Perceptual organization in moving patterns

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Is human motion perception based on a local piecemeal analysis of the image or do global effects play an important role? We used metastable apparent motion displays (Fig. 2) to try to answer this question. Two spots were flashed simultaneously on diagonally opposite corners of a square and then switched off and replaced by two spots appearing on the remaining corners. One could either see vertical or horizontal oscillation of the spots and the display was bistable just as a Necker cube is. We found that if several such bistable figures were randomly scattered on the screen (Fig. 3*b*), and presented simultaneously, then one always saw the same motion-axis in all of them, suggesting the presence of global field-like effects for resolving ambiguity in apparent motion. Surprisingly, the appearance of these displays could not be influenced by voluntary effort unless the speed of alternation was very slow. (Less than 3 frames per second.) It may be that if the events in the module that computes apparent motion are too rapid then it cannot be coupled with the "will" mechanism, which may have a long time constant.

Metastability is one of the most striking yet enigmatic aspects of perception[1-5]. Necker cubes (Fig. 1) and other bistable figures are often used to illustrate the point that perception is really a hypothesis on the state of affairs in the world rather than a passive response to sensory stimuli. One's perception of the cube changes dramatically as the mind hesitates between alternative three-dimensional representations. Indeed, when viewing such bistable figures it is often hard to believe that something has not changed physically in the stimulus.

This report is concerned with metastable apparent motion displays such as Fig. 2; a matrix of four dots forming the corners of a square. It was generated on a P-4 phosphor cathode ray tube (CRT) using an Apple 2 microcomputer and viewed from a distance of 1 m. The sides of the square subtended 40 min of arc and the dots themselves were 3 min of arc in diameter. A hand-held potentiometer could be used to vary the speed of alternation or stimulus onset asynchrony (SOA) continuously over a wide range: the SOA was varied by changing the duration of each of the two frames and there was no dark interval (ISI) interposed between the frames. The number by each dot refers to the time at which it is presented. Dots on two diagonally opposite corners are flashed first and then switched off, followed by two dots appearing simultaneously on the remaining two corners, with the procedure repeating in a continuous cycle. The two possible percepts, are indicated in the diagram as Percept 1 (vertical oscillation) and Percept 2 (horizontal oscillation) and the display is essentially bistable just as a Necker cube is[6]. However, we found it almost impossible to voluntarily switch from one percept to the other when the speed of alternation was higher than 3 frames per second (SOA = 350 ms). Subjects almost always experience hysteresis, that is, they tend to persist in seeing one of the percepts (either vertical or horizontal oscillation) and can switch the axis of motion only by looking away and looking back after some time has elapsed.

Another theoretically possible percept is either continuous clockwise (Percept 3) or anticlockwise motion but at short SOAs (350–400 ms), this was impossible to achieve even through intense mental effort. However, we made the curious observation that when the SOA was made sufficiently long (>465 ms) subjects could occasionally will themselves to switch the motion axis or even to see clockwise or anticlockwise motion. Six naive subjects were asked to view the display and we then varied SOA over a wide range using a hand-held potentiometer. We began with very slow speeds so that the subject could will clockwise (or anticlockwise) motion and then gradually increased the speed of alternation. When the SOA was smaller than 465 ms, subjects reported that they could no longer hold this percept (mean of 6 readings × 6 subjects, that is, 36 readings = 465 ms; s.d. = 33). They could now only see oscillation, and the axis of oscillation could no longer be influenced at will. Furthermore, we find that if Fig. 2 and its mirror-image are presented side-by-side then at slow speeds one can simultaneously 'will' clockwise and anticlockwise motion suggesting that eye movements cannot explain the effect. We conclude that axis-dominance remains absolute and unambiguous at small SOAs and that it can be coupled with the effects of will and attention only at SOAs longer than 465 ms. Hence using

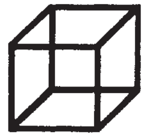

Fig. 1 An outline drawing of a transparent cube. The mind hesitates between the two alternative three-dimensional representations.

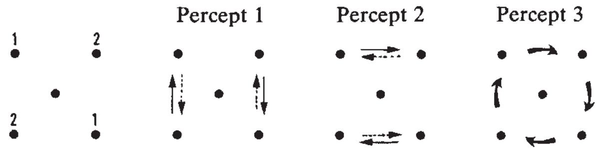

Fig. 2 The basic bistable motion display used in our experiment. (Numerals indicate order of presentation.) The three possible percepts are shown. (A fourth percept, anticlockwise motion, is not shown.)

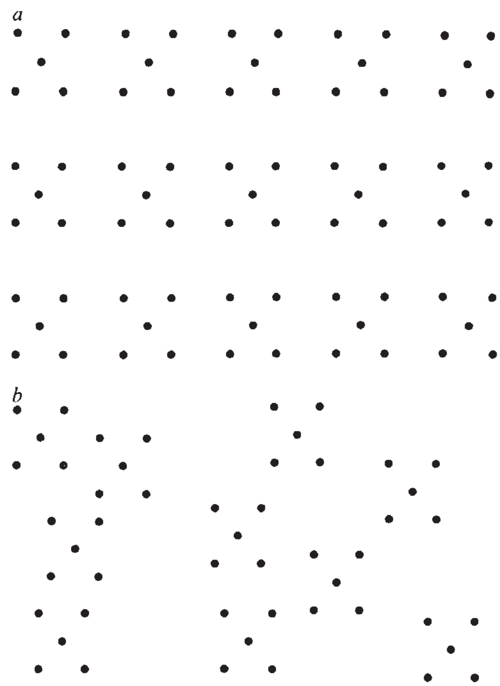

Fig. 3 *a*, Multiple bistable displays presented simultaneously. Identical oscillations are observed in *all* the displays. *b*, The squares (bistable dot-pairs) are randomly positioned and the same effect is seen showing that the presence of regular arrays is not necessary. The central dot within each display is present continuously and is perceived to be static.

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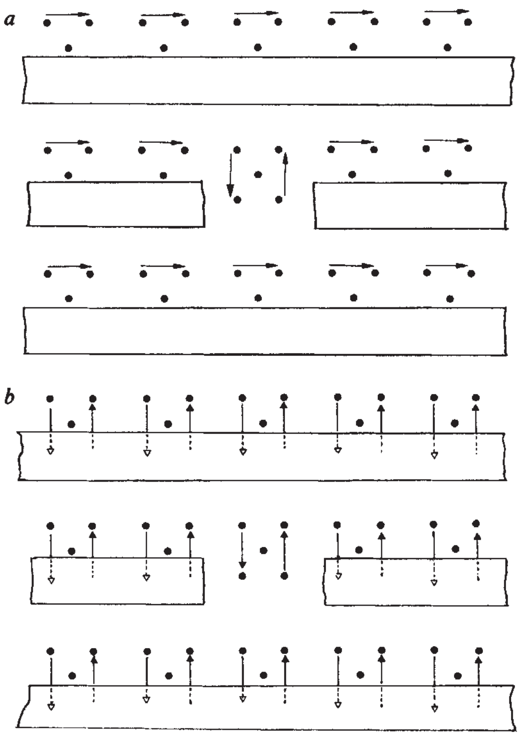

Fig. 4 *a*, The effect of unambiguous motion in the surround on a single bistable display in the centre. This was produced by mounting strips of adhesive tape on Fig. 3*a*. *b*, 'Occult apparent motion' seen behind the masking tape. The effect disappears if the central inducing figure is removed. This suggests that the presence of motion in one region of the visual field somehow creates a template that allows one to imagine similar motion in other regions.

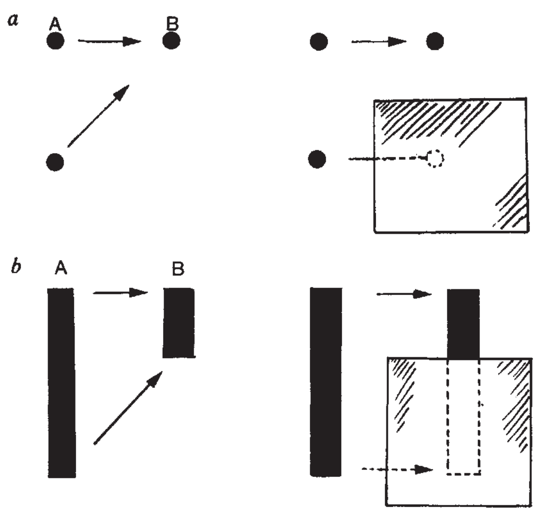

Fig. 5 *a*, The effect of a static occluder on the direction of perceived apparent motion. The bottom dot moves horizontally when the occluder is present. *b*, Same experiment as *a* using lines instead of spots. If the occluder is present the line 'slides' behind it but in the absence of the occluder the line appears to shrink and expand or to recede and advance.

short SOAs may be a good way to study metastability without worrying about contamination from higher centres.

We have now begun to use our bistable displays to address the more general question of whether motion perception is based on a piecemeal analysis of the image or whether global field-like effects are also important as emphasized by Gestalt writers[7,8]. Our strategy was to generate several bistable displays simultaneously on the screen (Fig. 3). Twelve naive subjects viewing these displays reported that all the oscillating dot-pairs seemed to 'lock-in'—that is, the displays always had the same motion axis. This was true even when adjacent displays were separated by several degrees. If one of the displays changed its motion axis then all the displays invariably changed with it simultaneously. This effect suggests the presence of a global field for resolving ambiguity in bistable displays for if the different displays were being processed independently there is no *a priori* reason why their oscillations should become synchronized. The presence of such a field is interesting for two reasons. First, if several Necker cubes or other similar reversible figures are simultaneously present in the visual field then they tend to undergo reversals more or less independently of each other[9]. This suggests that a field probably exists only for certain classes of visual displays such as the motion displays used in our study or the clusters of triangles described by Attneave[1]. Second, the effect seems to be inconsistent with the 'independence-assumption' of Ullman[10] according to which apparent motion should be based on strictly local computations and there ought to be no global field-like effects.

To rule out tracking eye movements as a possible explanation we created two clusters of figures (such as Fig. 3) side-by-side so that one of them was rotated by an angle of exactly 45° in relation to the other in the frontoparallel plane. In this display the effect was still present separately in each of these clusters. Since one cannot track simultaneously in two directions, this result suggests that for each cluster of figures a separate field must exist that synchronizes the elements within it. It should be noted, however, that there are at least two different ways in which an apparently field-like effect of this kind could arise. Either it could be based on cooperative interactions between adjacent quasi-independent modules or it could be produced by feedback signals from higher centres introducing the same bias in all the modules.

We then wondered whether an unambiguously moving array of dots in the surround could influence the perception of a single ambiguous figure (similar to that in Fig. 2) in the middle. To explore this we generated Fig. 3*a* again on the CRT screen and confirmed that all the oscillating pairs had become synchronized, as in our previous experiment. We then used long strips of white tape to mask off the lower half of each horizontal row of figures (Fig. 4*a*). A small window was then cut in the middle so that one of the ambiguous figures alone was allowed to become fully visible. By this simple procedure we were able to create unambiguous horizontal motion throughout the surround. Not surprisingly we found that this imposed a slight tendency to see horizontal motion in the central ambiguous figure, but the effect was very small. In fact by using voluntary effort one could easily uncouple the central ambiguous figure from the surround and decide to see vertical motion. Hence the coupling between an unambiguous and an ambiguous figure is probably much weaker than the coupling between adjacent ambiguous figures—although of course we had no simple way of measuring the strength of this coupling. This observation suggests that the synchronization of ambiguous motion displays does not arise due to cooperativity but due to some other more high-level mechanism.

While watching this display we made a curious observation. As pointed out above we could easily uncouple the centre from the surround so that vertical motion was seen. But to our astonishment we found that on some occasions when this happened the dots in the surround also moved vertically to imaginary locations behind the strips of masking tape. Since there is nothing in the retinal stimulus that would lead one to expect this, we have dubbed this illusion 'occult apparent motion' (Fig. 4*b*). Six naive subjects were confronted with this display and they all confirmed that they could see this effect. Interestingly, the effect took time to evolve as when viewing Julesz's random-dot stereograms, and two of the subjects had to be told what to look for, that is, they did not report the effect spontaneously. We then simply masked off the central ambiguous figure and found that the illusion disappeared and was replaced by the appearance of unambiguous horizontal motion in the surround. The illusion could be seen even if the surrounding figures were several degrees (say 3°) away from the central one. It was as though the particular hypothesis the brain had selected to resolve ambiguity in the centre was being automatically applied throughout the visual field. And in the absence of sufficient evidence the brain resorts to simply postulating the required dots behind the occluders.

An informal observation along these lines was made recently by Shepard[11]. Shepard's stimulus was a vertical bar rapidly alternating with a horizontal bar and one could see motion in either one of two different quadrants. Sometimes voluntary effort was ineffective in switching perceived motion from one quadrant to the other and so he had to occlude suitable portions of the display in order to encourage motion to be seen in the other (non-occluded) quadrant. He reports that on doing this he sometimes continued to see motion behind the occluder for a while but does not state how long this tendency persisted. Our effect (occult apparent motion) may, in a sense be regarded as the spatial equivalent of this persistence effect noted by Shepard.

We find that occult apparent motion is visible only if the SOA is sufficiently long. This may reflect the minimum time required by the brain to invoke the occlusion hypothesis. If the SOA is made smaller than 645 ms (mean for four subjects = 645 ms: s.d. = 84), the effect vanishes and the dots in the surround oscillate horizontally even when the dots in the central ambiguous figure are making vertical excursions. Oddly enough the presence of the masking tape, though helpful, is not essential. If the room lights are switched off, so that the tape is no longer visible, one can still see occult apparent motion. This suggests that under appropriate circumstances one can see apparent motion towards an invisible light spot hidden by an invisible occluder! Subjects reported that a faint subjective outline of the tape was visible corresponding to where it should have been physically present.

One does not have to use ambiguous displays to produce occult motion. The effect can also be seen, though less vividly, in displays such as Fig. 5*a* in which two light spots in the first frame (A) are alternated with a single light spot in the second frame (B). If the cardboard occluder is not shown then observers always see both spots moving towards the single one and fusing with it as expected. But if the occluder is added, the bottom spot appears to move horizontally to hide behind the occluder although there is no stimulus corresponding to it in frame B. The effect is even more striking if a long thin line is used instead of two separate spots (Fig. 5*b*). We have shown these displays to six naive subjects and all of them confirmed that they could see the illusion. As in the case of Fig. 3, the percept of the spot sliding behind the occluder was more striking at long SOAs (>500 ms).

The effects reported here, synchronized motion (Fig. 3) and occult apparent motion (Figs 4,5) suggest that spatial induction effects can be very compelling and may play an important role in perception. Whenever the brain applies a rule to resolve ambiguities in a given local region, there is a strong tendency to apply the same rule throughout the visual field and the system will go to tremendous lengths to achieve this.

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Specificity of cortico-cortical connections in monkey visual system

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When the primate primary visual cortex, area 17, is stained for the mitochondrial enzyme cytochrome oxidase[1], it shows a striking polka-dot pattern (cytochrome oxidase blobs). Area 18, the second visual area, shows a cytochrome-oxidase pattern of coarse alternating thick and thin stripes running perpendicular to the 17–18 border and separated by lighter (interstripe) regions. Here we show that the thin cytochrome oxidase stripes, and possibly also the thick stripes, in area 18 receive projections specifically from the blobs in area 17, and that the interstripe regions of 18 receive projections from the interblob matrix of area 17. This indicates a specificity of cortico-cortical connections far exceeding the demands of topographical mapping. Together with our physiological results, it suggests that within the pathway from area 17 to area 18 different kinds of information may be handled separately and in parallel.

Many major cortical and subcortical areas of the brain are known to be subdivided into columns, stripes or lattices. Areas as diverse as visual, auditory and somatosensory cortices, caudate nucleus and superior colliculus exhibit such subdivisions by local heterogeneities in physiological responses, anatomical connections and staining characteristics[2–9]. M. Wong-Riley (personal communication), using a stain for cytochrome oxidase in area 17 of squirrel monkey, discovered a regular series of densely labelled patches in layers 2 and 3. It was subsequently shown that in sections cut parallel to the surface these patches form a quasiregular array of round or oval blob-like regions 0.2 mm in diameter and spaced 0.5 mm apart[10,11]. In macaque

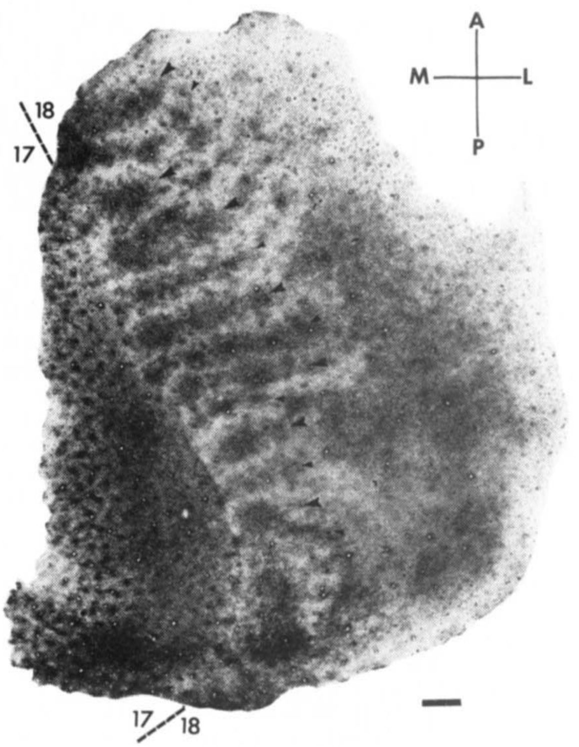

Fig. 1 Tangential section through a flattened squirrel monkey occipital lobe. Area 17 is on the left, and 18 on the right. The pattern in 18, although somewhat irregular, is roughly one of alternating thick and thin stripes, as indicated by large and small arrowheads. Scale bar, 1 mm.

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