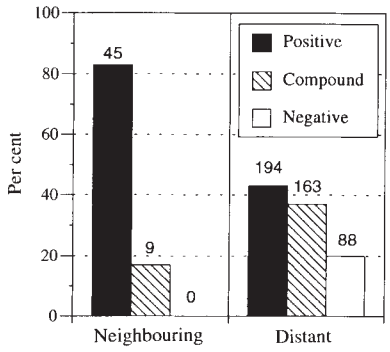

FIG. 4 Distribution of cross-correlogram patterns in neighbouring and distant neurons. Time-averaged cross-correlograms between pairs of neighbouring neurons are, in most cases, characterized by positive peaks. Note that negative cross-correlograms are completely missing in the population of neighbouring neurons. The number of neuronal pairs in each class is given above the bars. The difference between the two populations is statistically significant at a level of 0.001 ($\chi^2 = 318.77$).

of precise coincidences (with jitters of only ±2.5 ms) reached values up to 620%.

The wide peaks and troughs (tens to hundreds of milliseconds wide) indicate that the time-constraints of the underlying processes are loose. The mechanisms of such dynamic correlation (including precise coincidences) are unknown. The correlation could emerge from repeated volleys of direct synaptic interactions between the neurons; or, more probably, it could arise from changes in the pattern of activity of a large number of neurons, interacting with the sampled neurons in a correlated manner. Regardless of the mechanism, however, the modifications of correlation between two neurons in relation to stimulation and behaviour most probably reflect changes in the organization of spike activity in larger groups of neurons. Indeed, recent model studies have shown that similar dynamic organization can be accomplished in large networks, even without associated modifications of the synaptic weights[15–17].

Our results also support and extend anatomical and physiological findings indicating that functional groups are organized in spatial clusters[3,11,18–22]. Our findings suggest that neighbouring neurons tend to share common inputs of the same sign (either inhibitory or excitatory), whereas the effects on more distant neurons (in our study 500–1,000 μm apart) are mixed. Therefore, when the common drive is increased, neighbouring neurons tend to be activated in unison, enabling them to operate as a coherent functional group for a short while. Concurrently, the negative correlation between neurons in one group and those in another, more distant group can accentuate the demarcation among groups. Thus, the spatio-temporal organization of activity in the network allows for the rapid association of neurons into a functional group, at the same time dissociating such a group from concurrently activated, competing groups. □

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1. Ahissar, E. *et al. Science* **257,** 1412–1415 (1992).
2. Gray, C. M., Engel, A. K., König, P. & Singer, W. *Vis. Neurosci.* **8,** 337–347 (1992).
3. Eckhorn, R. *et al. Biol. Cybernet.* **60,** 121–130 (1988).
4. Vaadia, E. & Aertsen, A. in *Information Processing in the Cortex: Experiments and Theory* (eds Aertsen, A. & Braitenberg, V.) 81–102 (Springer, Heidelberg, 1992).
5. Murthy, V. N., Aoki, F. & Fetz, E. E. in *Oscillatory Event Related Brain Dynamics* (eds Pantev, C., Elbert, Th. & Lütkenhöhner, B.) (Plenum, London, in the press).
6. Barlow, H. B. *Perception* **1,** 371–394 (1972).
7. Barlow, H. B. in *Information Processing in the Cortex: Experiments and Theory* (eds Aertsen, A. & Braitenberg, V.) 169–174 (Springer, Heidelberg, 1992).
8. Newsome, W. T., Britten, K. H. & Movshon, J. A. *Nature* **341,** 52–54 (1989).
9. Aertsen, A. M., Gerstein, G. L., Habib, M. K. & Palm, G. *J. Neurophysiol.* **61,** 900–917 (1989).
10. Toyama, K., Kimura, M. & Tanaka, K. *J. Neurophysiol.* **46,** 191–201 (1981).
11. Ts'o, D. Y., Gilbert, C. D. & Wiesel, T. N. *J. Neurosci.* **6,** 1160–1170 (1986).
12. Fetz, E. E., Toyama, K. & Smith, W. in *Cerebral Cortex* Vol. 9 (ed. Peters, A.) 1–47 (Plenum, New York, 1991).
13. Nelson, J. I., Salin, P. A., Munk, M. H. J., Arzi, M. & Bullier, J. *Vis. Neurosci.* **9,** 21–37 (1992).
14. Abeles, M., Prut, Y., Bergman, H., Vaadia, E. & Aertsen, A. in *Brain Theory: Spatio-Temporal Aspects of Brain Function* (ed. Aertsen, A.) 149–181 (Elsevier, Amsterdam, 1993).
15. Aertsen, A., Erb, M. & Palm, G. *Physica* D**75,** 103–128 (1994).
16. Hansel, D. & Sompolinsky, H. *Phys. Rev. Lett.* **68,** 718–721 (1992).
17. Kaneko, K. *Physica* D**41,** 137–172 (1990).
18. Gray, C. M. & Singer, W. *Nature* **338,** 334–337 (1989).
19. Kruger, J. *Vis. Neurosci.* **5,** 135–142 (1990).
20. Selemon, L. D. & Goldman-Rakic, P. S. *J. comp. Neurol.* **297,** 359–376 (1990).
21. Michalski, A., Gerstein, G. L., Czarkowska, J. & Tarnecki, R., *Expl Brain Res.* **51,** 97–107 (1983).
22. Thomson, A. M. & Deuchars, J. *Trends Neurosci.* **17,** 119–129 (1994).
23. Palm, G., Aertsen, A. M. H. J. & Gerstein, G. L. *Biol. Cybernet.* **59,** 1–11 (1988).
24. Abeles, M. *J. Neurosci. Meth.* **5,** 317–325 (1982).

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Neuronal correlates of inferred motion in primate posterior parietal cortex

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For many types of behaviours, it is necessary to monitor the position or movement of objects that are temporarily occluded. The primate posterior parietal cortex contains neurons that are active during visual guidance tasks: in some cases, even if the visual target disappears transiently[1,2]. It has been proposed that activity of this sort could be related to current or planned eye movements[1,2], but it might also provide a more generalized abstract representation of the spatial disposition of targets, even when they are not visible. We have recorded from monkey posterior parietal cortex while the animal viewed a visual stimulus that disappeared, and then, depending on experimental context, could be inferred to be either moving or stationary. During this temporary absence of the stimulus, about half of the neurons were found to be significantly more active on those trials in which the stimulus could be presumed to be moving rather than stationary. The activity was thus present in the absence of either sensory input or motor output, suggesting that it may indeed constitute a generalized representation of target motion.

Two rhesus monkeys were trained to maintain fixation within a 1° window while they viewed the trial types shown in Fig. 1*a*. On full vision trials, a stimulus 0.25° across appeared 12° from the fovea, and then, after a brief delay, moved towards the fixation spot. On occlusion trials the stimulus appeared as above, but then disappeared without moving and reappeared at 2° eccentricity moving towards the fixation spot, with the reappearance timed to be consistent with the stimulus moving continuously during the time that it was not visible. Full vision and occlusion trials were randomly interleaved during a block of trial presentations. Blocks of full vision and occlusion trials were interleaved with blocks of a third trial type, blink trials. On these trials, the stimulus appeared and disappeared exactly as in the occlusion trials, but then it reappeared in the same location, as if it had been stationary during the time it was not visible. Until the reappearance of the stimulus, the visual stimulation was identical on the occlusion and blink trials, the only difference being that the animal presumably inferred that the stimulus was moving during the time it was invisible on occlusion trials and inferred that the stimulus was stationary during the same period on blink trials.

We recorded responses to these stimuli from 106 neurons in the posterior parietal cortex (PP), in the lateral bank of the intraparietal sulcus and the fundus and anterior bank of the superior temporal sulcus. Figure 2 shows the average responses of two PP units to the three different trial types. The data shown are only for the preferred trajectory in each case. The histograms are synchronized (long vertical line) on the start of movement for the full vision trials, or on the disappearance of the stimulus for the occlusion and blink trials. On the occlusion and blink histograms, the small vertical line below the x-axis indicates the reappearance of the stimulus. Thus, all the activity between the synchronization and reappearance marks was evoked with the stimulus not visible (corresponding to the shaded area in Fig. 1*a*). Both cells responded vigorously to the moving stimulus on the full vision trials. There was also appreciable activity following disappearance of the stimulus on the occlusion trials, but not on the blink trials. This activity on the occlusion trials was not a simple sensory 'off' response because the visual stimulus was identical on the blink trials. Of the 106 cells examined, 48 (45%) showed a significantly different firing rate (averaged over the time that the stimulus was not visible) on the occlusion trials versus the blink trials (two-tailed t-test; $P<0.05$). All 48 were more active on the occlusion trials. Figure 3*a* shows the distribution among all the units of a modulation index (MI) obtained by dividing the mean response of the occlusion trials by that of the blink trials, with the responses averaged as described above. The indices of most cells were greater than unity; the median MI was 1.38. Population histograms among the 48 PP units that showed a significant difference between the two trial types ($O>B$ units) are shown in Fig. 3*b*. The fourth column is a difference histogram between the occlusion and blink trials. This difference in activity was sustained throughout the time that the stimulus was not visible.

A trivial explanation for the different responses between the occlusion and blink trials is that as the two were necessarily presented in separate blocks of trials, the animals' general state of arousal could have been lower during the blink blocks. Were this the case, it would be expected that the responses might differ throughout the trial, and not just subsequent to the disappearance of the stimulus. However, for the visual on-transient evoked by the initial onset of the stimulus prior to its disappearance, there was no significant difference between the two trial types among the 48 $O>B$ units (activity averaged over the 125-ms period following stimulus onset, a period before the beginning of the peristimulus–time histograms (PSTHs) in Figs 2 and 3; two-tailed paired t-test; $P>0.20$; median MI, 1.05. For comparison, $P<0.001$ for the same two-tailed paired t-test for the period following the disappearance of the stimulus). Thus the difference seen between occlusion and blink trials was not due to general differences in arousal between the two trial types. Another difference between the two trial types could be activity related to expectation of reward, because reward delivery occurred later

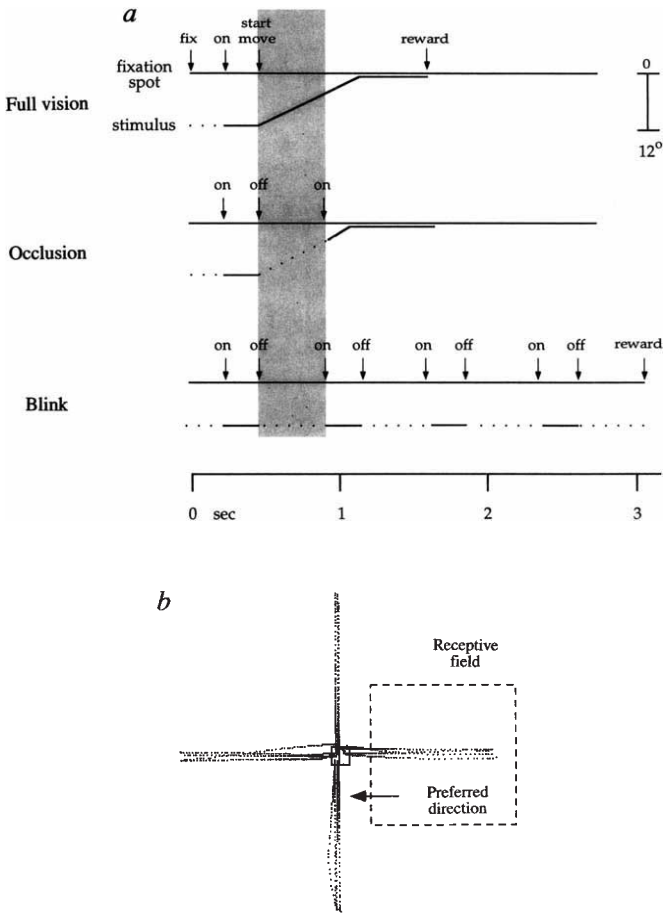

FIG. 1 Visual stimuli. *a*, Schematic of the three trial types. Time is shown on the horizontal axis; distance of the stimulus from the fixation spot on the vertical axis. Solid lines indicate that the stimulus is visible, dashed lines that it is not visible. Spike data were analysed over the shaded region—a time interval corresponding to, on the full vision trials, the start of movement until the stimulus was within 2° of the fixation spot or, on the other two trial types, the disappearance of the stimulus until its reappearance. On blink trials, the disappearance and reappearance of the stimulus was repeated four times to enhance the percept that the stimulus did not move. On full vision and occlusion trials, the animal received a juice reward after the stimulus reached the fixation spot; on blink trials the reward was delivered after completion of the fourth blink cycle. For comparison with the occlusion trials, data from blink trials were only examined during the first cycle, but the cells' responses generally did not change, or otherwise they declined on the later cycles. *b*, Typical stimulus trajectories, sampled at 75 Hz. While searching for units, trajectories were chosen randomly from trial to trial. Once a unit was isolated, its receptive-field size and directional preference were determined and then only four task trajectories were presented, spaced at 90° intervals, with the angle adjusted (while maintaining the 90° spacing) such that one traversed the receptive field of the unit, close to its preferred direction. As the trajectories were always centripetal, we necessarily selected units that had a major component of their preferred direction toward the fovea. During data collection, one block consisted of full vision and occlusion trials, randomly interleaved with respect to trial type and trajectory. The block continued until the animal had successfully completed two trials of each type and trajectory, for a total of 16 trials. The next block consisted solely of blink trials, again randomly interleaved with respect to the four initial locations, each repeated twice for a total of 8 trials. The timing of the disappearance and reappearance of the stimulus of each blink trial was identical to the timing of one of the corresponding occlusion trials of the previous block. This two-block alternation was then repeated 5–6 times for each unit, for a total of 10–12 repetitions of each trial type for each starting location. The trajectories used on full vision and occlusion trials were actually generated and stored during a previous block of trials in which the animal guided the stimulus to the fixation spot using a joystick. This accounts for the somewhat irregular trajectories exemplified in *b*. These movement trials will not be discussed; all the data herein were collected with the animals passively viewing as the stored stimulus templates were replayed. The start of each trial was indicated to the animal by a brief tone, with the pitch lower on the blink block so that the animal could distinguish the block type. Apart from this tone, the animal had no other way of distinguishing an occlusion trial from a blink trial on the first trial of a new block, because the visual stimulus was identical until the reappearance of the stimulus. But any such confusion should have only diluted differences in response between the two trial types. Stimuli were presented on a video monitor refreshed at 75 Hz, placed 57 cm from the animal.

on the blink trials than on occlusion trials. A subset of the $O > B$ units (28/48) had bilateral receptive fields. For these units, the null-trajectory trials (for example, those trajectories moving from left to right in Fig. 1*b*) also traversed the receptive field. Responses from these cells (Fig. 4) showed no difference between occlusion and blink trials following the disappearance of the stimulus for these null-trajectory trials (Fig. 4; two-tailed paired *t*-test; $P > 0.50$; median MI, 0.91), suggesting that the difference on preferred direction trials could not be attributed to non-spatial factors such as anticipation of reward.

In addition to the sustained differences following the disappearance of the stimulus, there was a statistically significant increase in the signal before the disappearance of the stimulus for the preferred directions and a decrease for the null direction (averaged activity compared between occlusion or full vision versus blink trials for the period from 120 ms to 20 ms before the disappearance; one-tailed paired *t*-tests; $P < 0.001$). As the animals knew that the stimulus would reliably disappear a few hundred milliseconds after it appeared, the directionality of this early activity suggests that it may be related to the animals' expectation of the impending direction of motion.

In summary, a large proportion of neurons in monkey PP were more active following the disappearance of a visual stimulus on trials in which the animal could have inferred that the invisible stimulus was moving rather than stationary. The difference in activity was not immediately related to sensory input, because the stimulus was identical between the two trial types. It has long been appreciated that the activity of PP neurons can be influenced by extraretinal as well as visual sources[3,4]; several studies have even reported responses in PP in the complete absence of visual stimuli during eye-movement tasks[1,2,5,6]. As these tasks involve motor actions, the activity could be related to the intention or execution of the movement. In the present study, however, the animals had no behavioural requirement beyond maintaining fixation, and never made eye movements to the stimulus. Thus the difference in activity between the occlusion and blink trials could not be related in a straightforward way to either sensory input or motor output. The only difference between the two trial types would seem to be the animals' inference that the invisible stimulus were either moving or stationary. The difference in activity could be a neuronal correlate of such inference. Signals of this sort might contribute to the extraretinal responses observed in visual guidance tasks such as smooth pursuit; for example, the activity in cells in the medial superior temporal area that persists when the pursuit target is transiently

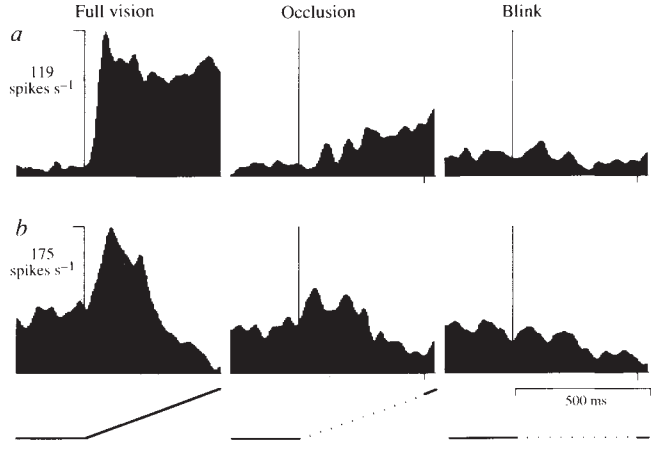

FIG. 2 Responses for preferred-trajectory trials from two PP units. *a*, Peristimulus–time histograms (PSTH) from one cell for the three trial types. *b*, Data from a different cell. Histograms were smoothed by convolving with a gaussian with a standard deviation of 5 ms. Each PSTH was compiled from 12 trials, synchronized (long vertical line) on the start of movement for the full vision trials, or on the disappearance of the stimulus on the occlusion and blink trials. The short vertical line below the *x*-axis on the occlusion and blink trials represents the earliest reappearance of the stimulus among the 12 trials used to compile the PSTH (as the timing among trials was not uniform). The traces at the bottom show the timing of the disappearance of the stimulus, as described for Fig. 1*a*. Single-unit recordings were made using tungsten electrodes (Microprobe Inc.) or glass-insulated Pt–Ir electrodes, introduced into cortex through a guide tube[7]. All surgery was performed aseptically and under full anaesthesia in accordance with Baylor College of Medicine and USDA regulations. The locations of recording sites were verified histologically in one animal; the second animal is still under study.

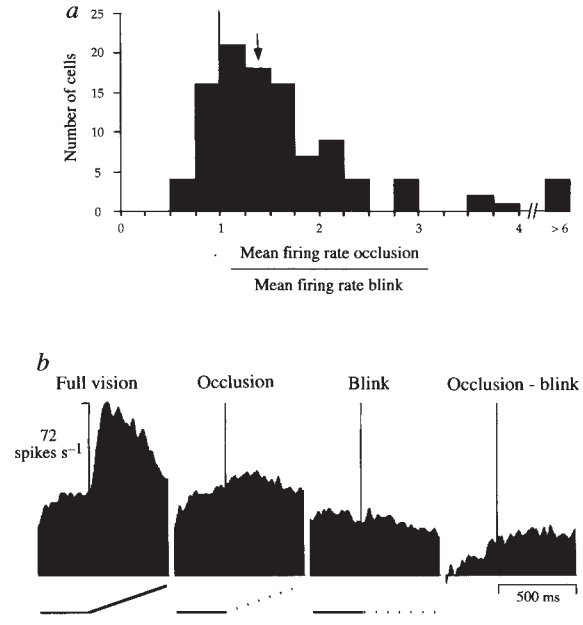

FIG. 3 Population responses. *a*, Distribution among all 106 units of the value of the mean rate of firing during occlusion trials divided by the mean rate during blink trials. Mean rates were calculated from the disappearance of the stimulus until its reappearance. Baseline activity was not subtracted in computing the ratio; this would have increased the absolute value of the modulation indices. The vertical line demarcates a ratio of one, and the arrow indicates the median value for the distribution. *b*, Population PSTHs compiled by calculating the average firing rate for each bin across the 48 PP neurons that showed a significant difference in mean firing rate between occlusion and blink trials. PSTHs were synchronized and smoothed as described for Fig. 2. The fourth column is a difference PSTH calculated by a bin-by-bin subtraction of the blink PSTH from the occlusion PSTH. A population PSTH was also compiled in identical fashion among 18 neurons recorded from area MT. The mean response on occlusion trials was not significantly greater than that on blink trials, averaged over the period following the disappearance of the stimulus (one-tailed paired *t*-test; $P > 0.50$; median MI, 0.90). For all cells, eye position was monitored using a scleral search coil system[8,9] and stored at 200 Hz. An analysis was then performed for every preferred trajectory trial among the 48 $O > B$ units (~600 trials of each type) to test whether eye movements differed in a systematic fashion between the occlusion and blink trials during the period that the stimulus was not visible. For every pair of successive eye-position samples, the component of the instantaneous eye velocity parallel to the preferred stimulus trajectory was determined. The distribution of these velocities (~60,000 for each trial type) was then compiled and compared between occlusion and blink trials. No significant difference was found (Mann-Whitney test; $P > 0.05$. Median velocities were very close to zero in both cases: $-0.0072°$ per second for occlusion trials and $0.0007°$ per second for blink trials).

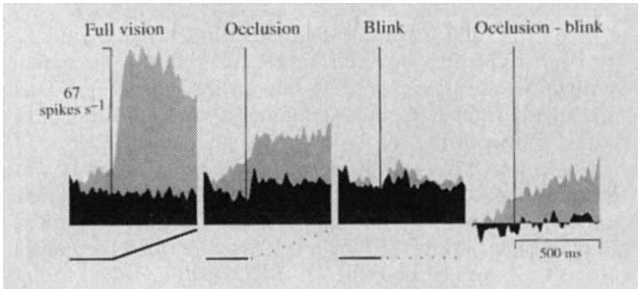

FIG. 4 Comparison of preferred and null-trajectory trials for the 28 $O>B$ units with bilateral receptive fields. Cells were defined to have bilateral receptive fields if their response to the onset of the stimulus was not greater for the stimulus corresponding to the preferred direction compared to the null direction (activity averaged over the 125-ms period following stimulus onset; one-tailed t-test; $P>0.05$). Twenty-eight of the 48 $O>B$ cells met this criterion. PSTHs were synchronized and smoothed as described for Figs 2 and 3*b*. Preferred-direction responses are shown in grey, null-direction responses in black.

extinguished or stabilized on the retina[1]. This activity might be related to the animal's presumption that a target is moving through space, rather than, or in addition to, motor-related signals such as efference copy from the motor system. □

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1. Newsome, W. T., Wurtz, R. H. & Komatsu, H. *J. Neurophysiol.* **60,** 604–619 (1988).
2. Andersen, R. A., Bracewell, R. M., Barash, S., Gnadt, J. W. & Fogassi, L. *J. Neurosci.* **10,** 1176–1196 (1990).
3. Mountcastle, V. B., Lynch, J. C., Georgopoulos, A. P., Sakata, S. & Acuna, C. *J. Neurophysiol.* **38,** 871–908 (1975).
4. Robinson, D. A., Goldberg, M. E. & Stanton, G. B. *J. Neurophysiol.* **41,** 910–932 (1978).
5. Barash, S., Bracewell, R. M., Fogassi, L., Gnadt, J. W. & Andersen, R. A. *J. Neurophysiol.* **66,** 1095–1108 (1991).
6. Barash, S., Bracewell, R. M., Fogassi, L., Gnadt, J. W. & Andersen, R. A. *J. Neurophysiol.* **66,** 1109–1124 (1991).
7. Crist, C. F., Yamasaki, D. S. G., Komatsu, H. & Wurtz, R. H. *J. Neurosci. Meth.* **26,** 117–122 (1988).
8. Robinson, D. A. *IEEE Trans. biomed. Engng* **10,** 137–145 (1963).
9. Judge, S. J., Richmond, B. J. & Chu, F. C. *Vision Res.* **20,** 535–538 (1980).

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Seeing the forest but only half the trees?

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In visuo-spatial neglect after right hemisphere damage, patients fail overtly to notice and respond to stimuli on the side of space contralateral to lesion[1,2]. Nonetheless, these neglected stimuli may covertly influence their performance in other tasks less direct than overt detection or identification[1]. We report here a new type of dissociation between two forms of conscious perceptual awareness in a patient with left neglect. J.R. was shown hierarchical drawings in which a larger (global) form, such as a geometric figure or an alphabetic letter, is composed of smaller (local) forms (dots, circles, or letters). She gave accurate verbal reports of the global structure of these stimuli (Navon figures[3]), yet when required to cross out the smaller subfigures, she only cancelled those on the right of each global figure. Conscious perception of the whole does not automatically lead to visual awareness of all the parts thereof.

J.R., a 59-year-old right-handed woman, initially presented in 1993 with a right hemiplegia from which she rapidly made a full recovery and returned to work; a computed tomography (CT) scan showed a small lacunar infarct of the left thalamic region. A year later, she suffered a right hemisphere stroke, with left hemiplegia, left visual extinction, and gross left visuo-spatial neglect. The weakness improved in the left leg and to a lesser extent in the left arm, but the other symptoms persisted over three months after the second stroke. Florid left neglect was repeatedly found on three diagnostic tasks: presented with random arrays of simple figures to cancel, J.R. crossed out the stimuli on the right-hand side of the page, neglecting all those on the left. Requested to bisect horizontal lines, she placed her transections significantly to the right of centre. When copying complex line drawings, J.R. made relatively accurate representations of the right side of figures but omitted the left sides without acknowledging that the copies were incomplete. Drawing from memory was considerably better. CT scan showed infarction of frontal and parietal cortex with probable subcortical involvement. The lacunar infarct from the earlier episode was still visible.

The following observations were made in the second and third months after the second stroke. J.R. was presented with Navon figures of the types illustrated in Fig. 1. Each stimulus, black on a sheet of white A4 paper, was placed on the desk top immediately in front of her. In free vision, and with no time constraint, J.R. was requested to (1) describe what she saw on the page; (2) cancel all the smaller subfigures (with a pen held in the right hand); (3) put down the pen when all components had been cancelled and describe again what she had seen. The figures varied in overall size and in the spacing between their constituents; some global figures were simple geometric forms, others were letters; the constituent (local) figures were dots (1 mm), circles (15 mm in diameter), or letters (5 mm × 5 mm).

J.R. invariably gave a correct verbal description of each locally consistent stimulus. Figure 1*b* (180 × 180 mm), for example, was reported as a large circle of small As; Fig. 1*c* (110 × 80 mm) was reported as a large E made of smaller Hs. Despite these accurate reports (before and after cancellation), J.R. never crossed out the subfigures on the left of the overall configuration. The same failure was seen when the cancellations were made in invisible ink, and is thus not due to attentional capture by the additional marks made by visible ink. Our dataset comprises over fifty observations of the type shown in Fig. 1; there were no counter-examples under the testing conditions described.

A number of shallow explanations can be ruled out. The conjecture that J.R. only 'saw' the right half of each square or circular configuration, but 'completed' the global percept by reporting the simplest closed figure compatible with what was seen[4] is false: when shown 'full' figures (Navon squares and circles) randomly interspersed with 'half' figures, J.R. reported only the squares and circles as squares and circles ($n=10$), while correctly describing the left-truncated figures as half-squares or half-circles ($n=10$). By contrast, when shown circles and squares in which the (lateral) halves were composed respectively of Es and Fs (or Cs and Xs), reliable local completion occurred. All global stimuli were correctly reported as circles or squares, but J.R. claimed that the (correctly named) local elements on the right extended throughout each global figure ($n=10$). When the (lateral) halves of a circle were respectively composed of blue and red dots, the colour of the right half was reported for all the dots of the circle ($n=10$).