

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Preserved figure–ground segregation and symmetry perception in visual neglect

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A CENTRAL controversy in current research on visual attention is whether figures are segregated from their background preattentively[1–8], or whether attention is first directed to unstructured regions of the image[9–13]. Here we present neurological evidence for the former view from studies of a brain-injured patient with visual neglect. His attentional impairment arises after normal segmentation of the image into figures and background has taken place. Our results indicate that information which is neglected and unavailable to higher levels of visual processing can nevertheless be processed by earlier stages in the visual system concerned with segmentation.

C.C. is a 69-year-old man with right-hemisphere damage and severe left neglect[14,15] (see Fig. 1 for case details). He ignores information on the left even though he has no left visual field loss. His neglect can therefore be characterized as an attentional rather than sensory deficit. We examined whether this deficit applied to the left side of unsegregated space, as would be predicted by purely spatial models of visual attention[9–13], or to the left of perceptual figures derived by preattentive segregation processes, as would be predicted by object-based models of attention[1–8]. He was presented with displays such as those in Fig. 2. A rectangle presented on a black screen was divided by a pseudorandom contour into a small bright green section and a large dimmer red section. The green section could be on the far left (upper panel of Fig. 2) or the far right (lower panel of Fig. 2). With appropriate colouring, normal observers see such displays as green shapes against a shapeless red background. This figure-ground segregation arises because the green shapes are smaller and brighter[16].

C.C.'s task was to remember the dividing contour between the red and green section on each trial, deciding whether it matched a probe line presented after each display (for example, in Fig. 2 the probe matches for the upper panel but not the lower panel). If his attentional deficit applies to the left side of an unsegregated representation of visual space, C.C. should perform less well when the green shape appears at the left of the rectangle (as in the upper panel of Fig. 2) as the dividing

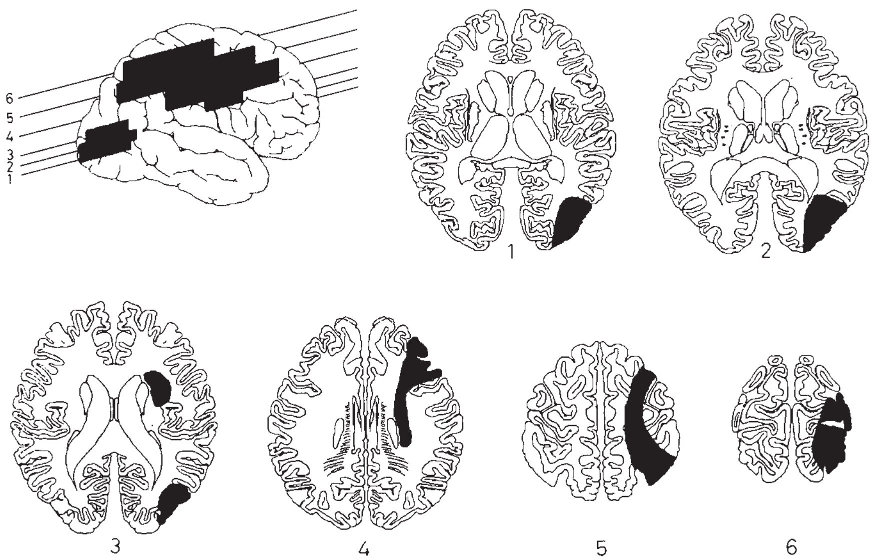

FIG. 1 Reconstructed computerized tomographic scan for C.C., a right-handed retired plumber who suffered a right-hemisphere stroke and sustained left hemiparesis and left neglect. The method for reconstruction is described elsewhere[26]. A right lateral view and transverse sections are shown, with shading indicating damage. The scan reveals infarction of the watershed territory of the right anterior and middle cerebral arteries. The damage extends anteriorly into area 8 and posteriorly into the superior parietal lobule. C.C. had no visual-field loss, but consistent left-sided extinction on double simultaneous stimulation. He showed severe left neglect on the conventional measures of line bisection and line cancellation, and in a new measure; when asked to detect the presence or absence of a small crack on either side of two-dimensional block shapes, he detected the crack for 37/40 shapes with a crack on the right, but for only 5/40 shapes with a crack on the left. All studies were conducted in the month following the stroke in the sequence described.

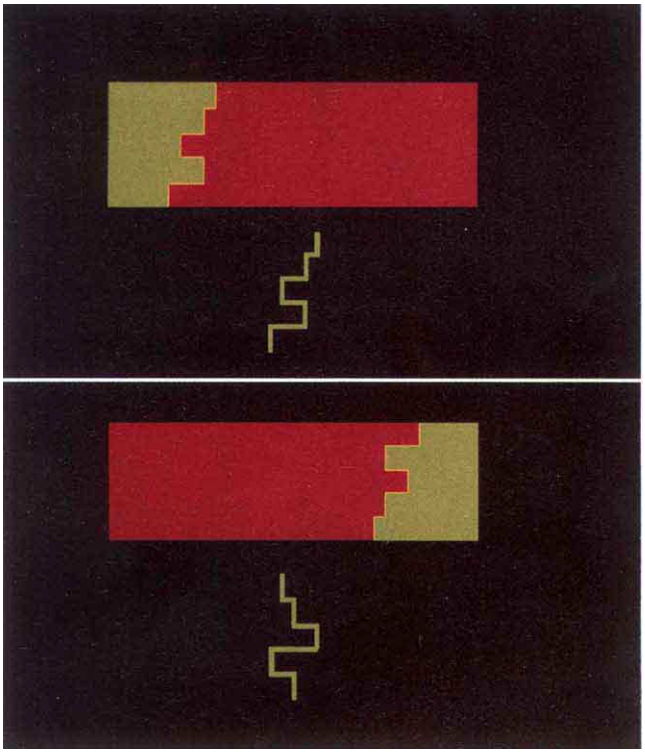

FIG. 2 Two example displays from the first experiment. The task was to report verbally whether the dividing contour in the $9.5^\circ \times 3.2^\circ$ rectangle matched the probe line, which was presented immediately below the rectangle following its offset as shown. The smaller region of the rectangle (on average 3.2° wide) was always bright green (~3.8 footlamberts (ftL)), the larger region a dimmer red (2.4 ftL) against a black background (0.15 ftL). In the upper panel, the small green figure is on the left, and a matching probe is illustrated. In the lower panel the small green figure is on the right, and a mismatching probe is illustrated. The green figure was equally likely to be on the left or right, and 50% of the probes matched in both cases. The dividing contours and probes always had 5 pseudorandom 'steps'. Using an IBM PC-AT microcomputer and a Mini-Micro VGA monitor, the rectangle was presented for 2 s, followed by a gap of 100 ms, and then the probe until a same/different response was made. Central fixation was required during each rectangle display. There were 160 trials in random sequence. C. C. correctly rejected mismatching probes on 33/40 trials when the green figure was on the left, but on only 21/40 trials with green figures on the right. He correctly accepted matching probes on 31/40 trails when the green figure was on the left, and on 19/40 trials with green figures on the right. Thus, C.C. performed well above chance for displays with the green figure on the left, as in the upper panel, but was at chance when the green figure was on the right, as in the lower panel. This difference in performance is significant ($P < 0.01$).

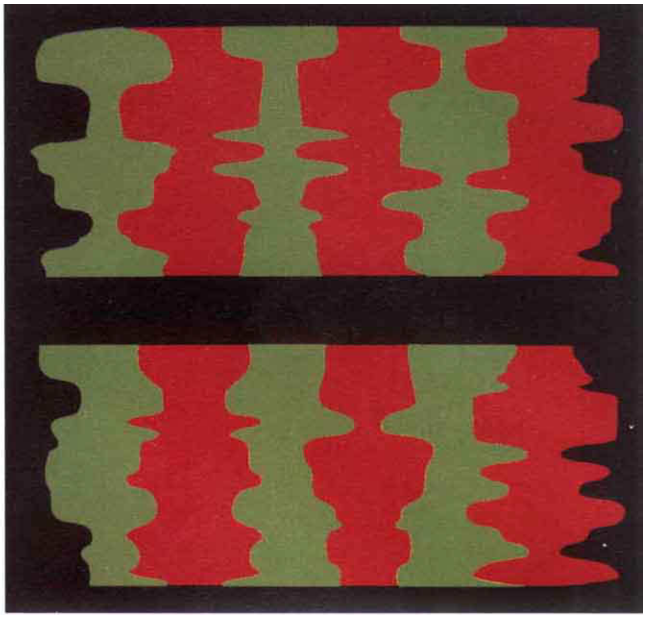

FIG. 3. Two examples of displays from the second study. Readers should be able to experience the effect of symmetry on figure-ground segregation for themselves. With the lower example covered, the upper figure is typically seen as green shapes against a red background because of the symmetry. Conversely, with the upper example covered, the lower is typically seen as red figures against a green ground. Each display comprised 6 pseudorandom shapes, alternating red and green, and subtended $13.4^\circ \times 6.3^\circ$ in total. With equal probability, either the red shapes were three different symmetrical shapes, and the green shapes asymmetrical, or the reverse. The rightmost shape was equally likely to be symmetrical or asymmetrical, and to be red (4.3 ftL) or green (3.8 ftL). The colours were roughly matched for salience in pilot studies with healthy observers. The displays were presented until a response was made, and there were 120 trials. With red symmetrical shapes, C.C. responded 'red' on 21/30 trials when the rightmost shape was red, and 26/30 trials when the rightmost shape was green. With green symmetrical shapes, he responsed 'green' on 29/30 trials when the rightmost shape was green, and 20/30 trials when the rightmost shape was red. Thus, there was no significant tendency to pick one colour rather than another (58/120 red responses, 62/120 green responses), or to respond with the colour of the rightmost shape (64/120), but a strong tendency to pick the colour of the symmetrical shapes (96/120, $P < 0.01$). This effect of symmetry was indistinguishable from that observed in the speeded responses of two age-matched, neurologically healthy men. The colour of the asymmetrical shapes is chosen on a small proportion of trials where other factors (such as relative size) override symmetry because of pseudorandom fluctuation in the shapes employed.

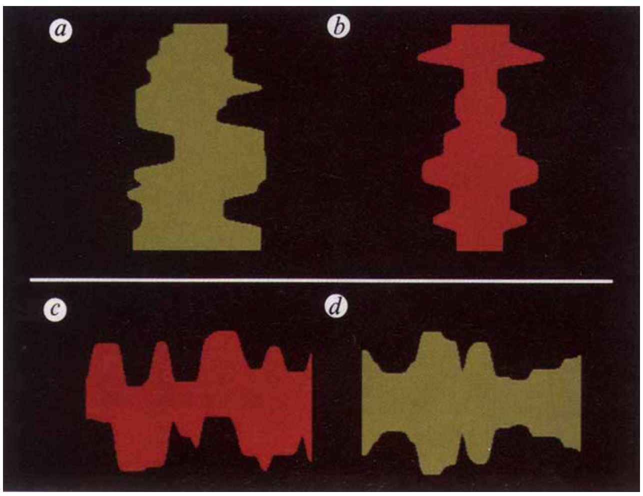

FIG. 4 *a, b,* Two example displays from the explicit vertical symmetry task. Each display comprised a single shape from the figure-ground displays of the preceding study. The shapes were 6.3° tall and on average 2.2° wide, and were equally likely to be red or green. In either case, 50% were symmetrical. A green asymmetrical shape (*a*) and a red symmetrical shape (*b*) are shown. Individual displays were presented until a response was made, and there were 120 trials. C.C.'s performance was at chance; he responded 'symmetrical' to 31/60 symmetrical shapes, and 'asymmetrical' to 34/60 asymmetrical shapes, with no effect of display colour. *c, d,* Two examples of displays from the explicit horizontal symmetry task, conducted immediately after C.C.'s chance performance in judging vertical symmetry. A red asymmetrical shape (*c*) and a green symmetrical shape (*d*) are shown. The displays were exactly as for the vertical symmetry task, except that the monitor was rotated 90° clockwise. Normal observers find symmetry judgements harder around the horizontal than vertical[27]. But C.C.'s abnormal difficulty in judging vertical symmetry is caused by his neglect for the left of figures, which should not disrupt judgements of symmetry about the horizontal axis. C.C. responded 'symmetrical' to 56/60 symmetrical shapes, and 'asymmetrical'' to 59/60 asymmetrical shapes. This performance is significantly better than that for vertical symmetry ($P < 0.01$).

contour is further to the left of the display and the patient in this case. But the opposite prediction follows if C.C.'s neglect applies to the left side of perceptual figures after the normal operation of figure-ground segregation. He should perform worse when the green shape is on the right of the rectangle (as in the lower panel of Fig. 2) because the dividing contour now falls to the left of the perceptual figure, although the contour is further to the right of the display and the patient.

The results supported the figural prediction (see legend to Fig. 2), demonstrating that the critical variable was the location of the dividing contour in relation to the green figure, rather than in relation to the patient or to the display as a whole. This implies that, like normal observers, C.C. saw the green shapes as the perceptual figures whether they appeared on the right or the left, implying that figure-ground segregation operated normally across the display (his phenomenal descriptions of 'green shapes at either side' on debriefing are also consistent with this). Thus, C.C.'s left neglect arises at a stage of attending to figures provided by a preceding, and unimpaired, segregation stage. This two-stage account of his neglect is in accordance with recent two-stage characterizations of normal vision[8]. Our results are consistent with a recent report that visual neglect can apply to the contralateral side of objects[17]. They go beyond this by demonstrating that the 'objects' concerned are figures derived by segregation processes operating normally in both visual fields. The intact segregation between green and red shapes is also consistent with a previous report that colour perception can be preserved in the contralateral field for some neglect patients[18]. Our data extend this to show that such preserved perception can support figure-ground segregation.

Our next experiment tested directly whether C.C.'s visual system represents left-sided information at a preattentive stage of figure-ground segregation, but subsequently loses this information for the derived figures at an attentional stage. Symmetry about the vertical exerts powerful effects on figure-ground segregation in normal observers; other factors being equal, symmetrical shapes are seen as figures against asymmetrical grounds[16]. We examined whether C.C. also showed this effect. Because symmetry depends on the correspondence between reflected sides, sensitivity to symmetry requires representation of both the right and left sides of shapes at the segregation stage.

We presented C.C. with displays of alternating red and green pseudorandom shapes (Fig. 3). Either the red shapes or the green shapes were symmetrical. C.C. was told: "Sometimes we are going to show you red shapes on a green background, sometimes green shapes on a red background. Just tell us which colour the shapes are, red or green". He showed the usual effect of symmetry on figure-ground segregation, tending to report the colour of the symmetrical shapes, with no bias towards reporting the rightmost colour (see legend to Fig. 3).

This normal effect of symmetry demonstrates that, at the preattentive segregation stage, both sides of perceptual figures must be represented in C.C.'s visual system. But our first experiment found that he neglects the left side of perceptual figures at a subsequent stage of attending to them. C.C.'s phenomenal descriptions of the present displays suggest that this applied for the symmetrical figures as well. When asked to explain his responses at the end of the study, he replied that his chosen shapes 'looked closer and brighter', but did not mention the symmetry which is so striking to a normal observer. In the next task, we required C.C. to judge explicitly the symmetry of individual shapes from the figure-ground displays (Fig. 4*a* and *b*). His responses were at chance level (see legend to Fig. 4). This inability to make explicit symmetry judgements contrasts dramatically with the preserved effect of symmetry on figure-ground segretation. The contrast arises because the two tasks reflect distinct stages of visual processing. Figure-ground segregation occurs preattentively, at a stage where left-sided information is represented. Explicit symmetry judgements require a subsequent stage of attending to perceptual figures, at which the patient neglects left-sided information. His inability to make explicit vertical symmetry judgements was not due to failure to understand the task, as he was able to judge whether our nonsense shapes were symmetrical about the horizontal axis (Fig. 4*c* and *d*). This task requires comprehension of comparable instructions, but does not require left-sided information.

C.C. retains intact figure-ground segregation despite his severe left neglect. He segregates figures from their background normally, even when they appear on his left (our first study), and even when their segregation depends on vertical symmetry (our second study) which requires that both the right and left sides of these figures are represented. His deficit arises in a subsequent stage of attending to these figures, at which he neglects the left of figures wherever they appear, and thus cannot judge explicitly whether they are symmetrical about the vertical.

The dissociation between severe left neglect and intact figure-ground segregation strongly supports recent models of normal visual function, which postulate a preattentive segregation stage providing candidate objects to a subsequent attentional stage[1-8]. Our findings about symmetry perception also demonstrate that neglected information that is unavailable for verbal report may nevertheless be represented implicitly, confirming previous reports[19,20] which have remained controversial[21-23]. This conclusion is in accordance with comparable dissociations between implicit processing and verbal report in other areas of neuropsychology[24,25]. □

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