

# Illusory surfaces affect the integration of local motion signals

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## Abstract

A 2IFC paradigm was used to measure speed discrimination thresholds for pairs of Gabor patches. When one of these patches was phenomenally placed over an illusory surface (IS), we observed higher thresholds relative to control conditions without ISs. Additional controls demonstrated that this effect was due to the placement of the patch on a different phenomenal depth plane rather than to the mere presence of an IS. We conclude that (i) ISs can affect the long-range integration of local motion signals, and (ii) long-range motion integration obeys a coplanarity principle.

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## 1. Introduction

Any system trying to compute motion is faced with a difficult challenge and cannot rely on local measurements alone. First, when a contour crosses the visual field, its direction and speed are locally ambiguous. Early motion-sensitive neurones have small receptive fields and are selective for orientation and direction. Therefore, different combinations of object direction and orientation can give rise to the same neuronal response (Hubel & Wiesel, 1968; Movshon, Thompson, & Tolhurst, 1978), producing the so-called *aperture problem* (Hildreth, 1984, 1987; Nakayama, 1985; Stumpf, 1911; Wallach, 1935). Second, local motion responses are all affected by independent noise. For these two reasons, integrative processes must play a fundamental role in the visual computation of object motion. Integrating motion signals across space serves the purpose of disambiguating local speeds and directions, as well as improving signal-to-noise ratios. To perform integration, however, the visual system cannot generally apply a simple averaging scheme, as signals arising from

multiple objects in the visual field must be parsed appropriately into those that belong to the same object, and those that come from separate objects (Braddick, 1993). To do so, it is generally believed that motion integration takes into account the spatial structure of the stimulus. Although there are some empirical data in support of this expectation (Shimojo, Silverman, & Nakayama, 1989; Verghese & Stone, 1997; Verghese, Watamaniuk, McKee, & Grzywacz, 1999), the nature of the motion integration process is still largely unknown.

Here we report experiments on the effect of the formation of illusory surfaces (ISs) on motion integration. As a special kind of spatial structure in the stimulus, ISs provide a unique advantage. The gratings carrying motion information can be kept always exactly the same, even if the static context is manipulated to produce an IS and therefore a different spatial layout than in a control condition. This advantage is used here to investigate whether ISs can affect integration, and whether this effect is due to the formation of the IS per se or to the depth stratification that brings the surface nearer to the viewpoint than its inducers.

Numerous considerations suggest that an effect of ISs on motion integration is plausible. For instance, Liden and Mingolla (1998) have found that an illusory frame can support the barberpole effect, although in a slightly less effective manner than when the frame is formed by luminance-defined contours (see also Mosca & Bruno,

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1999; Tommasi & Vallortigara, 1999). The phenomenology of ISs (Kanizsa, 1955, 1974, 1979), studies of single cell responses (Sheth, Sharma, Rao, & Sur, 1996; von der Heydt, Peterhans, & Baumgartner, 1984), as well as fMRI results (Mendola, Dale, Fischl, Liu, & Tootell, 1999) converge in suggesting that IS may be processed by the same neural units that integrate luminance-defined contours at early stages of visual processing. Finally, ISs are perceived to lie on a different depth plane than their inducers (Kanizsa, 1955), and depth placement is a known factor in the integration of local motion signals (Shimojo et al., 1989). However, a direct test of the effect of ISs on motion integration has never been performed. To perform such test, we measured speed discrimination thresholds in pairs of translating gratings within Gaussian windows (Gabor patches). It is generally held that an increase in threshold is a signature of less efficient integration (Verghese & Stone, 1995, 1997). In our experiments, pairs of Gabors were presented such that there was no information about a depth difference between them, apart from the fact that one of them was surrounded by a context inducing an IS. If the presence of the IS interferes with integration efficiency, speed discrimination thresholds should increase relative to control conditions with contexts that do not induce an IS.

## 2. General plan and overview of experiments

In all experiments, we used the minimum number of local motion signals necessary to detect integration, namely, two. To create an IS we used a configuration introduced by Albert (1992) (see also Albert, 1995, 2001) in which a set of lines induces the perception of a square (this “magic square” and its control configuration can be seen in Fig. 1). We chose this configuration because it allowed us to create a control configuration with the same local elements, at the same distance from the grating, but no IS. In the control configuration there is no IS because the corners are not a generic view of lines hidden by a square surface (Albert, 2001).

In a first experiment, we compared thresholds with an IS to thresholds in the control configuration, and manipulated viewing conditions and contrast. In monocular viewing conditions, we expected a difference between ISs and controls. In binocular viewing conditions, we did not expect a difference because of conflicting information about stratification in depth. Finally, with low inducers contrast we did not expect a difference because low contrast reduces the strength of the IS (Kanizsa, 1979). These predictions were basically confirmed. Results demonstrated a consistent threshold increase in ISs in the least ambiguous condition (monocular viewing condition). However, there were large individual differences in the conditions of information conflict. For this

reason, we used larger samples in all subsequent experiments.

The second experiment compared the magic square to a sectored-circle IS, to insure that what we are studying is not specific to the magic square display. We expected an effect of the illusory surface in both conditions, and this prediction was again confirmed. However, the two kinds of IS did not yield effects of comparable magnitude. We argue that this difference is again consistent with a causal role of ISs. Given the configurations that we used, the magic square had spatial features more favourable to inducing a strong IS (i.e., a larger support ratio). It is therefore not surprising that it produced a stronger effect on thresholds.

The third experiment added binocular disparity information to the displays, in such a way that the depth specified by disparity was not compatible with an opaque surface occluding the inducers. The inducers were located closer to the observer and the grating was seen through an illusory frame at a different depth. Given that this manipulation inhibited the formation of a surface and did not lead to a perceived difference in depth between the two motion signals, we did not expect a difference in threshold. This prediction was confirmed.

Given the results of the first three experiments, the existence of an effect of ISs on motion integration seems well established. However, ISs may affect integration in two different ways. The integration of local motions may be hindered because the motion signals are perceived as belonging to different surfaces, or because they appear to lie on different depth planes. The fourth experiment<sup>1</sup> aimed at separating these two factors. By a suitable modification of our basic displays, we compared a *continuity hypothesis* (surface formation is critical) with a *coplanarity hypothesis* (stratification in depth is critical). We found evidence in favour of the coplanarity hypothesis.

In a final control (Experiment 5), we also insured that the observed differences were related to the integration of motion signals and was not due to other figural factors.

## 3. General methods

*Stimuli and procedure.* Stimuli were displayed on a Sony F500T9—Trinitron monitor driven by a G4 Macintosh computer. This monitor has a resolution of 33 pixels/deg at a viewing distance of 57.5 cm. The nonlinear gamma function of the monitor was linearized and verified with a photometer. The background luminance of the display was always 40 cd/m<sup>2</sup>.

<sup>1</sup> We are grateful to one of the anonymous reviewers for suggesting that we perform this experiment.

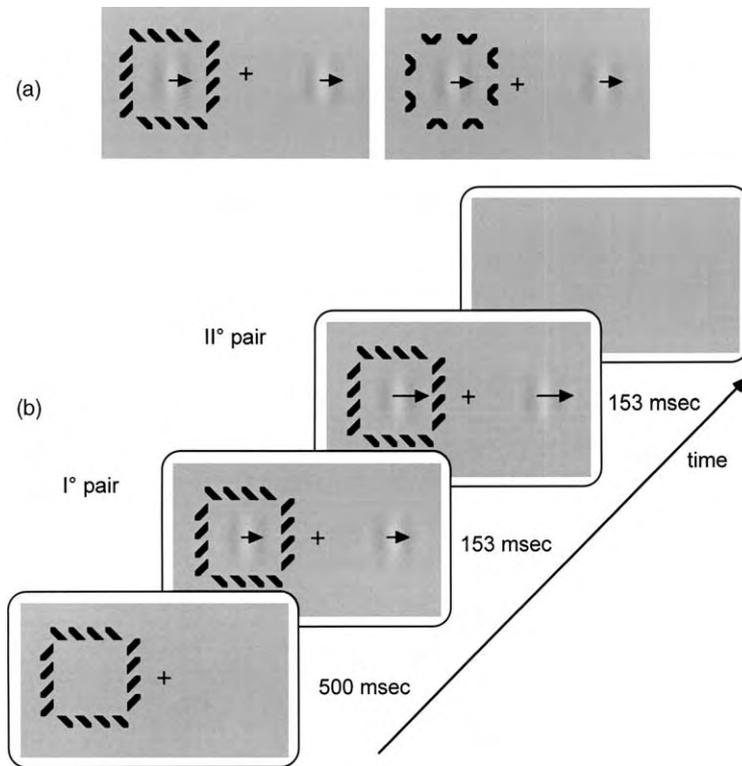


Fig. 1. (a) Example of stimuli used in Experiment 1. In each configuration there were two sinusoidally modulated gratings. The orientation of the gratings was always vertical. In the magic square configuration a set of lines induced the perception of an illusory square. In the control configuration the same inducers were rotated and therefore the illusory surface was not perceived. (b) Each trial started with the presentation of the inducers for 500 ms. Next, the first and second displays (the motion signals) were presented for 153 ms. Finally, a grey screen was presented until response. The observers pressed “1” or “2” if they judged that the motion was faster in the first or second pair, respectively. The speed difference between the two pairs was adjusted by an adaptive procedure.

The stimuli were pairs of Gabor patches, i.e. moving sinusoidal gratings windowed by a stationary two-dimensional spatial Gaussian with SD of 0.4 deg in both dimensions. Examples of the stimuli are shown in Fig. 1. The spatial frequency was fixed at 1.5 c/deg, and the orientation was always vertical. The direction of motion of the gratings (left or right) was randomised in each trial. The two contrast levels of the Gabor patches used in Experiment 1 were 8% (low contrast) or 50% (high contrast). The 8% level was chosen as a level low enough to be near threshold for all of our participants whilst not too low to make the task impossible. The experiment was programmed in C by the authors using some of the VideoToolbox functions (Pelli, 1997).

As can be seen in Fig. 1, the two Gabor patches were positioned on the left and the right of a fixation mark, which was present throughout the experiment. The patches themselves did not translate on the screen. In the magic square displays, one of the patches was perceived inside (on top of) an IS. The square boundaries were created by inducers that were darker than the background (approximately 0 cd/m<sup>2</sup> in the standard condition, and 36.5 cd/m<sup>2</sup> in the condition in which inducers contrast was reduced). In the control configuration half of the lines were rotated so that their

terminators coincided. As a consequence the IS was no longer perceived (Albert, 2001). The position (right or left of fixation) of the magic square or control was randomised in each trial.

Each trial started with a warning beep, followed by the first pair of Gabors, a blank screen for 500 ms, and then the second pair. Each display was a movie of 13 frames, which lasted 153 ms in Experiment 1 and 150 ms in all other experiments. In each movie, the motion of both Gabors had the same speed, but speed could change from the first to the second pair. After the second pair, observers were asked to press one of two keys, depending on whether they perceived faster motion in the first or the second pair. Feedback was provided in each trial. The subsequent trial started 1 s after the response.

Motion sensitivity was measured using a two-interval forced choice (2IFC) procedure. The task was to compare the speed of the two configurations (standard and test) that were presented in the two successive pairs. The presentation order for the standard and test configurations was randomised. The speed of the standard was fixed to 5.1 deg/c in Experiment 1 and 3.6 in all other experiments.

In all but the first experiment, we used a stereo system to control the apparent position in depth of the display

elements. Stereo images were presented through a Nu-Vision stereoscopic system. This system uses an infrared emitter to drive a pair of liquid-crystal glasses that can turn from transparent to opaque in synchrony with the presentation of images intended for the left and right eye. When using this stereo system, the effective vertical resolution and refresh rate of the monitor were halved (512 pixels at 60 Hz in each eye).

We used an adaptive procedure (3 up–1 down staircase, Levitt, 1971) to sample the speed differences between the two movies (for a similar method see Verghese & Stone, 1995). The staircase terminated after 24 reversals. Thresholds were determined by fitting a Weibull psychometric function to the raw data. The fitting procedure minimised the  $\chi^2$  of the fit of the data, which was computed by weighting the data points with their SDs, assuming a binomial distribution. The 82% threshold for speed discrimination was determined from the Weibull fit.

#### 4. Experiment 1

In this experiment we used pictorial stimuli. Under normal viewing conditions, depth information in a pictorial configuration is ambiguous. This means that the depth stratification due to the formation of an IS in our displays was incompatible with that specified by binocular disparity (which is zero for pictorial stimuli). If this conflict interferes with the perception of an IS, this may prevent us from observing an effect. For this reason, we decided to compare thresholds in two viewing conditions: monocular and binocular. When a pictorial stimulus is seen monocularly, the depth ambiguity is not completely removed (our observers did not stabilize their head using a bitebar, or did they view the displays through an artificial pupil). However, the ambiguity is greatly reduced, and Shimojo et al. (1989) as well as others (Bruno, Bertamini, & Domini, 1997) have indeed reported differences between monocular and binocular viewing of pictorial displays involving occlusions. Thus, there are strong reasons to expect stronger evidence of stratification effects on integration with monocular displays. In addition, we also expect more variability in the binocular displays due to the conflicting depth information.

We tested motion sensitivity for two levels of contrast of the gratings. We varied this factor because it has been suggested that motion integration should be more clearly detectable at lower contrast values of the motion signals (Wuerger, Goodwin, & Bertamini, 2000). Furthermore, if we are correct in expecting motion integration to be affected by the presence of an illusory surface then such effects should be modulated by the salience of the illusory surface. Although consistent polarity is not necessary for the formation of an illusory

surface, many studies suggest that, other things being equal, the strength of the illusory surface depends on the luminance contrast between the inducers and the background (e.g., Petry & Meyer, 1987; Spillmann & Dresch, 1995). By decreasing the salience, i.e. the contrast between inducers and background, we should observe a decreased effect of the illusory surface.

##### 4.1. Method

Three observers participated in three separate sessions: monocular, binocular, and monocular with reduced inducer-to-background contrast. One of the three observers was the first author, whereas other two were not aware of the hypothesis that motivated the study.

A 2 configurations (illusory vs. control)  $\times$  2 Gabor contrast (high vs. low) design was used. The four conditions were interleaved in each session. Observers took part on different days in the three versions of the experiment. The other details concerning the stimuli and procedure are described in Section 3.

##### 4.2. Results and discussion

Thresholds for speed discrimination (in degrees per second) are presented separately for each observer in Fig. 2. The three rows show results for each of the three experimental conditions: monocular (top), binocular (middle), and monocular with reduced inducers-to-background contrast (bottom).

In the monocular condition, there was no clear difference between the thresholds for the IS and control configurations when the gratings contrast was high. When the contrast of the gratings was low, the threshold in the illusory configuration was higher than in the control configuration for all three observers. In the binocular condition the variability was higher and there was no consistent difference between the IS and control configuration, as predicted.

The last row of Fig. 2 shows the thresholds for the monocular presentation with reduced-inducers-to-background contrast. In these conditions, we did not observe any consistent difference between the IS and control configurations at both high and low Gabor patch contrasts.

It is possible that with high contrast gratings we observed a ceiling effect in all conditions. On the other hand, with low contrast gratings there were differences between the thresholds in the monocular condition. Thus, a monocularly perceived illusory surface appears to affect the integration of motion signals across its boundaries, as predicted. This conclusion is supported by the fact that the difference between the illusory and control conditions was not found when the contrast of the inducers was reduced. In this condition the salience of the illusory surface was reduced and thus the effect of

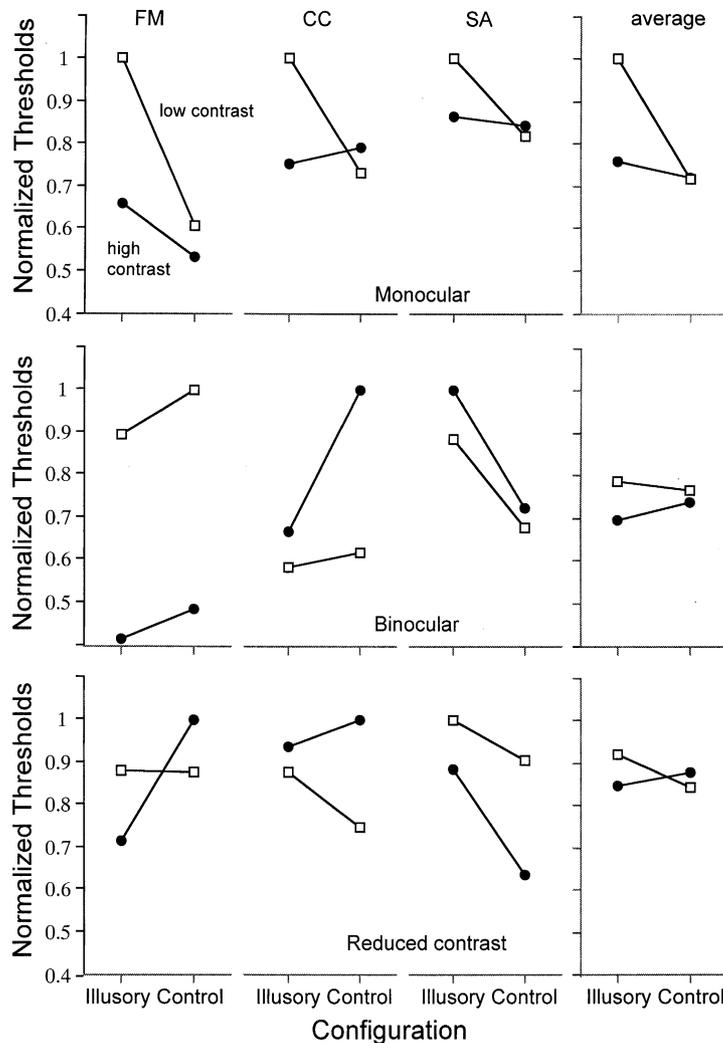


Fig. 2. Data from Experiment 1. The 82% thresholds for speed discrimination are presented separately for each observer as a function of type of configuration (illusory vs. control). Averages are presented in the right column. Data normalised to the highest threshold value of the observer for ease of comparison. Top row: monocular condition. Middle row: binocular condition. Bottom row: monocular with reduced inducer-to-background contrast condition. Open squares: low contrast gratings. Solid circles: high contrast gratings. There is high variability in the binocular condition and also with reduced contrast, however there is a pattern in the monocular low-contrast condition. See text for discussion.

surface formation and stratification in depth was also decreased. For reasons that will become apparent after the presentation of our Experiment 4, however, we suggest that this reduction of sensitivity occurs because motion on an IS is perceived to lie on a different phenomenal depth plane with respect to its background, not because of the mere presence of the IS.

## 5. Experiment 2

In this experiment we studied the effect of surface formation and information about stratification in depth using two different illusory configurations: the magic square configuration that we used in all experiments, and a different configuration with sectorized circles (see Kanizsa, 1955). We compared each illusory configura-

tion with a control configuration having rotated inducers (Fig. 3). Based on the data from Experiment 1, we used monocular presentations and low contrast gratings. In addition, we measured two baselines. The first baseline consisted of two motion signals without any static context. Static context can affect motion sensitivity, so we expect thresholds to be much higher without any static reference other than the fixation mark. The second baseline had one of the signals framed by a square outline the same size as the illusory square. If the presence of the IS acts as a static reference frame (not present in the control condition), then the illusory condition should show a change in the same direction as the baseline with luminance boundaries. This is not our prediction because we believe that the IS does not simply provide a new static reference.

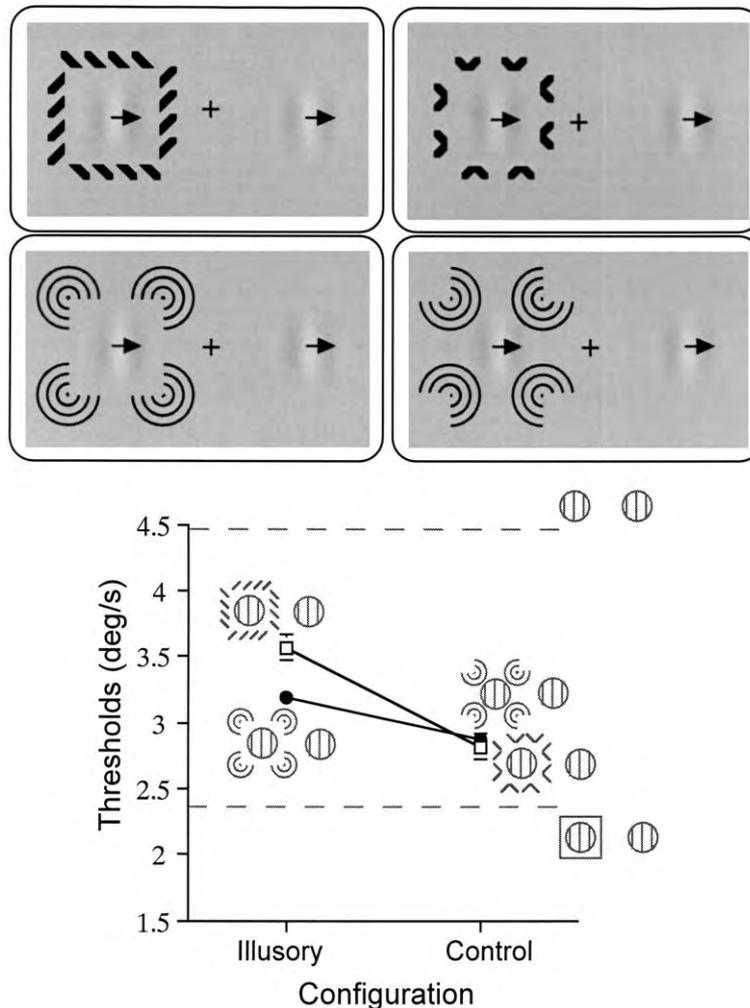


Fig. 3. Data from Experiment 2. Average thresholds for speed discrimination are plotted as a function of type of configuration (illusory vs. control). Open symbols, magic square configuration. Solid symbols, sectored circles configuration. Error bars are  $\pm 2$  SE across observers. Dashed lines, thresholds for the two baseline conditions.

### 5.1. Method

Thirteen University of Liverpool students participated for course credit. They had normal or corrected vision. A 2 configurations (illusory vs. control)  $\times$  2 illusions (*magic square* vs. *pacman*) design was used. Moreover two new baseline conditions were also interleaved in each session for a total of six conditions. Stimuli, equipment and procedure are described in Section 3. Although the same monitor was used, participants always wore an eye patch as well as the stereo glasses, even if the monitor was placed in stereo mode only to ensure constant testing conditions across studies. The nominal monitor resolution was  $1280 \times 1024$  pixel at 120 Hz, but given the stereo mode the effective resolution in the unpatched eye was  $1280 \times 512$  at 60 Hz, corresponding to a resolution of 33 pixels/deg at a viewing distance of 57.5 cm. On the basis of the previous findings, the contrast of the gratings was always 8%. Unlike the previous experiment, the speed of the stan-

dard was fixed to 3.6 deg/c and each motion sequence lasted 150 ms.

### 5.2. Results and discussion

Fig. 3 shows the thresholds for speed discrimination in degrees per second. Dashed lines indicate the thresholds that were observed in the two baseline displays. We compared the speed differences in the illusory and control configurations using paired *t* tests.

Before considering the differences between the illusory and control configurations, we evaluated these baseline thresholds. As is shown in Fig. 3, the configuration without any static element yielded the highest threshold. Conversely, the configuration with the outline square was the lowest. A likely explanation for this result is that these baselines correspond to the two extremes of a continuum. On one extreme, without static elements there is motion relative to a global, distal frame of reference (“absolute” motion). On the other extreme,

with the square outline there is motion relative to proximal landmarks provided by the static contours. It is known that, other things being equal, speed thresholds for “absolute” motion are higher than for relative motion (e.g., Mack, 1986).

Consider now the differences between experimental configurations. In both the magic square ( $t(11) = 7.36$ ,  $p < 0.001$ ) and sectorized circle ISs ( $t(11) = 3.97$ ,  $p = 0.002$ ) the thresholds were higher than the corresponding control configurations. Note that this cannot be due to the presence of a modal contour in the IS displays, but not in the controls. If the contours of the IS acted as static elements that provided stronger relative motion signals than the controls, the thresholds for the illusory conditions should be lower than that for the control conditions. In other words, if the effect were similar to introducing contours that form a proximal frame of reference, the direction of the change should be in the direction of the square outline displays. However, the opposite holds true.

Finally, note that the difference between the IS and the control thresholds was more pronounced with the magic square displays than with the sectorized circles. This difference is also consistent with a causal role of IS on motion sensitivity. Shipley and Kellman (1992) convincingly demonstrated that a critical predictor of IS perceptual strength is the ratio of the portion of the IS perimeter defined by luminance edges to the total perimeter of the IS (“support ratio”). A quick computation showed that in our display the magic square IS had a support ratio of 0.35 whereas the sectorized circle IS had a support ratio of 0.11. Therefore, a parameter that is known to affect the strength of IS also affects the magnitude of the effect on motion integration, suggesting that the latter is indeed due to some feature of the IS.

To further test our hypothesis that the formation of the IS influences the integration process, we have used binocular disparity information to directly manipulate the stratification of the inducers in an additional control experiment.

## 6. Experiment 3

To further corroborate the interpretation that the effects observed in the previous experiments were due to IS, not to the mere arrangement of the inducing patterns, we used stereo information to position the IS inducers *in front* of the background. Under these conditions, the resulting percept is no longer of an IS in front of the inducers but of an illusory square aperture. If the threshold differences that were observed in Experiments 1 and 2 were due to the effect of the formation of a surface, then displays in which the surface has been turned into an aperture should not produce the same

effect, even if exactly the same inducing patterns are presented.

### 6.1. Method

The same thirteen students who took part in Experiment 2 also participated in Experiment 3. Stimuli and procedure are described in Section 3 except for the changes that are detailed below. A 2 configurations (illusory vs. control)  $\times$  3 viewing conditions (monocular replication, inducers-in-front, monocular inducers) design was used. The monocular replication condition was intended as a replication of Experiment 2. However, in this case only the dominant eye was exposed to the displays, whereas the other eye was presented with a medium gray screen (see Fig. 4). In the inducers-in-front condition, conversely, both inducers and the motion signals were presented in both eyes, but the inducers had a small positive disparity (0.18 deg). This caused the inducers to appear in front of the background. Thus, the illusory boundaries of a square were perceived, but there was no IS: the Gabor was seen through an illusory square aperture. Finally, the monocular inducers condition was a hybrid where the inducers were presented monocularly but the motion signals were presented binocularly. We included this condition to test for possible differences in thresholds when motion signals were presented to one or two eyes.

### 6.2. Results and discussion

Fig. 4 shows the thresholds for speed discrimination in degrees per second. Again, we compared the speed difference for the illusory square (or frame) configuration and the control configuration using paired  $t$  tests.

In the monocular replication ( $t(11) = 6.34$ ,  $p < 0.001$ ) and monocular inducers conditions ( $t(11) = 3.87$ ,  $p = 0.003$ ) we found again a significant difference between the IS and control thresholds. On the other hand, in the inducers-in-front condition we did not observe any difference between the two thresholds ( $t(11) = 0.48$ ,  $p = 0.635$ ).

These results show that it is not the mere presence of illusory boundaries that interferes with the integration of local motion signals. When the same local inducers are present but the square boundaries appear to delimit an aperture rather than a surface, no interference is observed. We conclude that the integration of local motion signals is affected by the formation of the surface itself. At present, exactly how the process of integration may take surfaces into account is not known, but an integration rule that could account for our results is a *coplanarity principle*: combine local motion signals that appear to lie on the same phenomenal plane, segregate those that appear to lie on different planes. This rule is consistent with the results of other

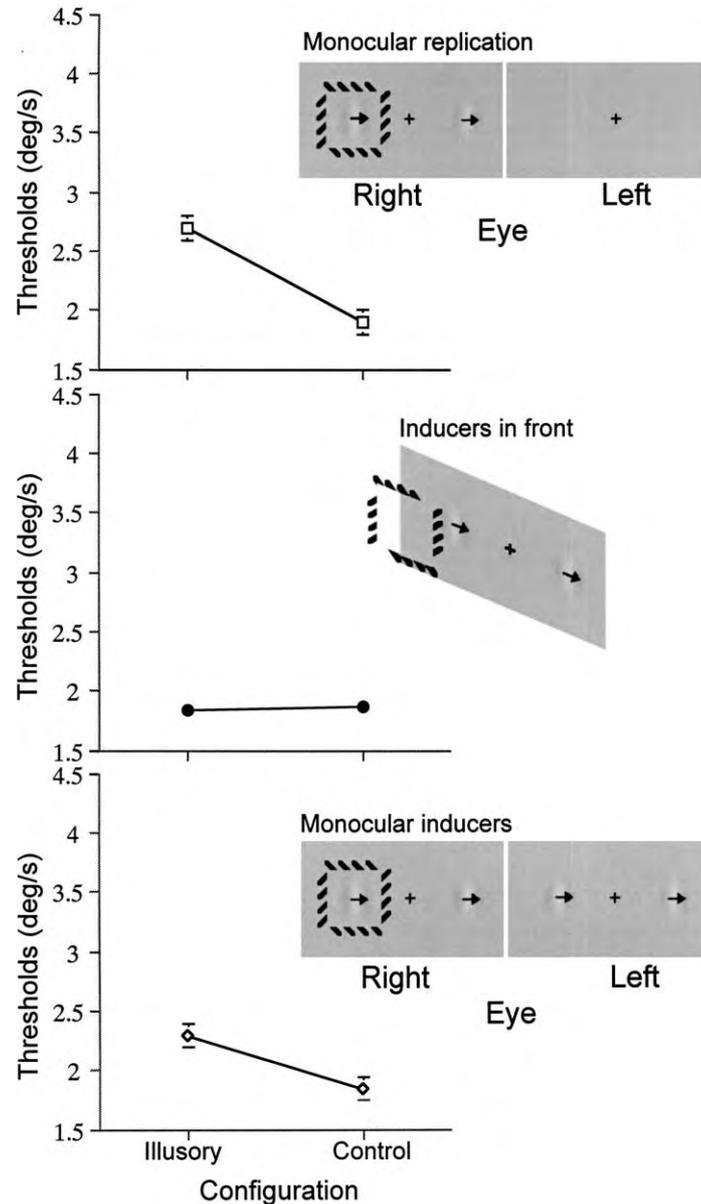


Fig. 4. Data from Experiment 3. Average thresholds for speed discrimination are plotted as a function of type of configuration (illusory vs. control). Open squares, monocular condition (a replication of Experiment 2). Solid dots, inducers-in-front condition. Open diamonds, monocular inducers condition. Error bars are  $\pm 2$  SE across observers.

studies of motion integration (Shimojo et al., 1989). Based on the results of Experiments 1–3, however, there is also another integration rule that may be responsible for our observed thresholds. The motion integration process may function according to a *surface continuity principle*: combine local signals that appear to belong to a continuous common surface, and segregate those that appear to belong to separate surfaces. Our displays in Experiments 1–3 could not distinguish between these two alternatives, because one of the motion signals was presented on a different surface (the IS) than the other, but this also caused the former signal to appear on a different depth plane. To distin-

guish between these two alternative possibilities, we performed another experiment.

#### 7. Experiment 4

To distinguish between coplanarity and continuity, we presented both motion signals in our displays over ISs. If coplanarity is responsible for the difference between illusory and control configurations, then thresholds should not be affected relative to the control configuration, even though ISs are perceived in the experimental condition. As can be seen in Fig. 5, the two

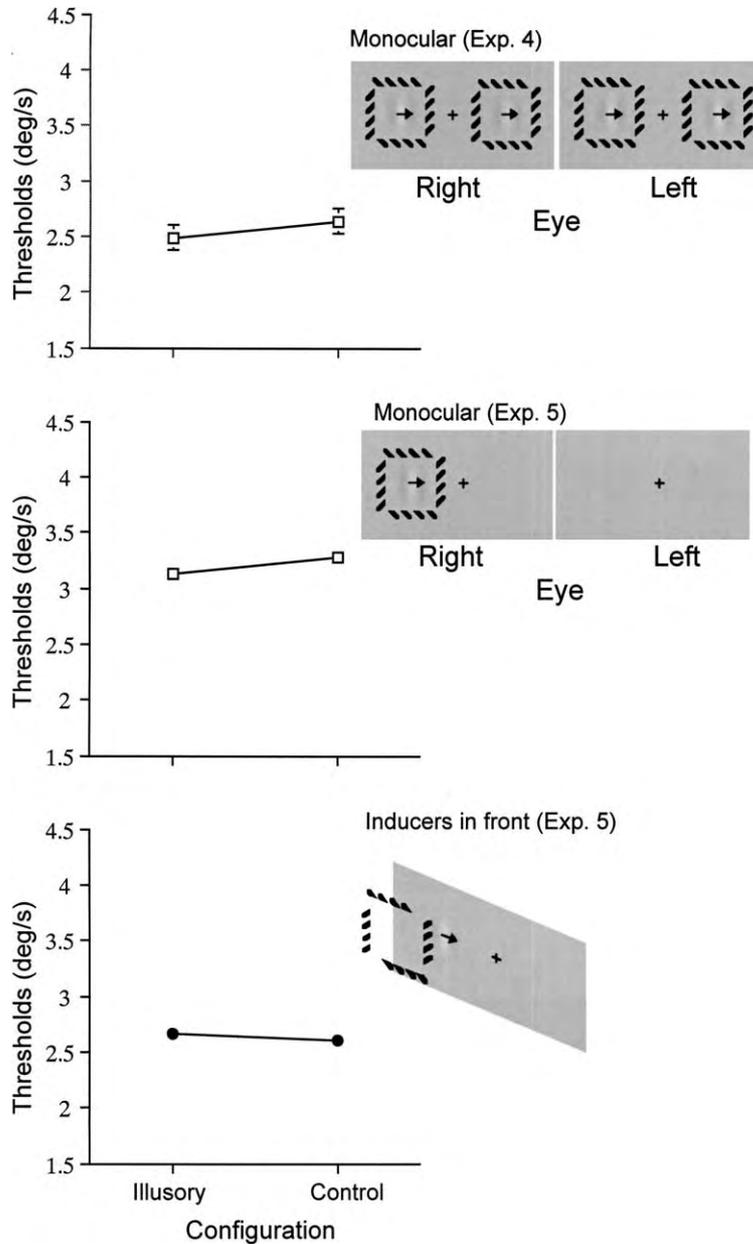


Fig. 5. Data from Experiments 4 and 5. Average thresholds for speed discrimination are plotted as a function of type of configuration (illusory vs. control). Open symbols, monocular condition. Solid symbols, inducers-in-front condition. Please note that in Experiment 5 there was only one motion signal (Gabor). Error bars are  $\pm 2$  SE across observers.

motion signals belong to different surfaces but are on the same depth plane. On the other hand, if the effect is due to continuity, i.e. signals located on different surfaces, then there should be an effect on the thresholds.

7.1. Method

Thirteen University of Liverpool students participated for course credit. They had normal or corrected vision. Two configurations (illusory vs. control) were compared. Stimuli were the same as in the previous experiments, except that both Gabor patches were pre-

sented on an IS or control configuration (see Fig. 5). To keep the testing conditions as comparable as possible to those of Experiment 3, participants always wore an eye patch as well as the stereo glasses.

7.2. Results and discussion

Fig. 5 shows the thresholds for speed discrimination in degrees per second, which were analysed as in the previous experiments.

We did not find a difference between the thresholds for the IS and control configurations ( $t(12) = 1.92$ ,

$p = 0.079$ ). This result supports the hypothesis that coplanarity is the key to integration.

## 8. Experiment 5

Although unlikely, it is possible that our results were produced by some uncontrolled effect of the different configurations on the speed signals, such that signals embedded in an IS were weaker than those in the control configurations. To control for this possibility we compared speed discrimination thresholds in the IS and control configurations using a single Gabor. We placed the Gabor at the same eccentricity as in the previous experiments and surrounded it with either a magic square or a control configuration. To evaluate all our viewing conditions, we included both the monocular repetition and the inducers-in-front conditions that were used in Experiment 3.

### 8.1. Method

Thirteen University of Liverpool students participated. They were naive with respect to the problem and the hypotheses until after the data were collected. A 2 configurations (illusory vs. control)  $\times$  2 viewing conditions (monocular replication vs. inducers-in-front) design was used. Stimuli and procedure are those described in Section 3, except that in this experiment we used only one motion signal instead of two.

### 8.2. Results and discussion

Fig. 5 shows the thresholds for speed discrimination in degrees per second, which we analysed as in the previous experiments. In both the monocular replication ( $t(11) = 0.81$ ,  $p = 0.435$ ) and inducers-in-front conditions ( $t(11) = 1.03$ ,  $p = 0.805$ ) there was no difference between the thresholds for the IS and control configurations. These results rule out that the local configuration of the IS inducers had an effect on the strength of the motion signal, making it weaker relative to the configuration of the control condition. We conclude that our observed differences in the speed thresholds are indeed due to less efficient integration across the pairs of Gabors when one of them is on an IS.

## 9. General discussion

We investigated the process of integration of motion signals across space and the effects of the global spatial structure of the stimulus on this process. Illusory surfaces allowed us to observe the effect of surface formation and depth stratification in the absence of any difference between the motion signals that were pre-

sented. Our results show that when people perceive an illusory surface monocularly, and motion signals are distributed so that some are on the illusory surface and some are not, speed discrimination thresholds increase. We take this increase to signal less efficient motion integration (cf. Verghese & Stone, 1997).

Furthermore, we did not observe this effect on motion integration when the inducers were modified so that they did not form an illusory surface (the control configuration in all our experiments), when the inducers were perceived binocularly creating information conflict about the depth plane of the illusory surface (in Experiment 1), and when the inducers were perceived in front of the background (forming an illusory aperture rather than a surface, in Experiment 3). The binocular condition was associated with high variability as would be expected when there is conflicting information about depth. Finally, we did not observe the effect when both motion signals were presented on illusory surfaces (Experiment 4). Taken together, these results converge in suggesting that the motion integration process obeys a simple coplanarity principle. In all our experiments, when the manipulation consistently supported an interpretation of the motion signals as being on the same phenomenal plane, integration remained efficient; whereas when one of the signals appeared to be on a different plane, efficiency was reduced.

From an ecological standpoint, it is possible to argue that both continuity and coplanarity should be important when integrating motion. Thus, it is partly surprising that continuity did not have a significant role in our findings from Experiment 4. Nonetheless, coplanarity has been shown to drive integration when combining local signals to solve the aperture problem (Shimojo et al., 1989), in induced motion (DiVita & Rock, 1997), and in the integration of luminance ratios to compute surface lightness (Gilchrist, 1977). It is possible that assessing coplanarity, based on local depth measurements, is less computationally expensive than assessing continuity, which requires representing spatial relationships between surfaces. In general, however, relating continuity to objectness is not simple, as solid objects are complex entities consisting of many surfaces, and neither continuity nor coplanarity are necessary or sufficient in themselves to define an object (see also Feldman, 2003). We suspect that there may be conditions in which both factors have an effect, and future studies might reveal the spatial range in which they are effective.

The issue of perceived depth also raises a question about effective speed perception. It is possible that when signals are perceived at different depths but have the same angular velocity they are assigned different speeds (because of speed constancy, McKee & Welch, 1989). Perhaps the difference in perceived speed caused in turn a decrease in threshold. We do not believe this to be the case, for McKee and Welch (1989) have looked specifi-

cally at the issue of thresholds for signals that had different depth as specified by binocular disparity, and found that thresholds for angular velocity were unaffected by variability in perceived depth.

Most researchers agree on the importance of spatial structure on the integration of motion signals, but the debate is still open on the role of different aspects of spatial structure. For example, several studies (Anderson, 1999; Liden & Mingolla, 1998; Mosca & Bruno, 1999; Mosca, Bruno, & Bertamini, submitted for publication; Shimojo et al., 1989; Tommasi & Vallortigara, 1999) have tested the effect of different spatial cues on motion integration process, such as binocular disparity, Da Vinci stereopsis, and *T*-junctions. In the context of this general problem, our results are interesting in that they show an effect of coplanarity in the absence of any local depth cues (i.e. *T*-junctions, binocular disparity) in the illusory surface displays. This suggests that the motion integration process is sufficiently complex to take into account the long-range *spatial* integration of contour information and the resulting stratification of surfaces into depth planes.

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