FIG. 3 Seasonal variations in the oxygen isotopic composition of water extracted from suberized root/stem (○) and leaves (□) of pioneer perennial plants found in the study area (Fig. 1). Tissue samples were collected in summer (May, no summer rains) and autumn (November, after the first rain in the region was recorded). The arrows indicate the average $\delta^{18}O$ value for leaf or root/stem water for all plant species sampled. Isotopic composition was analysed as for Fig. 2.

to-leaf enrichment—in contrast to the expected effects of the lower humidity at that time[23]. Thus, the results in Fig. 3 indicate that in summer the plants become increasingly isolated from their environment, in terms of water uptake and evapotranspiration[24]. After the first winter rain and possibly flood, the renewed utilization of fresh water results in a decrease of stem water $\delta^{18}O$, and the consequent restoration of transpiration is associated with increased isotope enrichment in the leaves. Yet it is still remarkable that the plants were capable of discriminate use of flood water, which is chemically distinct from the bulk of soil water found in their root zones. Such a feature, shared by several different plant species, may be a prerequisite for plant invasion of highly stressful environments, allowing for the early onset of terrestrial biospheric activity. □

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A brain-damaged patient with an unusual perceptuomotor deficit

Umberto Castiello*†, Marina Scarpa‡
& Keree Bennett§

* Dipartimento di Psicologia, Università di Bologna, Viale Berti Pichat 5, 40127, Bologna, Italy
‡ Clinica Neurologica, Università di Modena, Via del Pozzo, 71, 41100, Modena, Italy
§ European Medical Centre, Pieve di Cento, Bologna, Italy
† To whom correspondence should be addressed. Address from June 1995: Department of Psychology, Cippsland Campus, Monash University, Churchill, Victoria, Australia

WHEN interacting with objects, the pattern of movements is influenced by such object characteristics as size and position[1–4]. Little is known about the effect of higher level categorical encoding of objects upon movements. Here we present evidence for an approval-for-action process which takes into account such encoding. For the brain-damaged subject L.P., the ability to complete actions involving two objects in central vision is influenced by the semantic or functional relationship between the objects. Even though she
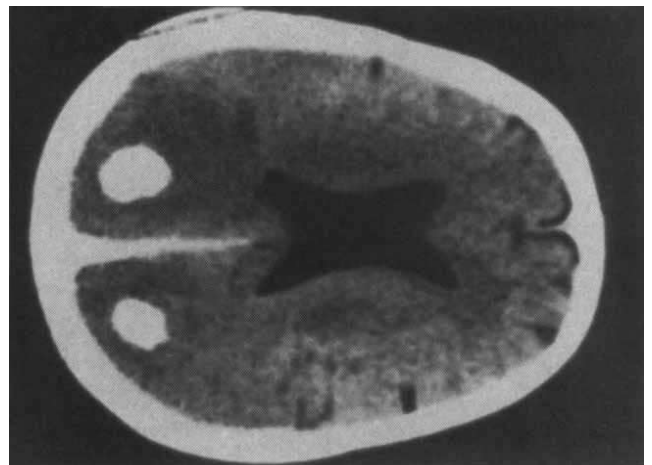

FIG. 1 L.P. suffered a left-hemisphere stroke with transient right hemiparesis in May 1993. A computed tomography (CT) scan at that time showed a left occipital lesion. The CT scan shown here demonstrates bilateral lesions (cortical mark is a slide crease). It was performed in April 1994 after L.P. complained of difficulties when putting objects together, and of intermittent problems with dressing, reading, writing and watching television. 'As my pen approaches my grandson's scribbles, the tip disappears and I cannot draw. However I can write my name'. 'At times I construct complicated LEGO forms. Yet, sometimes I cannot join pieces'. She reports: 'I see only the bottle or its lid but can screw on the lid; only the toothbrush or the tube but can squeeze out the toothpaste'. Across 15 assessment sessions during the six-month period following the second CT scan, the subjective reports and clinical picture have remained constant. L.P. identifies single elements rather than the whole of a complex picture ('telegraph boy'[17]; 'cookie theft'[18]). When presented with two pictures or objects she immediately reports seeing only one. (Note, however, that exposure time was not manipulated). There are no visual field defects (Goldman Perimeter), voluntary ocular movements are normal, and visual acuity is 10/10. L.P. is able to read single words (80/80[18,19]) and can identify single objects: 260/260 for objects/non-objects[20], 99/99 for objects viewed from different angles[7], and 32/32 for objects with similar functions but different forms[21]. L.P. has no signs of apraxia or optic ataxia[11,22,23]. She performs common hand gestures and facial expressions, and demonstrates and mimes the use of everyday objects. She does not misreach or show inappropriate grasp apertures for a variety of targets. There are no signs of unilateral neglect, extinction, split-brain syndrome, dementia or psychiatric dysfunction.

perceives only one object, she can integrate two related objects into a coordinated action. If the objects are not related she is unable to integrate them into a single motor act. We propose that selection-for-action systems[5] include processes which gate conceptually the behavioural disposition to action.

L.P. is a 66-year-old retired primary-school teacher with bilateral, calcarine sulcus, occipital lesions (Fig. 1). She reports seeing only one of two objects placed within central view. The selected object is correctly identified irrespective of its semantic category, or visual field position. In addition to this form of simultanagnosia[6][8], her ability to point to, or manipulate together, two objects is disturbed when the objects are not functionally or categorically related.

When the objects are related, her movements are performed in a unified manner, with coordinated manipulation appearing to be normal, and independent of perceptual judgements. This applies to objects that she would frequently put together. For example, when a pen and its cap are in central view she reports seeing only one or the other, yet she can pick up both objects and join them together. Unified bimanual movements are also found for pairs of three-dimensional objects, or pictures of objects, within the same 'living things'[9,10] semantic category. If

two related pictures are placed together in central view, she uses the left index finger to point to one and the right index finger to point to the other (Fig. 2, upper panel). With the index fingers thus placed, she can separate the pictures, moving both. When the pictures are placed apart she can move them together (Figs 3 and 4, upper panels).
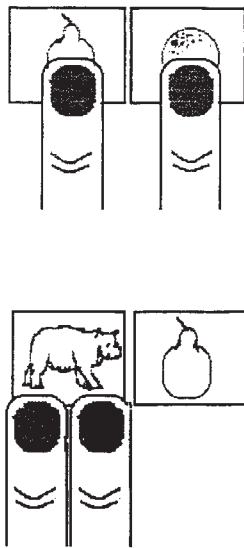

FIG. 2 Pointing task. L.P. was asked how many pictures (objects) she could see. Upon replying, she was instructed to point to them. Two pictures, pasted onto cards (3 cm × 3 cm), were presented side by side, or one above the other, with no overlap and in central view. The semantic relationship between the cards was manipulated. From 40 pictures[20], the following pairs were presented: 15 'living semantic'[9,10], from 5 cards for each animal, vegetable and fruit category; 15 'non-living' semantic[9,10] from 5 cards for each tool, furniture and vehicle category; 30 non-semantic; and 5 associative, non-semantic (for example, grapes/wine barrel). Five pairs, presented one on top of the other, were formed for each 'living', 'non-living' and non-semantic category for objects (n = 20) within the subject's home (for example, fruit and toys). All pairs and the following experimental design were used for all assessed tasks. Three trials were tested for each pair. Presentation order followed an ABBA design. The position of each picture (object) was randomized. Exposure time was unlimited but L.P. always responded immediately. Upper panel. 'Living' category. L.P. points to both fruits (pear and orange) yet reports seeing only one. This same result applied for 100% of trials for pictures and objects from this category. She often asked how she could point to two if she sees only one. Lower panel. No semantic relationship. L.P. points to and reports seeing only one card (bear or pear). She pointed to the bear for one trial and to the pear for two trials. Similar results were found for pairs from the 'non-living' and associative categories. The exception was when L.P. pointed to both the 'bed' and 'pillow' pictures, indicating that 'non-semantic' objects which are usually linked together in a motor act can be integrated at the motor level.
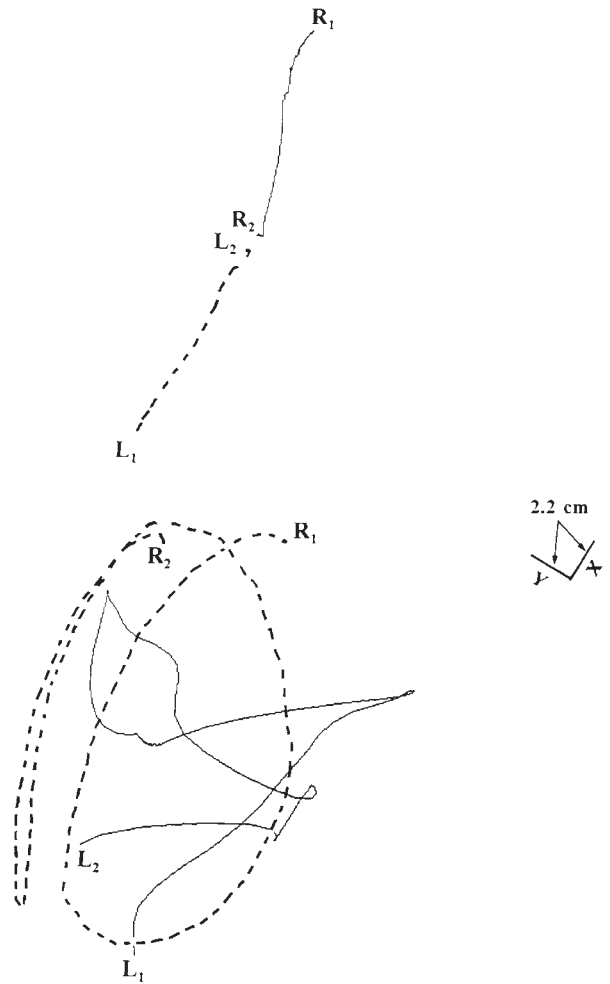

FIG. 3 L.P. was asked to put the pictures (objects) together. For bimanual movements, one was to the left and one to the right of a central point (15–60 cm apart). For unimanual movements, one was central and the other was to the right or left (10–30 cm). The subject was seated and the video view was from approximately 1 m to her left and 0.5 m above her head. The experimental design is explained in the legend of Fig. 2. For each video frame, a reference point was placed on the centre of each card (Videotrack, BTS). Broken line, left card trajectory; solid line, right card trajectory. L1 and R1 are initial positions of left and right cards; L2 and R2 are final positions. Upper panel. 'Living' semantic category. The subject places the cards (bear and alligator) together, and reports seeing one after completion of the task. L.P. also performs unimanual movements without difficulty. Lower panel. No semantic relationship. The subject begins by picking up each card (bed and lemon), but cannot bring the cards together, moving them back and forth instead in an iterative manner. Trajectories of the card movements are not consistent from trial to trial. With unimanual movements, L.P. cannot bring a laterally placed card to a central card. These results apply for all 'non-living' semantic pairs (except for bed and pillow) and for all associative non-semantic pairs. L.P. was also filmed putting together ten objects with two parts (for example, pen and pen cap), and when putting something on her finger (for example, a ring). Again, the relationship between the component parts was manipulated to form ten 'usual' pairs and ten 'unusual' pairs (for example, pen cap and tablet bottle). Each action was performed ten times. Although dextrous with 'usual' pairs, she cannot bring together 'unusual' pairs.

With object pairs that have other associative and categorical relationships her movements are completely different. She cannot bring together objects that do not usually go together. For example, she cannot complete the action of placing a pen cap on a tablet bottle; the actions taken to avoid colliding with the bottle nevertheless indicate implicit knowledge of its presence. She cannot insert her finger into a bottle top, despite correctly aligning both the finger and the top. Unified movements are also impossible with pairs of objects or pictures within the same 'non-living'[9,10] semantic category, and with those which have no semantic relationship. They are also impossible for pairs that do not usually go together but have an associative, non-semantic relationship. When pointing to picture pairs of these three kinds, L.P. uses both index fingers to point to one or the other picture (Fig. 2, lower panel). If the examiner places L.P.'s index fingers
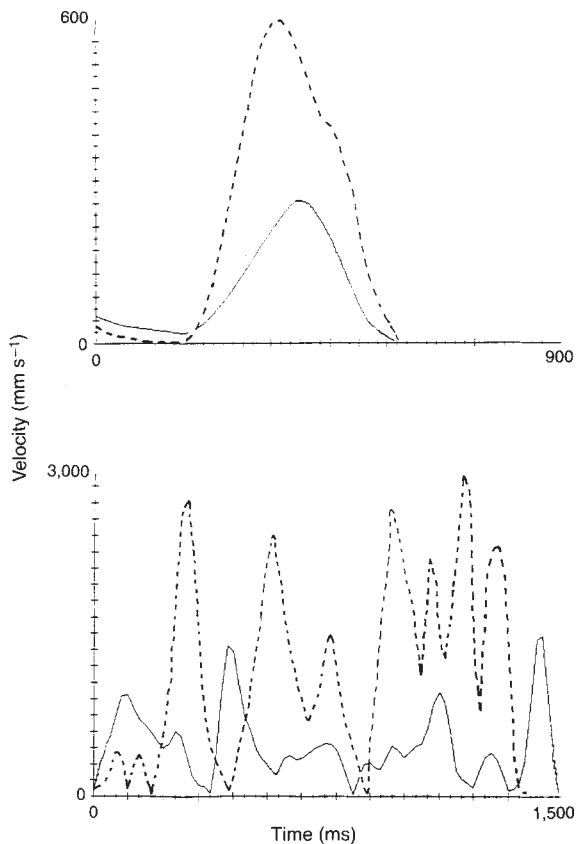

FIG. 4 Velocity profiles of the movements shown in Fig. 3. The Elite[24] processing package was used to filter the Videotrack data, and to construct velocity profiles. Upper panel. When bringing together pictures of the bear (left hand; broken line) and alligator (right hand; solid line), the movement of each card shows a single velocity peak. The similar timings of the velocity peaks and of the end of the card movements, suggests that the limbs have been coupled successfully for the execution of a common task[25–27]. Lower panel. In contrast, the bimanual action of bringing together pictures of a bed (left hand; broken line) and a lemon (right hand; solid line) demonstrates a completely different pattern. As indicated by the presence of several velocity peaks, the movement of each card is divided into several submovements. The times at which the peaks of velocity occur for the left hand do not coincide in time with those for the right hand. This, together with the asynchrony in completing the actions, suggests that the hands are acting independently, without bimanual coordination or integration. Also of interest is the high amplitude of the velocity peaks: each submovement is performed extremely rapidly. (Note that the abscissa and ordinate axes differ for the upper and lower panels). The time taken to complete the entire movement is also very long. In fact, L.P. would often continue to move the unrelated card or object pairs about in a random and disorganized manner, until taking an apparently arbitrary decision to finish the movements.

on different pictures, L.P. moves only one picture when asked to separate them. She cannot bring two separated pictures together at all (Fig. 3, lower panel): she begins the bilateral movement, but then moves the pictures in an iterative (Fig. 4, lower panel), almost circular, manner, to finish up placing the pictures often near their original positions. The uni-manual movement of bringing a laterally placed picture or object to lie beside one that is central is also not possible.

Dysfunction is present even at a representational level. To test this, picture pairs were placed face down and apart, and the examiner stated the identity of each. Despite seeing identical blank green cards, and not having seen the pictures, L.P. cannot bring together unrelated pairs.

Dysfunction is confined to central vision. While fixating centrally, L.P. correctly states the number and identity of peripherally presented objects, irrespective of their categorical or functional relationship. She can also separate them or bring them together in peripheral vision (10–30°).

This perceptuomotor deficit is characterized by visuomotor dissociations between objects in central view. A constant dissociation is for the process of consciously seeing the objects. A dissociation that is not constant, but is dependent upon the relationship between the objects, is for the performance of integrated motor acts with the objects. When the relationship is functional, motor dissociation is not present. Although this suggests preservation of familiar actions, such an explanation cannot account for the absence of motor dissociation when the objects share a 'living things' semantic category, that is, for objects (or pictures) that may not normally be put together (for example, bear and alligator). This result, together with the presence of motor dissociations for other relationships between objects, suggests that high-level visual processes (for example, semantic categorization[7], assessment of object use and sense[11], and evaluation of relationships between objects) influence covert attention to the objects and motor unification of the objects.

'Implicit' or 'covert' knowledge also appears to influence attentional and motor unification. L.P. consciously uses two objects together, even though she does not report seeing both objects. (This dissociation parallels that of an agnosic patient who could act accurately upon objects using visual properties which she did not report seeing[12].) Further, and without underestimating the contribution from previous visuomotor experience, L.P. does not need low-level visual processing for unification. Even when identification of the objects is indicated verbally, conceptual gating according to the relationship between the objects continues to influence attentional and motor performance.

These results support a complex role for the occipital region in the synthesis of categorical, functional and spatial information about objects within a head-centred coordinate representation, and in the linking of this information, via inferotemporal and parietal areas[13,14], to motor systems[15,16]. This selection-for-action includes a definition of the relationship between objects to be integrated within a unified motor act. □

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Independent neural mechanisms for bright and dark information in binocular stereopsis

Julie M. Harris[*][†] & Andrew J. Parker[*]

* University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK
† The Smith-Kettlewell Eye Research Institute, 2232 Webster Street, San Francisco, California 94115, USA

EARLY visual processing is organized into a number of independent channels. In the retina, increments and decrements of brightness are processed independently by different groups of neurons[1]. For psychophysical measurements of human vision, independence can be tested statistically. Using this criterion in a depth judgement task, we show here that, for binocular stereo vision, increments and decrements are treated independently, at least as far as the level at which information from the left and right eyes is first combined. At later stages of stereo processing, the information from the two channels is no longer independent. Because the signals for stereo vision are first combined at the visual cortex, these results suggest that the neural 'on' and 'off' channels remain independent right up to early cortical stages. Theoretical studies of stereo vision have proposed that visual features in the views of the two eyes are matched on the basis of 'similarity'[2]. Our results show that stereo matching treats features as statistically independent (and therefore dissimilar) if they appear perceptually bright and dark relative to the background. If features differ perceptually but only in the degree of brightness or darkness, human stereo vision treats them as similar.

In the retina and the visual thalamus, the perceptual detection of increments and decrements of brightness is mediated by two independent sets of cells, the 'on' and 'off' cells[3,4]. There is physiological evidence that the two channels may be functionally segregated as far as the cortex: however, the anatomical[5,6] and psychophysical[7-10] evidence is less clear. We developed a new psychophysical test of whether brightness increments and decrements are processed separately at a cortical level. To support depth judgements with binocular stereo vision, information from the two eyes is first combined effectively at the primary visual cortex. We therefore required: (1) a stimulus and task that necessitated the merging of information from the two eyes before judgements could be made and (2) a measure that reflected how much of the available information was used by the observer when the stimulus contained either just one or both contrast polarities.

The use of a random dot stereogram[11] satisfies the first requirement. The stereogram consists of a pair of images containing randomly positioned dots. The two eyes' images are identical, except for small horizontal offsets of the dots. With each eye viewing one half-image, the horizontal disparities between the positions of the dots are interpreted by the visual system as if the dots were at different depths. If a task requires a stereo depth judgement, it tests performance at or beyond the stage at which stereo matching takes place, as the depth information is available only after binocular combination. In the particular task studied here, the stereogram depicted a step-change in depth that appeared as a vertical edge to the observer: the observer had to identify which side of the edge was nearer (Fig. 1).

The second requirement can be satisfied by measuring the statistical efficiency of stereopsis. The measure of efficiency is essentially a comparison between the performance of a chosen system and that of an ideal observer, whose performance can be manipulated by adding noise to the stimulus[12]. Efficiency gives a measure of the proportion of image information used by the test system. Thus for a dot stimulus, efficiency provides an estimate of the effective number of dots used to solve the task.

In previous work, we measured stereo efficiency using a random dot stereogram that depicted a step-edge in depth[13,14]. Noise was added by jittering the disparity of each dot. Such noise limits the ability of even an ideal detector to decide which side of the step-edge has the greater average disparity. For this task, human efficiency is low because of an inability to exploit all the information within the target[13]. With this type of random dot stimulus that has a noisy, jagged depth profile, one main reason for the low efficiency may be that only a few dots in the pattern are correctly matched between the left and right eyes[14]. The problem faced by the visual system is that there are many alternative pairings of individual dots in the right and left images, most of which need to be discarded as incorrect. If the correct dots are not matched binocularly, their disparity signal is never made available to later stages of processing and thus efficiency will be low.

We considered that, if brightness increments and decrements are processed separately at the dot-matching stage, stereo efficiency should be improved by making half the dots dark and half light, because for each distinct and independent set of dots there will be fewer possible matches overall and therefore fewer incorrect matches to be discarded. With completely independent binocular matching of increments and decrements, stereo efficiency should improve by a factor of 2. If less than a factor of 2 is found, this would indicate a partial dependence: either a degree of statistical correlation between the channels or some other form of interaction.

Statistical efficiency was measured for the detection of a step-edge in depth (Fig. 1). In the first experiment, half the dots were lighter and half darker than the grey background. Performance with these mixed targets was compared against performance with stereograms containing only light or only dark dots. Figure 2a shows the effective number of dots used by an observer when the stimulus contained either dots of one contrast polarity, or dots of both polarities. Observers behaved as if they were using more dots when the stimulus contained both light and dark dots than either when only light or when only dark dots were present. Figure 3a shows the ratio of the efficiency found in the 'mixed contrast' condition to the efficiency found in the 'single contrast' condition. A ratio of 1 would indicate that the same efficiency was found in each condition, but the actual ratios are close to 2, which represents a doubling of efficiency. This suggests that the simultaneous presence of increments and decrements of brightness provided the observer with two statistically independent samples, one from the dark dots and one from the light.

In the second experiment, stimuli were created in which all dots were dark relative to the background, but the dots were at two different contrast levels ('dark' and 'darker' relative to the background). For these stimuli, the effective number of dots