taxonomic significance can be attributed to this aspect of the biology of early hominids during these phases of human evolution. However, future estimates of age at death for the majority of sub-adult early Plio-Pleistocene fossil hominids, based on this study and new dental developmental data, should help quantify the nature of changes in rates of growth in specific anatomical regions, and enable these changes to be traced through the hominid fossil record.

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Subjective contours capture stereopsis

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Stereoscopic depth perception is based on measuring tiny differences between the two eyes' images which arise as a result of binocular parallax[1]. Julesz[2] used random-dot stereograms to demonstrate that stereopsis may be based on a simple point-to-point comparison of the two eyes' images and does not require the presence of monocularly visible forms or contours. Here we present a new class of stereograms which illustrate that monocular subjective contours[3–5] can influence the matching of elements in a stereogram even though the elements themselves convey no disparity information. More specifically, the depth seen from such contours is automatically attributed to texture elements and lines that are enclosed by these contours—an illusion that we call 'stereoscopic capture'.

Figure 1*a* depicts a well-known illusion known as the 'wallpaper effect'. When patterns consisting of repeating stripes are viewed binocularly they can convey any one of a number of different depth planes[6]. However, at any given instant the entire pattern is seen to occupy only one single plane; the exact plane seen seems to depend mainly on the angle of convergence. Figure 1*b* shows a square defined by subjective contours[3–5]. Such contours can be produced by means of appropriately aligned black disks from which right-angled sectors have been removed. The brain interprets this figure parsimoniously as an opaque white square with its four corners occluding the four black disks (and not as four sectored disks which have been deceitfully aligned by the experimenter). One has the strange impression of a contour connecting these aligned edges even though no contour exists physically—hence the name subjective contours. Whether these contours are physical, physiological or truly 'subjective' is a much debated semantic issue that need not concern us here.

We constructed a stereogram using two subjective squares similar to that of Fig. 1*b* by introducing small horizontal disparities between the vertical edges of the cut-out sectors (Fig. 1*c*). Perception of depth in these stereograms is most vivid when the disparities convey a square standing out in front of the disks. If the two images are now interchanged, stereopsis disappears and, surprisingly, the subjective contours also become weak; perhaps because it is now difficult to make any sense out of the whole figure[7,8]. These stimuli and all subsequent ones described here were generated on a CRT screen using a Macintosh microcomputer. The visual angle subtended by the black disks was 0.5° and the subjective square itself subtended 2°. The horizontal disparity between the vertical edges of the cut sectors was 20 arc min.

Our next step was to superimpose a template of Fig. 1*c* on several kinds of wallpaper to generate 'wallpaper stereograms' (Figs 2, 3, 4). In Fig. 2 we simply used repeating vertical rows of spots (see figure legends for additional details). This stereogram was then shown to eight subjects who were experienced psychophysical observers but were unaware of the purpose of the experiment. They were shown both crossed and uncrossed versions (that is, with a square depicted in front or behind the plane of fixation) and asked to report what they saw. With crossed stereograms (Fig. 2*a*) all eight subjects saw the square defined by the subjective contours as standing out clearly in front. Interestingly, the corresponding dot-rows on the wallpaper were also carried forward with the plane—an effect we call 'stereoscopic capture'. As the disparity of the squares equalled several multiples of the periodicity of the dot-rows, this finding implies that the subjective surface in depth created by the subjective contours was somehow pulling the dots with it even though the dots themselves do not convey any specific disparity information (in fact they convey zero disparity in relation to the background). When the subjects viewed uncrossed stereograms, no such effect was seen; neither the subjective surface nor the stereoscopic capture effect was observed (Fig. 2*b*; see legend for further details).

In Fig. 3 we used continuous vertical lines instead of rows of dots in the background. Subjects reported that the illusion was just as compelling here as in Fig. 2. Surprisingly, the capture effect was strong enough to overcome the physical continuity of the vertical lines and caused apparent breaks to appear on the lines at the upper and lower edges of the subjective square. Again, as in Fig. 2, the illusion disappeared completely when the pictures received by the two eyes were interchanged and subjects now reported seeing rivalry and diplopia instead of capture.

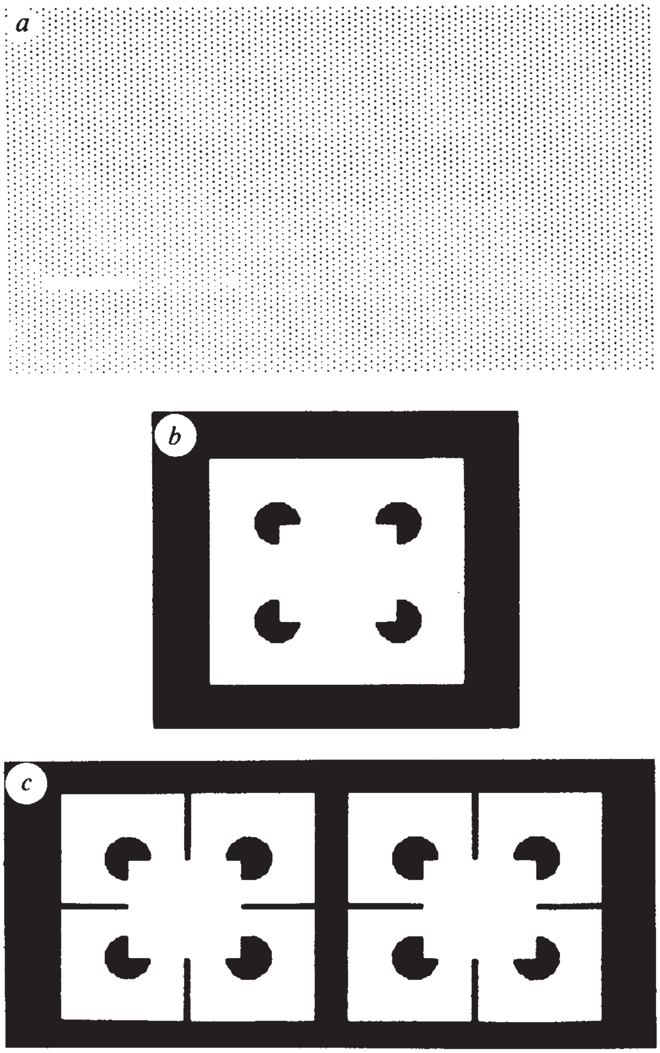

Fig. 1 *a*, A well-known stereoscopic illusion called the wallpaper effect. If the reader brings the pattern very close to his nose and changes his angle of vergence while viewing this display he will perceive corresponding changes in the plane of perceived stereoscopic depth. *b*, A square defined by subjective contours. Observers usually perceive an opaque white square whose corners partially occlude the four black disks. Faint 'subjective' lines are seen to delineate the square even though no physical lines exist. *c*, A stereogram produced by using two subjective squares similar to that in *b*. Small horizontal disparities are introduced between the vertical edges of the cut sectors. When the two eyes' patterns are fused, a subjective square stands out in stereoscopic depth.

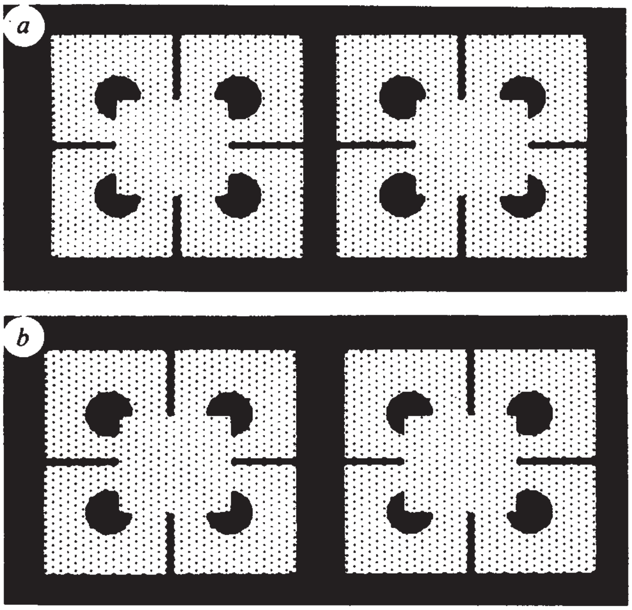

Fig. 2 *a*, Produced by superimposing a template of Fig. 1*c* on a repeating wallpaper pattern. The inter-dot separation between the elements constituting the wallpaper is 5 arc min. A subjective square stands out in front of the background and carries the wallpaper with it even though the elements on the wallpaper are at zero disparity. This is an example of stereo capture (see text). *b*, Identical to *a* but with the two eyes' pictures interchanged to reverse retinal disparities. The illusion is destroyed and replaced by rivalry and diplopia. However, one of our subjects spontaneously reported that instead of stereo capture he now saw four portholes cut out of an opaque sheet of wallpaper. Through these portholes he could see the four corners of a smaller square piece of wallpaper and these corners pulled the corresponding rows of dots with them. This alternative and unusual percept of seeing four deeper corners is of considerable interest for it reinforces the view that it is indeed the subjective contours that drive the perceived depth. The observation was also confirmed by two other subjects on prompting but the remaining five subjects continued to experience rivalry and diplopia. The percept becomes more pronounced if the horizontal black lines are removed and if finer textures are used (for example, try fusing Fig. 3*b*).

Next we superimposed Fig. 1*c* on horizontal lines (Fig. 4*a*). As expected, none of the eight subjects observed capture when uncrossed disparities were used (as in Fig. 3). With crossed disparities, subjects reported that only the lines actually adjoining the sectors themselves were pulled forward. All the other lines on the square remained flush with the background and it was very difficult to break the continuity of these lines in order to partition them into two surfaces. Perhaps the brain is reluctant to attribute depth to horizontal lines as such lines do not normally convey disparity signals in the real world.

One could argue that the anisotropy observed here is between vertical as opposed to horizontal gradients of disparity (that is, between the vertical and horizontal edges of the illusory square) and not between vertical and horizontal gratings. We tested this possibility by using oblique gratings (Fig. 4*b*) and found that the illusory breaks on the lines could now be seen along both vertical and horizontal borders of the square. Further, when they were asked to compare the vertical and horizontal depth edges, none of our subjects could see any difference. This result suggests that the anisotropy observed in Figs 3 and 4*a* occurs not at the cyclopean level but probably at an earlier stage of stereo-matching.

Figure 4*c* depicts another version of stereo capture: here we have used dissimilar wallpaper textures for the images received by the two eyes. As the elements comprising these textures are uncorrelated for the two eyes, one would expect to see either binocular rivalry or random depth planes based on chance correlations. Seven of our eight subjects, however, reported seeing stereo capture; the dots corresponding to the square were seen to stand out in front despite the rivalry. Thus, the stereo capture illusion is strong enough to overcome rivalry of finer image features (high spatial frequencies), although the effect is certainly less striking than that observed in Figs 2, 3. This observation is consistent with the conclusions of Ramachandran *et al.*[9] that monocularly visible texture boundaries can support stereopsis even when the elements defining the textures are themselves uncorrelated.

We considered the possibility that vergence eye movements are involved in producing these effects—this seems unlikely for two reasons. First, one sees two different stereoscopic planes simultaneously in each of these stereograms, an outcome that would be impossible to achieve by simply using convergence alone. Second, we presented the stereograms (Figs 2, 3*b*) in a tachistoscope to three subjects. Crossed and uncrossed disparities were flashed in random sequence while they fixated a spot presented on the background just below the subjective square. When asked to report whether the elements within the

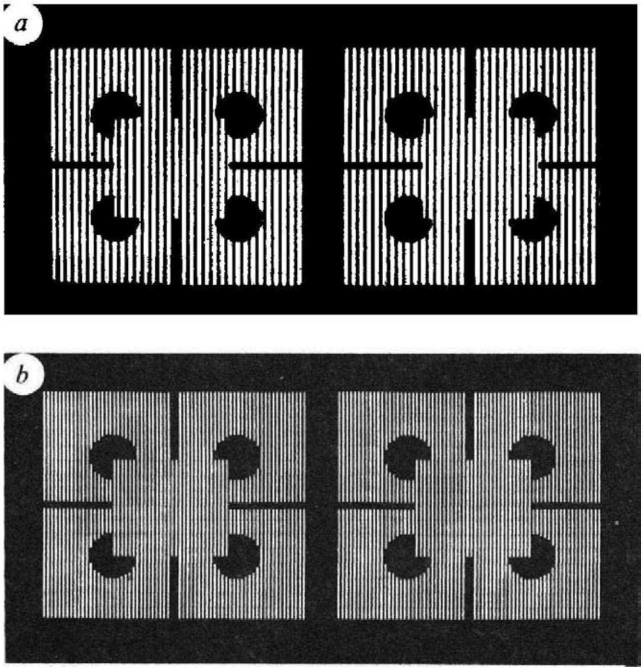

Fig. 3 *a*, A template of Fig. 1*c* superimposed on a pattern of repeating vertical stripes (spatial frequency of the stripes is 9 cycles deg^{-1}). A subjective square stands out clearly from the background, carrying the lines with it. Also, the capture effect is strong enough to overcome the physical continuity of the lines and causes apparent breaks to appear on the lines. *b*, Similar to *a* except that the disparity has been reduced to 10 arc min to enable easier fusion. The spatial frequency of the grating is 18 cycles deg^{-1}.

square appeared in front of or in the same plane as the fixation spot, they responded correctly on 51 out of 60 trials (3 subjects × 20 trials each). Similar results were obtained with Fig. 3*b* (54 out of 60 responses were correct), suggesting that eye movements are not responsible for the effect.

We found that stereoscopic capture was also very sensitive to the spatial phase relationship between the wallpaper and the sectored disks: the cut edges had to be 'phase-locked' with the lines so that the subjective square's disparity was an exact multiple of the periodicity of the lines. Thus, when the disks themselves were flush with the background, the subjective square occupied exactly the same plane as the enclosed wallpaper that was captured and this seemed to amplify the illusion. If a deliberate phase shift was introduced, capture was considerably reduced and replaced by the appearance of a transparent subjective square. This observation implies that the signal derived from the disparate subjective contours is not merely attributed to the elements of wallpaper; there must be some degree of mutual synergy between the two. In this respect stereo capture may turn out to be different from motion capture[10,11].

Our conclusions are also consistent with the elegant demonstrations of Mitchison and McKee[12] and Julesz and Chang[13], although neither of these studies specifically explored the role of image segmentation produced by illusory contours. Mitchison and McKee found that disparity signals derived from the endpoints of two horizontal dot-rows viewed binocularly could influence the matching of ambiguous repetitive elements in the middle. However, in certain conditions they could produce a dot-row that was tilted in stereoscopic space as a result of interpolation—an effect that we could not produce in our displays. When we superimposed a tilted illusory surface on closely spaced gratings (12 cycles deg^{-1}) the gratings remained flush with the background and showed no tendency to tilt with the illusory surface.

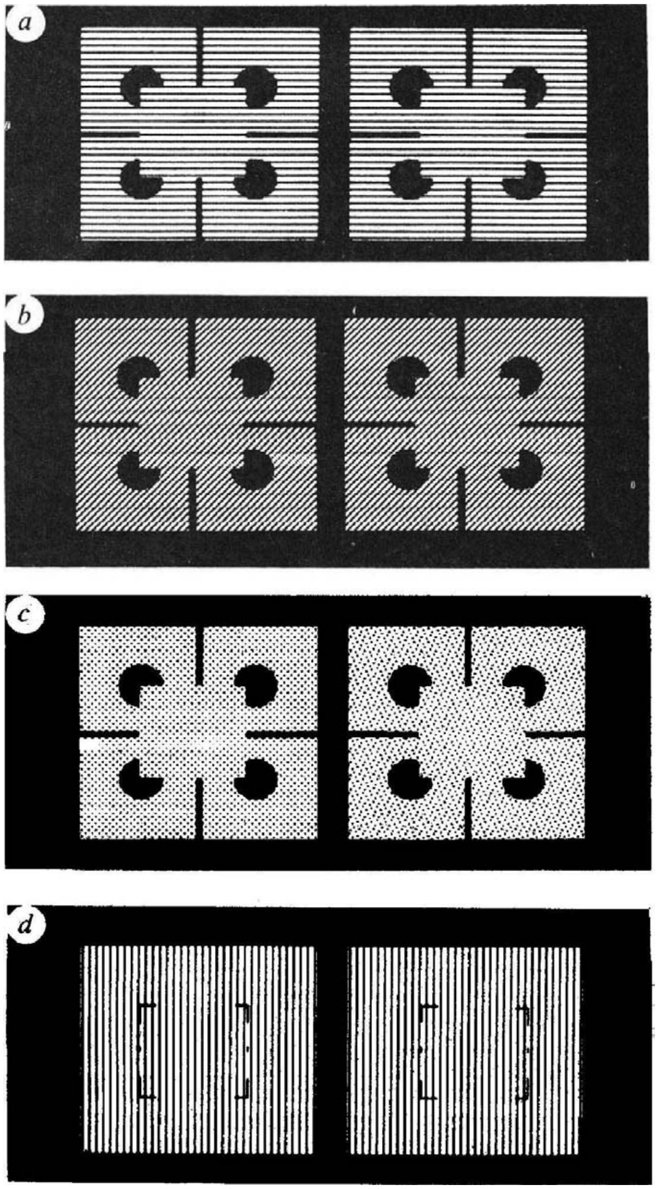

Fig. 4 *a*, Capture is considerably weaker if horizontal lines are used. The lines adjoining the sectors themselves are pushed forward but not the lines in between (they remain flush with the background and it is impossible to see subjective breaks). *b*, A stereogram similar to *a* and Fig. 2, except that we have used oblique lines instead of horizontal or vertical lines. The apparent breaks on the lines are equally obvious on both vertical and horizontal borders of the illusory square. *c*, Here we have used dissimilar textures for the two eyes to produce rivalry. Stereo capture can be seen despite the rivalry (especially on eccentric fixation) but the illusion is less compelling than in Figs 2 and 3. Note that although the textures are dissimilar, they probably have some overlap of their Fourier power spectra; this overlap may produce some chance correlations that are necessary for generating the effect, but we did not specifically explore this possibility. *d*, This stereogram is identical to Fig. 3*a* in every respect except that we have replaced the cut sectors with corners made of small line segments so that no illusory contours are visible. Although the disparity between these corners is identical to the disparity between the cut sectors in Fig. 3*a*, stereoscopic capture cannot be observed in this display, suggesting that the presence of an illusory surface is an important prerequisite. Some of the lines may occasionally appear to come forward due to convergence but it is impossible to partition the image into two well-defined surfaces.

Next, we wondered whether the stereo capture illusion depicted in Figs 2 and 3 was being produced by the illusory contours themselves or by the disparity conveyed by the cut sectors. Although there is no simple way of answering this question, we attempted to do so by using a 'control' stereogram of the kind shown in Fig. 4*d*. Here, we have replaced the cut sectors with corners made of tiny line segments so that no illusory contours are visible. When our eight subjects viewed this stereogram, they reported that the corners floated out in front of the paper but that the grating was not captured and pulled forward. This supports our contention that the creation of a subjective surface is an important prerequisite for producing stereo capture.

Thus, disparate subjective contours capture regions of zero disparity enclosed within these contours but not regions that lie outside the contours. When vertical stripes are used the effect is strong enough to overcome the physical continuity of the lines so that illusory breaks appear on them. The capture effect disappears if the sign of disparity is reversed, suggesting that factors such as overlay or occlusion are an integral part of the illusion. An anisotropy was observed between vertical and horizontal lines, the latter being resistant to capture. Capture was also phase-sensitive, the effect being most pronounced when the disparity of the illusory contours was an exact multiple of the grating periodicity. Finally, completely uncorrelated (and rivalrous) regions can also be captured to a limited extent.

It would be interesting to determine whether computational models[14] of stereopsis can be modified to account for these intriguing phenomena. We conclude that in many instances the brain may begin by segmenting the scene into contours and surfaces and that the information derived from such segmentation can have a profound influence on subsequent processing retinal disparities[9]. Certain cells in area V1[15-17] are thought to respond to small disparities and those in V2 to large retinal disparities[18-20] as well as illusory contours[21]. It is not inconceivable, therefore, that stereo capture results directly from synergistic interactions between these cells. For example, the wallpaper might excite cells corresponding to several depth planes in area V1 whereas the disparity of illusory contours would excite only a single plane in V2. The latter signal might then be fed back to V1 to select or 'highlight' the appropriate plane—a conjecture that is consistent with the observed anisotropy (Figs 3, 4*a*) and phase-sensitivity of stereo capture. Further experiments along these lines may help us to better understand the hierarchy of precedence rules in the brain that result in the construction of a three-dimensional visual world.

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Note added in proof: If disparities were introduced between the disks themselves and not just between the cut sectors, no capture was seen. This suggests that a simple spread of disparity signals cannot explain the effect; the presence of an illusory stereoscopic surface is required.

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Cycles of presence and absence of mother mouse entrain the circadian clock of pups

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Recent findings on neural and endocrine rhythms in infant mice and rats show that maternal coordination has an important role in setting the phase of the developing circadian clock both in the fetus and soon after birth[1-7]. However, less information is available about the influence of the mother on activity/rest cycles of infants. Separation of the mother from infants in guinea pigs, monkeys and rats[8-10] results in an increase in sleep disturbance (enhanced activity?). In this context it may be a common feature that during the postnatal period there is enhanced activity of pups during the hours when the mother is not nearby. Conversely, the social influences exerted by the mother while present with her young possibly leads to a relative rest stage. We have now tested this assumption in the night-active mouse *Mus booduga*. Our study addressed the postulate that the circadian activity/rest cycles of the pups are controlled by cyclic(?) presence and absence of the mother. The results reported here clearly indicate that the circadian locomotor activity of pups kept under continuous illumination or continuous darkness do entrain them to a regime of imposed 12:12-h cyclic presence and absence of the mother. The characteristics of this entrainment confer on the mother mouse the role of zeitgeber.

Pregnant females of the field mouse *M. booduga* (14-16 g) were captured from the fields surrounding the university campus. The pregnant mice were maintained in continuous darkness (DD) at a temperature of 28±1 °C and littered two to eight pups. For the first series of experiments two pups of either sex were selected from each litter. The animals for these experiments were from a total of 14 mothers and 28 pups. One pup was placed in continuous illumination (LL) of 0.5-0.7 lx incandescent light from day 5 of postnatal life whereas the other pup remained in DD. (A 12-h separation of the pups from the mother before day 5 resulted in excessive mortality.) Starting on day 5 until day 15, the mothers were presented for 12-h periods alternately to pups in LL during 06:00-18:00 h and to pups in DD during 18:00-06:00 h. The circadian rhythm of the mother mice would have been entrained to the imposed light/darkness (LD) cycles while being alternately berthed with the pups. Food and water were available at all times. By day 16 of postnatal life, pups of *M. booduga* can already run the activity wheel independently. Their locomotor activity was measured from day 16 onwards for about 4 weeks, individually using running wheels in the absence of the mother in the same lighting conditions as had prevailed before. The locomotor activity of the mother was also similarly recorded in DD from day 16 onwards. The revolutions of the wheels were monitored with an A620X Esterline Angus event recorder.

The mother mice began to be active at 18:00 h on day 1 of the recording (day 16 after littering the pups) and the activity rhythm free-ran thereafter on subsequent days. The circadian rhythms in the locomotor activity of the pups in LL and those in DD revealed onsets of activity on day 1 of the recording which were 180° off course relative to each other and free-ran on the subsequent days. For each pup, this onset of activity coincided with the time at which the mother had been removed during entrainment. Figure 1*a*-*c* illustrates these trends. From these results we infer maternal entrainment of the circadian clock of pups.

In a second series of experiments mother mice were again cyclically presented from day 5, but in this series the mice were presented beyond day 16 for a further 2-5 weeks. Sixteen days after littering, the mother mice were tethered by a 10-cm aluminium chain. The presence/absence (PA) cycles of the mother were continued as in the first series of experiments. The restricting chain meant that the mother mouse could not enter the activity wheel from the nesting cage whereas the pups could.