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Visual binding of luminance, motion and disparity edges

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Abstract

Visual binding of edge segments embedded in noise and created by luminance, motion and disparity contrasts were studied in three experiments. The results showed that path formation was limited by the same rules across all attributes tested. The first experiment showed that binding could be accomplished with either attribute used in isolation. The second experiment showed that closed paths were easier to detect than open paths irrespectively of the attributes used to create the path elements. No additive effects were found in either Experiment 1 or 2 when the path elements were created with several attributes superimposed on the same positions, compared to when only one attribute was used along the path. In Experiment 3 it was found that when another attribute was added between the positions of the first attribute along the path, so that two attributes alternated along the path, the performance of path detection was better than expected by probability summation estimated from the single attribute conditions. These results provide evidence for attribute-invariant Gestalt laws and provide clues about the underlying neural mechanisms.

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1. Introduction

How are fragments of coherent shapes in images put together to provide viewers with a unified perception of shapes, and how are various information bearing media (attributes) integrated in shape perception? The Gestalt psychologists proposed a set of laws for describing how perceptual linking of local texture elements is influenced by global context (Koffka, 1935). Texture elements tend to be perceptually grouped together, and be distinct from the background, if they are involved in common motion (common fate), they are aligned (good continuation), they form closed contours (closure), they are closely spaced (proximity) or similar to one and other (similarity). These laws have almost exclusively been demonstrated with luminance or colour-defined features. Luminance and colour are first-order information bearing media (attributes) and may be carried by single points in an image such as luminance intensities and colour values on the retinas. However, there are other information bearing media than luminance and colour available to the visual system. The description of second-order attributes (Cavanagh & Mather, 1990) re-

quires more than one point separated either in space or time (e.g., texture, disparity, and motion). Edges can be created and perceived in either first- or second-order attributes. Examples of second-order edges are the border between regions having different textures, depth contrast seen in random-dot stereograms (Julesz, 1964) and edges that may be seen in random-dot kinemato-grams due to motion contrast (Kaplan, 1969). Although the texture in such random-dot displays carries the disparity and motion signals, there is no luminance contrast to signal the presence of an edge created in second-order attributes. In technical terms there are no Fourier components signalling the edge. The questions addressed here are whether visual linking of edge elements created by luminance contrast, depth contrast (in the form of interocular disparity) and motion contrast obeys similar rules, whether facilitation occur if attributes are combined, and whether the grouping process is attribute specific. Shortly, does binding across attributes precede or follow linking across visual space? A path finding paradigm, developed by Field, Hayes and Hess (1993), was used in three experiments to investigate these issues.

The Gestalt laws are merely descriptive in that no mechanism of gestalt formation is implied, although Köhler's (1940) field-model is an exception. Somehow,

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information across attributes, and from feature detectors separated across cortical space has to be integrated into a visual impression of a figure or a ‘gestalt’. How integration across cortical space and attributes is accomplished has been addressed as the binding problem (for a review see Roskies, 1999). The binding of luminance edges, or the perceptual Gestalt laws of good continuation and closure have been extensively studied in both psychophysical and neurophysiological investigations of possible path ‘binding’ or linking mechanism.

1.1. Prior investigations of path linking

Most studies on path linking have used stimuli made of luminance-defined elements. The ability to detect straight lines composed of dots embedded in noise dots increases when their spacing is regular, they are collinearly arranged, and their separation is small (Smits, Vos, & van Oeffelen, 1985; Uttal, 1975). Variables other than spatial density influences line segregation since lines composed of spatially separated lines segments aligned with the global line are more easily detected than if the elements are orthogonal to the global line (Beck, Rosenfeld, & Ivry, 1989). Field et al. (1993) developed a technique where the positional cues to the path were absent. In their study observers were presented displays containing a large number of small luminance-defined Gabor elements (a one-dimensional sinusoid multiplied with a two-dimensional Gaussian luminance distribution). These path elements could form a smooth snake-like pattern. The task was to detect a patch of such elements whose orientation was aligned along a pre-determined path embedded in randomly oriented elements (Fig. 1a). The Gabor elements were joined at an angle $\pm\beta$ (the path angle, see Fig. 1b) randomly selected for each new path segment added to the pre-existing segments during the construction of the path. Observers could reliably detect the path when the distance between the elements was seven times their width, path curvature

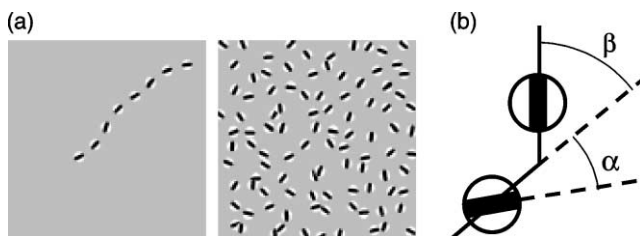


Fig. 1. (a) An illustration of the path detection paradigm, here displayed with luminance defined path elements. The path alone is shown in the left panel and embedded in randomly distributed and randomly oriented noise elements in the right panel. (b) Schematic view of two path elements on a path shown by the thin line segments. The path-angle (β) specify the curvature of the path, zero path-angle specify a straight line. The element-orientation (α) specify the orientation of the elements relatively the path orientation, zero element orientation specify a path where the elements are aligned along the path.

β was up to 60° , and the elements were aligned along the path ($\alpha = 0^\circ$, Fig. 1b) as opposed to orthogonal to the path ($\alpha = 90^\circ$). The linking was found to be phase invariant suggesting that the linking process occurs a stage beyond linear orientation filtering, although a slight phase selectivity has been found in later studies (Field, Hayes, & Hess, 1997). Also, path linking may traverse stereoscopic depth indicating a cortical site for the linking process (Hess & Field, 1995; Hess, Hayes, & Kingdom, 1997). This suggests that the linking process operates on rectified orientation selective cortical cells, such as complex cells, which are characterised by non-linear filtering. The contextual influence in linking of luminance defined path elements is further demonstrated with the closure effect whereby closed paths embedded in noise are easier to detect than similarly embedded open paths (Kovacs & Julesz, 1993).

Contrary to results from earlier demonstrations on failure of perceptual grouping at equiluminance (Livingstone & Hubel, 1987), McIlhagga and Mullen (1996) showed that path linking could be accomplished with path elements defined only by colour contrast. Mullen, Beaudot, and McIlhagga (2000) compared the performance between equiluminant red–green, blue–yellow and luminance-defined path linking. They found that performance on path linking was similar for a range of curvatures as well as other parameters tested for all three types of elements. However, the linking process is not colour blind since path linking is disrupted when the path elements alternate between different colour contrasts and phase (McIlhagga & Mullen, 1996; Mullen et al., 2000). Mullen et al. (2000) proposed that a common linking process operates in the visual system but that it remains sensitive to colour contrast and phase of its input.

A phenomenon closely related to the linking of aligned path elements is the perception of illusory contours that may be seen between spatially separate but aligned inducing edges where no contrast exist in the image (Kanizsa, 1955). In typical demonstrations and investigations of illusory contours the inducers are defined by luminance contrasts, although motion and disparity cues may be used. Poom (2001a) demonstrated high ratings of illusory contour strength between two inducers defined by different attributes (luminance texture, motion, and disparity contrasts). He also used a summation technique to demonstrate inter-attribute summation between a near threshold luminance line and illusory contours created by luminance, disparity, and motion cues (Poom, 2001b). These findings provide evidence for attribute invariant creation of illusory contours in the visual system.

1.2. The present investigations

Evidence for the existence of attribute invariant edge-orientation detectors has accumulated from both psy-

chophysical (Poom, 2000, 2001a,b; Rivest & Cavanagh, 1995) and neurophysiological studies (e.g., Marcar, Raiguel, Xiao, Maes, & Orban, 1992). This raises the question whether edge-linking processes operate on such attribute invariant detectors. In such case the binding across attributes would precede binding across space. To address this hypothesis visual path linking was investigated across path elements created with luminance, motion, and disparity contrasts. The paths were composed of path elements imbedded in similar noise elements so that the location cues were minimised. The path could be perceived by aligning the path elements (illustrated in Fig. 1a). Similar sampling density was provided by using the same density of random-dot micropatterns across the attributes to create the path elements (Regan, 1999) (Fig. 2). The experimental results from multi-attribute conditions were compared with predictions derived by probability summation from the outputs of hypothetical independent channels, cal-

culated from the results obtained when single attributes were used along the path. Briefly, the rules limiting linking of edge elements were the same across the attributes. For all the attributes the results from Experiment 1 showed that performance was severely degraded when the path elements were orthogonally oriented to the path compared to aligned with the path. Experiment 2 showed that closed paths were easier to detect than open paths irrespectively of the attribute used to create the path elements. Experiments 1 and 2 showed no path detection facilitation when several attributes were superimposed on the elements along the path compared to corresponding conditions when the attributes were isolated. Experiment 3 showed that path detection was possible when the attributes alternated along the path, and that the performance was better than predicted by probability summation derived from conditions when one of the attributes were shut off. Also, comparison between inter-attribute conditions in Experiment 3 and

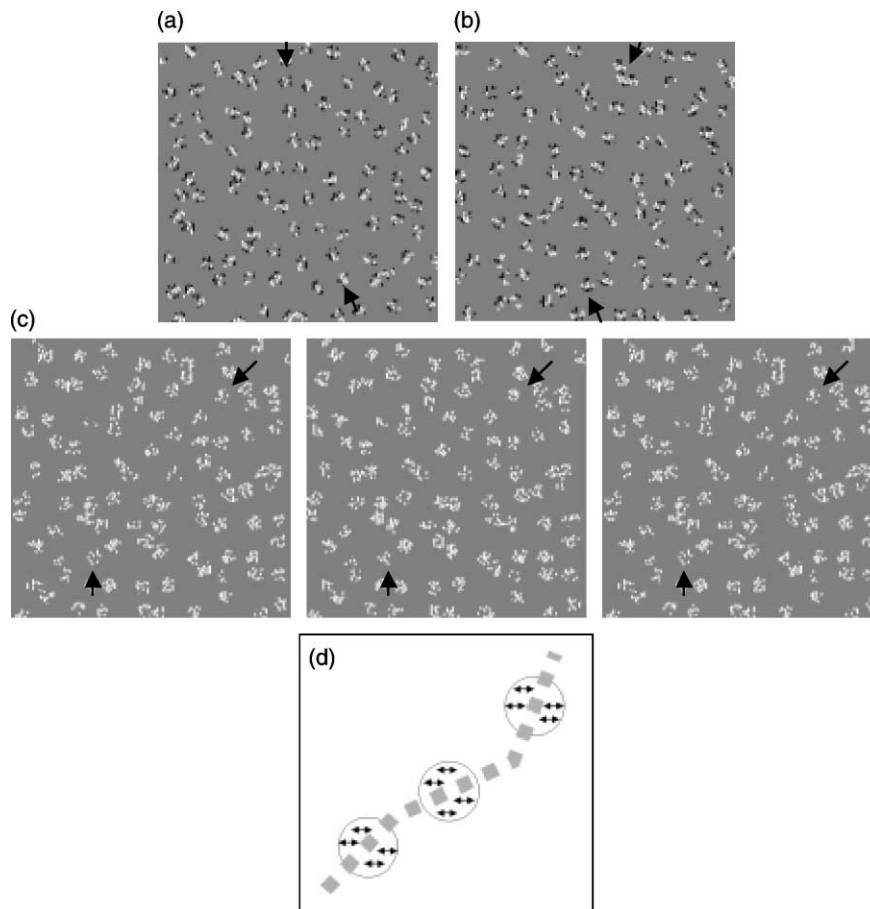


Fig. 2. Illustrations of the attributes used to create the paths in the experiments, the arrows show the path ends. (a) A luminance-defined path having the elements aligned with the path with path angle of 10° . (b) Orthogonally oriented to the path. (c) The stereopairs show the stimuli used in Experiment 1 in conditions when disparity was used to create the path elements. Crossfusion of the leftmost stereopairs or uncrossed fusion of the rightmost stereopairs reveal a path with path angle of 10° . (d) A schematic illustration of the path elements created by motion contrast used in the experiments. The flanking regions of each micropattern were oscillating back and forth, disappearing and reappearing as they passed the central bar. Horizontal unidirectional and synchronous motion was used for all micropatterns irrespectively of their orientations. The path is shown here by the dotted line but was composed of stationary dots within the bars in the micropatterns.

the single attribute conditions in Experiment 1 reveal better performance when the attributes remained the same along the path than when they alternated. These results are discussed regarding the possible location of binding across attributes.

2. Experiment 1

Luminance-defined target edge elements embedded in randomly oriented noise elements are perceptually grouped together and can be distinguished from the background when they are aligned but not when they are orthogonal to the path (Field et al., 1993). The distinctiveness whereby the target elements stand out depend on several factors, one is the path angle (β) whereby the target elements are aligned (Fig. 1b). Paths created with luminance-defined Gabor elements can be detected in randomly oriented noise elements for path angles up to 60° (Field et al., 1993). Experiment 1 attempts to compare linking of edge segments aligned along a pre-determined path where the segments are defined by luminance, motion, and disparity as a function of path angle. Also, linking of edge segments that are orthogonal to the path is examined. The attributes are used either alone, in pair-wise conjunction, or all three in conjunction superimposed on the same locations. The results obtained from the conjunction conditions were compared to predictions derived from probability summation of the output from hypothetical independent channels calculated from the results obtained when the corresponding single attributes defined the paths.

2.1. Stimuli

A version of the Field et al. (1993) path stimulus generation procedure was used to determine the positions of the path and noise elements in the display. The image was divided into an 11×11 grid of squares where each square contained the centre of only one element. The total size of the grid pattern was $8^\circ \times 8^\circ$. A random starting position about 3° from the centre of the image was selected. The next point in the path was defined by the endpoint of a line with distance equal to the grid spacing pointing toward the centre of the image plus or minus the path angle β as shown in Fig. 1b. The path elements consisted of micropatterns of randomly distributed dots as described below. An element was placed halfway between the starting and end points of the line. The subsequent endpoints were created with a vector aligned with the previous line segment plus or minus the path angle β . If the midpoint of the line segment was within a square that already contained the centre of another element, then the line segment was extended 0.25 times its original length. This variation of line length also prevented a regular spacing of the target elements that

could be used as a cue to path detection. The orientation of the individual path elements relative the path orientation (α in Fig. 1) could be varied. In Experiment 1 the orientations of the elements were aligned with the path ($\alpha = 0^\circ$, Fig. 2a with luminance-defined path elements and Fig. 2c with disparity-defined path elements) or orthogonal to the path ($\alpha = 90^\circ$, Fig. 2b). A random variation of $d\beta = \pm 10^\circ$ was added to the path angle to prevent any symmetrical patterns to emerge by accident. The noise elements were distributed so that each square contained the centre of only one element and the overlap between elements were minimised. The resulting stimulus contained 121 elements, eight of these composed the path and the rest was noise elements.

All micropattern elements were created with random dot patterns where the centre of the dots (about $0.08^\circ \times 0.08^\circ$) were restricted to lie within a circular area with a diameter of about 0.5° . Each micropattern had 30 possible dot locations, and the probability of placing a dot at a particular location was set to 0.5, so on average 15 dots created each micropattern. Micropatterns with luminance-defined bars were created with white bar-dots flanked on both sides by black dots (illustrated in Fig. 2a and b). All dots were displayed on a medium grey background. The disparity-defined bars were created by positional binocular disparity of uniformly white texture elements so the bar appeared in front of the flanking parts of the elements. This can be seen by fusing the stereopictures in Fig. 2c ($\alpha = 0^\circ$, $\beta = 10^\circ$). The interocular disparity creating the edges within the micropatterns was set to 0.1° . Motion-defined bars were created by relative motion among uniform white dots. Three frames created the motion sequences, dots within the bars of each element were stationary while the surrounding dots oscillated back and forth with amplitude of 0.1° , and frequency of 2.9 oscillations/s. Coherent horizontal motion was used for the motion of all 'background' texture (Fig. 2d). The moving dots disappeared and reappeared as they passed the border of the bars in the micropatterns. The depth-plane of the bars was the same as the depth plane for the motion and luminance elements when these attributes were mixed. The luminance, motion, and disparity contrasts were simply chosen to make sure that the bar dots could effortlessly be distinguished from the flanking dots, no other efforts were made to equalise signal strength. All bars were 0.2° wide and the same texture density was used for all stimulus attributes.

It is not known how edge-detecting cells sensitive to different spatial frequencies (or spatial scales) interact. Therefore, Gabor elements with a smooth luminance crest rather than a sharp edge have been used as oriented elements in previous path linking studies since they contain a minimum of spatial frequencies in the Fourier frequency domain (Field et al., 1993). However for several reasons it is difficult to create oriented elements

defined by motion and disparity that satisfy this requirement of smoothness. First, some sort of texture is required that carry second-order attributes such as motion and disparity signals. Second, in order to make a fair comparison between the path linking process for different stimulus attributes, it is important that the sampling density is comparable between them (Regan, 1999). These constraints lead to the creation of the path elements used in the present study, where the same dot density and sharp contrasts were used across all attributes. This procedure in constructing the micropatterns provided similar sampling density across the attributes since the average number of dots marked by luminance, motion or disparity contrast, to distinguish the oriented bars from the flanks in the micropatterns, was the same. A computer program was developed that created the pictures and displayed them on a 17 in. monitor with 75 Hz refresh rate. Stereopairs were presented at adjacent positions on the screen, and was viewed through a polaroid stereoscope that facilitated crossfusion. The viewing distance was 70 cm.

2.2. Method and procedure

Path detection was measured with a two-interval forced choice technique (2IFC). Pairs of stimuli, target embedded in noise and stimuli with only noise, was presented in random order. The presentation time for each stimulus in the pair was 1 s and the inter-stimulus interval was 0.4 s. The path angle (β) was used as an independent variable and the percent correct responses was the dependent variable. The path angle was held constant during each session. Blocks with variable number of sessions with different path angles were executed on separate days. In one condition the target elements were orthogonally oriented to the path and the path angle was fixed at 30° for observer L.P. and 20° for observer A.M. The observer responses were given on the computer keyboard by either pressing the left-arrow key when the path was perceived as present in the first presentation or the right-arrow key when the path was perceived in the second presentation. Feedback was given in the form of a soft beep if the wrong response was given. The next stimulus pair was presented on the computer screen after the space bar was pressed. Practice was given in the different stimulus conditions before each block of stimulus presentations. The author L.P. and a naive observer A.M. participated in the experiment. Both had normal vision. The percent correct responses were estimated with 60 trials for L.P. and 50 trials for A.M.

2.3. Results and discussion

The path could quite easily be detected for all attributes used to create the path elements as long as the

path angle was less than about 40° and when the edge segments were aligned along the path ($\alpha = 0^\circ$). Performance levels were similar between the conditions, indicating that the particular contrast levels used were not an important factor for achieving similar saliency across the attributes, or that they were accidentally similar. Three main results emerged. First, when the edge segments were orthogonal to the path ($\alpha = 90^\circ$) then the path detection performance became severely degraded and almost fell to chance levels for the path angles tested in the experiment as seen in Fig. 3 (path angle $\beta = 20^\circ$ for A.M., and $\beta = 30^\circ$ for L.P.). This also shows that the positional cues were very weak or absent for these path angles. Second, the performances in single attribute conditions were degraded identically with increase in path angle. Thus, the visual linking of the micropattern path segments used here seem to obey the same rules as linking of luminance-defined Gabor patterns as created

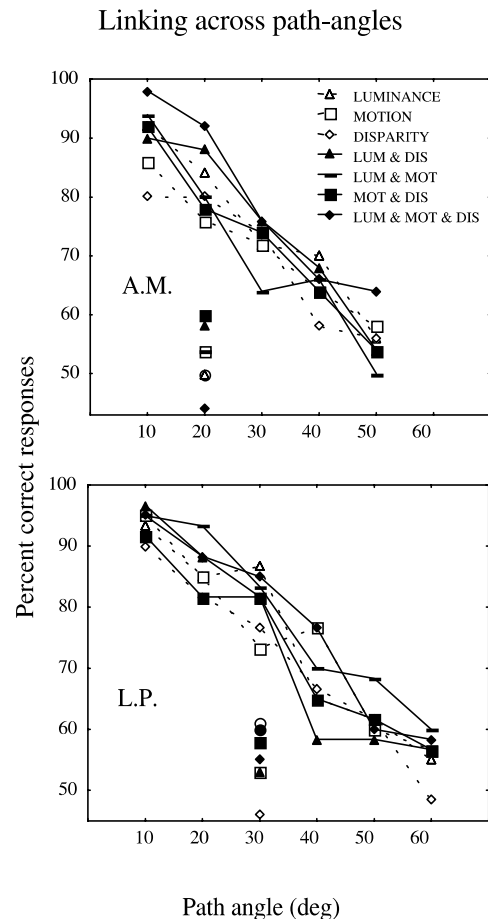


Fig. 3. The percent correct responses as a function of path angle for detecting paths composed of eight edge elements. Luminance, motion, and disparity edge elements were used alone, or in conjunction. Also shown are the results obtained when the path elements were orthogonally oriented to the path, for 30° path angle for L.P. and 20° path angle for A.M. When the path elements were orthogonal to the path performance becomes severely degraded compared to when they are aligned with the path.

by Field et al. (1993). Third, there seem to be no facilitation when several attributes were used in conjunction compared to the corresponding single attribute conditions. This issue is further investigated with the same set of data and compared with probability summation.

When several attributes operate in conjunction and if it is assumed that different attribute-specific channels mediate path detection, then the linking process occurs within each channel separately. The decision stage must act on the output from these channels and the theoretically best performance is obtained with probability summation. In detection tasks the proportion correct responses have a range between 0 and 1, and the corresponding probability-summation formula for N independent channels is

$$P'_{1,2,\dots,N} = 1 - (1 - P'_1)(1 - P'_2) \dots (1 - P'_N) \quad (1)$$

where $P'_{1,2,\dots,N}$ is the proportion of correct responses obtained in conditions where N attributes work in conjunction, and P'_1, P'_2, \dots, P'_N are the proportions of correct responses obtained for each attribute in isolation. In a 2IFC task the response format has a range between 0.5 and 1. The corresponding 2IFC task probability-summation formula is obtained by transforming the full range P' values to half range P values with $P = 2P' - 1$. Substitution into (1) gives the probability summation formula in a 2IFC task with N attributes:

$$P_{1,2,\dots,N} = 1 - \frac{2^N}{2} (1 - P_1)(1 - P_2) \dots (1 - P_N) \quad (2)$$

The results from the multi-attribute and the corresponding single attribute conditions from Fig. 3 are redrawn in Fig. 4 and compared with the corresponding probability summation calculated with Eq. (2) from the results obtained when one attribute was used to create the path. So, the salience of each attribute is taken into account in the predictions for probability summation. Probability summation of the output from independent channels predicts that the performance should be better when several attributes are used in conjunction compared to when each attribute works in isolation (as long as the percent correct responses in the single attribute conditions are above 50%). However, the results show that when two or three attributes are combined there is a complete lack of facilitation. One interpretation of the results is that when several attribute specific channels are activated the decision stage uses only one channel. However this would not be an optimal strategy since probability summation would improve the performance when independent channels are activated. Another interpretation is that no label exists to separate edges from the different attributes used here by the edge linking process since the channels are not independent or that there is only one single channel.

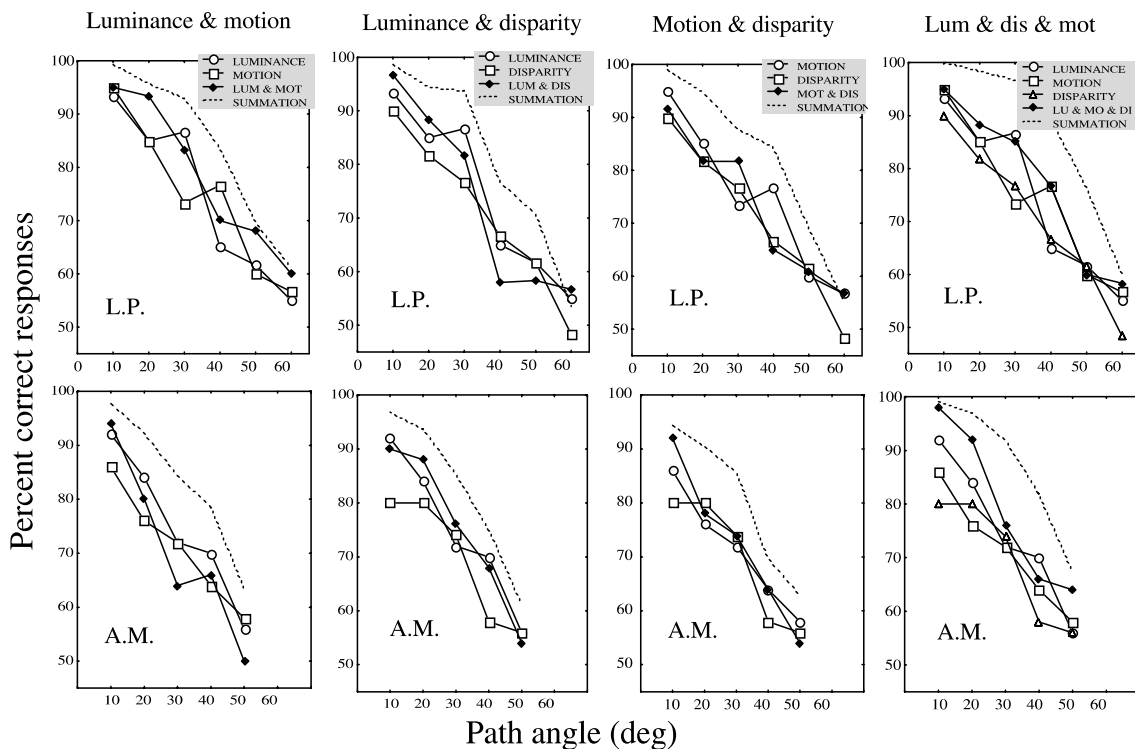


Fig. 4. The estimated probability summation is shown by the dotted lines and is calculated from the results obtained when only one attribute was used to create the path. No facilitation was obtained when several attributes were superimposed to create the path, compared to the corresponding single attribute conditions. Thus, performance was worse than predicted by probability summation.

3. Experiment 2

The aim of Experiment 2 is to proceed the examination of the rules limiting the linking process across the attributes. This time regarding the ‘closure effect’ whereby closed paths created by aligned luminance Gabor elements are more easily detected than similarly created open paths (Kovacs & Julesz, 1993). When path segments are aligned along closed paths, both closure and good continuation act together to signal the path. However, only good continuation is present to signal open paths. It has been proposed that the closure effect is mediated by reverberating activity of neural edge signalling elements along the contour, the activity spreads along the contour and loops back on itself (Pettet, McKee, & Grzywacz, 1998). Such reverberating activity traversing along the path cannot occur when the path is open. Computational modelling have shown that such reverberating activity may arise from excitatory interactions between cells with aligned orientation preferences, and that such reverberation may facilitate path detection (Yen & Finkel, 1998). Experiment 2 attempts to investigate if the closure effect is attribute invariant for luminance, motion and disparity-defined linking of path elements. As in Experiment 1, its also investigated if the linking is facilitated when several attributes are superimposed and act in conjunction.

3.1. Stimuli

The closed and open paths, composed of 12 target elements were initially created by the same rules. The positions of the corners (vertex) in the closed path were initially located along a circular path with radius of 1.5° , and were spaced with regular intervals plus a random perturbation of ± 0.3 times the distance between the corner positions. A sinusoid with three periods and amplitude of 10% of the radius of the circular path was then added to the circular path. The resulting closed path has three bumps and the edge elements are irregularly located along the path (Fig. 5b). The open paths were

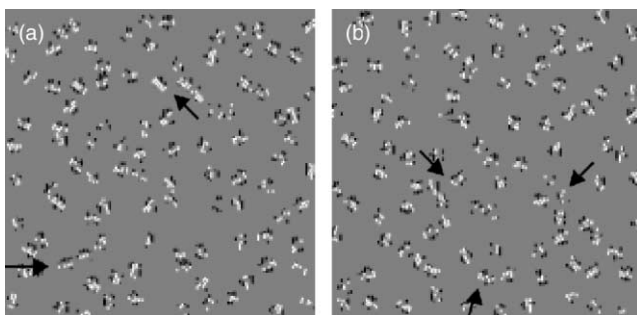


Fig. 5. (a) An open S shaped path and (b) a closed path, created by luminance-defined path elements. The arrows show the locations of the paths.

initially closed ones that was cut somewhere in a randomly chosen position along the path and thereafter unfolded creating an S shape that was randomly oriented in the display (Fig. 5a). This procedure made the total curvature for closed and open paths identical, although the curvature changes sign along the open paths. The orientations of the path-elements were randomly assigned a value between a maximal deviation range (α -range) that was used as an independent variable while the path detection was measured with the 2IFC technique. When the path deviation range is $\pm 90^\circ$ there is no correlation between path orientation and local edge-element orientation. Twelve targets among about 121 elements created the path in both closed and open path conditions.

3.2. Procedure

The procedure was identical to the procedure used in Experiment 1. The author L.P. and one naive observer P.J. participated in the experiment. The percent correct responses were calculated from 50 trials in each stimulus condition.

3.3. Results and discussion

Closed paths were easier to detect than the open paths across all attributes and attribute conjunctions used in the experiment (Fig. 6). Thus, the closure effect is invariant with respect to the attributes used to create the path elements. Also, as a replay of Experiment 1, when several attributes act in conjunction no facilitation occur and hence the performance is less than expected by probability summation of independent channels (Fig. 7a and b).

Most models of path or edge linking processes consist of two stages, where at a first stage local edges are detected which are linked at a subsequent stage (Grossberg & Mingolla, 1985; Heitger & von der Heydt, 1993; Marr, 1982; Parent & Sucker, 1989). These two-stage models have received empirical support since the contextual modulation of local stimuli takes longer than the response evoked by the local features. This result has been interpreted in terms of a fast feed-forward processing of local features and a slow feedback contextual modulation of the original message (Zipser, Lamme, & Schiller, 1996). There is massive feedback of axonal projections from cortical sites such as prefrontal cortex to visual areas V1 and V2 that may be used to modulate local information. Also, lateral connections intrinsic to both V1 and V2 may be used in that process. It has been shown that the short-range process is dependent of contrast and sign (Wehrhahn & Dresch, 1998), and that long-range processes are almost independent of contrast and sign (Dresch & Grossberg, 1997).

Binding across attributes can take place at either the first or second stage in the two-stage model. Early

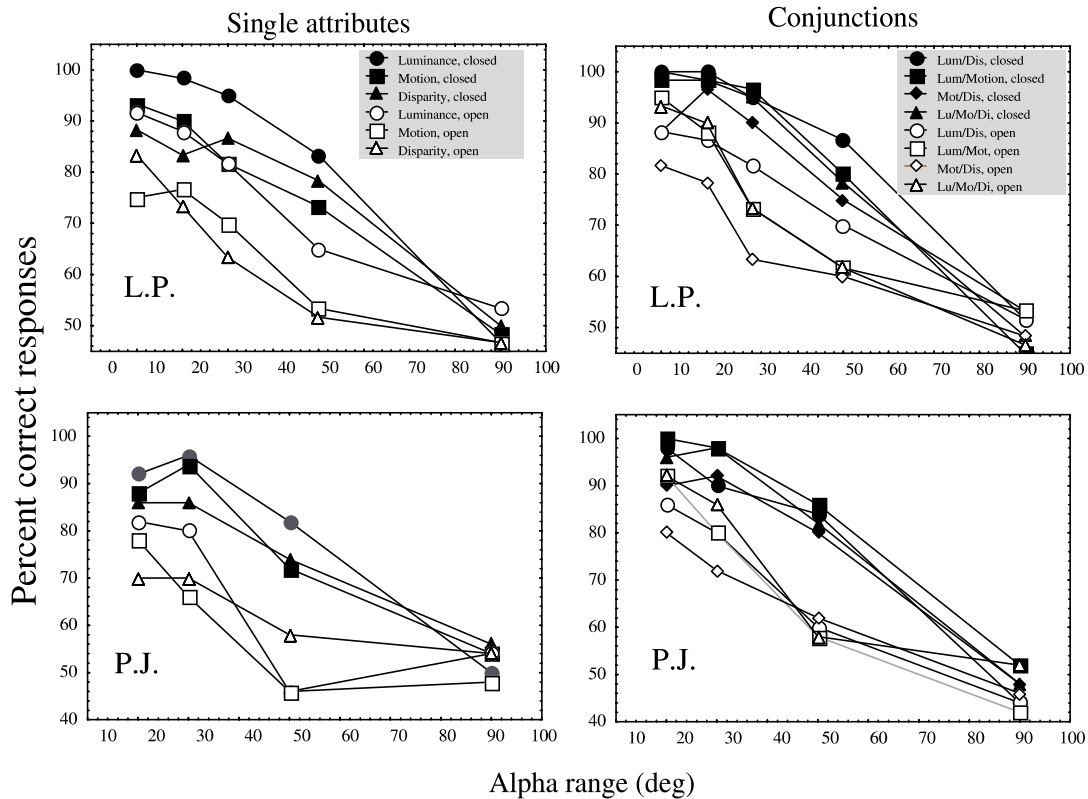


Fig. 6. The percent correct responses as a function of element orientation range (α -range) for closed and open paths created by eight path elements. Luminance, motion, and disparity edge elements were used alone or in various conjunctions.

binding of edges across attributes may imply facilitation of local orientation detection before the path linking process, and late binding across attributes may occur at the linking stage. So, both early and late binding of attributes may imply facilitation of path detection. Interestingly, the loss in performance in contour linking tasks when curvature increases, and when colour or luminance were used to define the edge elements, in the Mullen et al. (2000) experiments could not be compensated for by increased contrast. This may explain why the accidental choice of contrast levels (contrasts in luminance, motion, and disparity) used in Experiments 1 and 2 resulted in similar detectability across the attributes, since the linking process is insensitive to the contrast level. Similarly, when the contrast (in any attribute) within each micropattern is above threshold, then it may not be possible to increase the orientation signals of individual path elements by superimposing contrasts of other attributes to the same dots in the micropatterns (so that the sampling density is held the same). The absence of facilitation found by adding attributes in Experiments 1 and 2 is accounted for if binding of local edges across attributes takes place at the first stage, followed by a second-stage attribute invariant and contrast insensitive edge linking process. This issue is further examined in Experiment 3.

4. Experiment 3

McIlhagga and Mullen (1996) showed that path detection is possible in equiluminant conditions when the same colour polarity and contrast are used along aligned path elements, but when polarity or contrast alternates between the path elements, path detection becomes severely degraded. They concluded that although the linking of luminance and colour-defined path elements is similar, the process remains sensitive to colour contrast and phase of its input. An attribute-invariant linking process can be demonstrated if paths created by alternating attributes along the path can be detected with better performance than if only one of the attributes, involving only half of the elements, is used to create the path. If the performance in inter-attribute conditions is disrupted, or if the path perceptually segregates in two separate paths, then it might be suspected that the attributes feed different linking processes and that each process is blind to the other attribute (McIlhagga & Mullen, 1996). This issue is investigated in Experiment 3 for paths created by aligned luminance, motion and disparity contrasts. The results from inter-attribute conditions were compared with predictions derived by probability summation from the corresponding single attribute conditions.

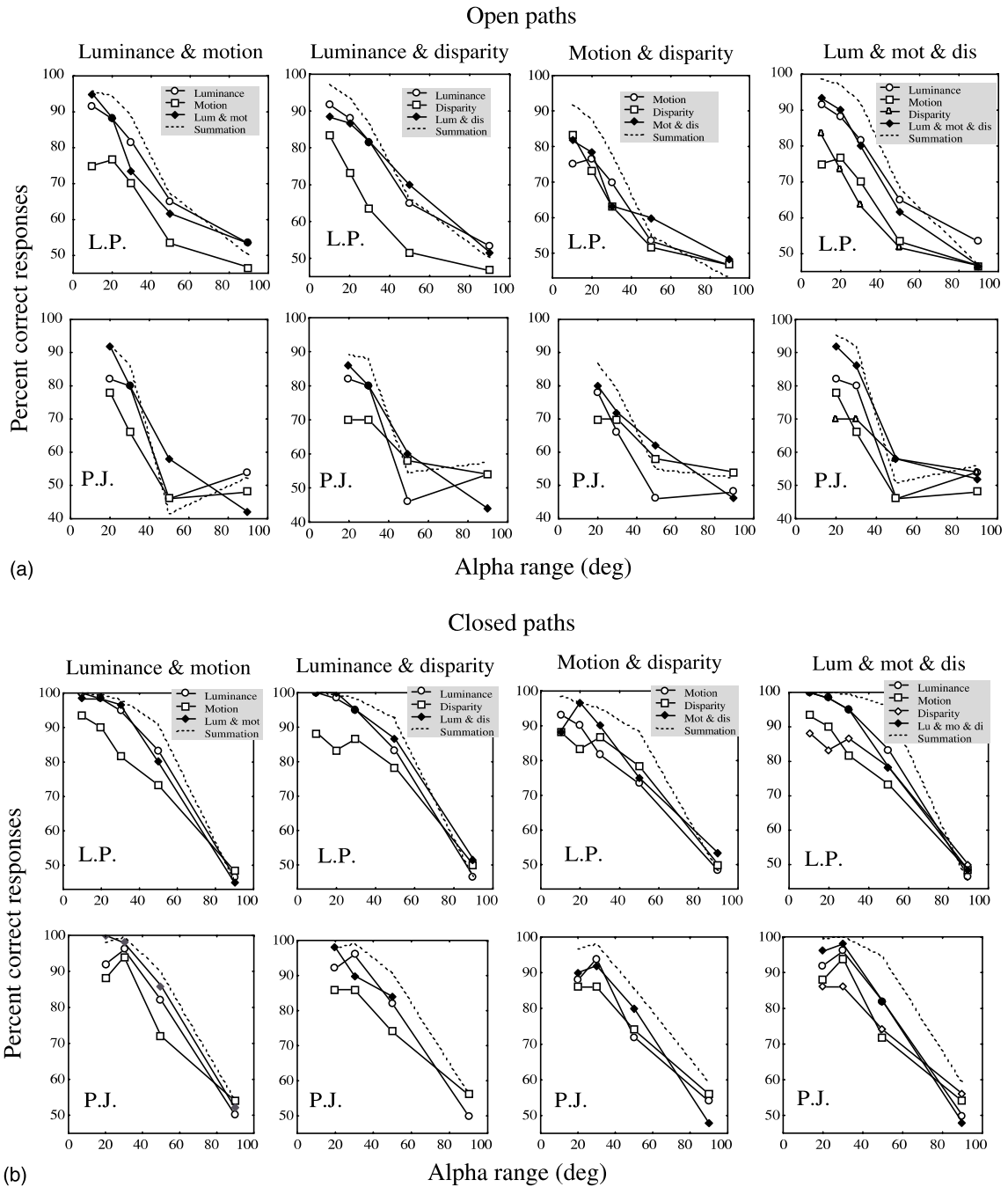


Fig. 7. The estimated probability summation for (a) open paths and (b) closed paths are shown by the dotted lines and is calculated from the results obtained when only one attribute was used to create the path. No facilitation was obtained when several were superimposed to create the path compared to the corresponding single attribute conditions. Thus, performance was worse than predicted by probability summation for both open and closed paths.

4.1. Stimuli

The same stimulus generation procedure as used in Experiment 1 was used in Experiment 3. The path angle (β) was varied for paths created by eight elements. However, the attributes were not superimposed as in the previous experiments, instead the attributes used to create the path elements alternated along the path in

inter-attribute conditions. This is illustrated by the stereogram in Fig. 8 with a path composed of alternating luminance and disparity edge elements (path angle = 10°). In the inter-attribute conditions four micropatterns of one attribute were alternated with four micropatterns of the other attribute along the target path. The path was embedded in noise micropatterns created by the same attributes as used in the path. The attribute was

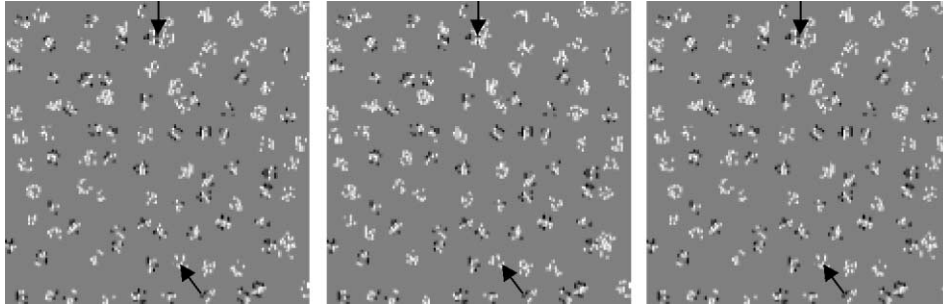


Fig. 8. An example of the stimuli used in Experiment 3. Crossfusion of the leftmost stereopairs or uncrossed fusion of the rightmost stereopairs reveal a path composed of alternating path elements created by luminance contrast and disparity contrast (arrows show the path ends). The micropatterns aligned along the path (path angle is 10°) were created by luminance or disparity contrasts, and alternated between these attributes along the path. Each randomly oriented noise pattern was randomly assigned one of the attributes used to create the path. In single attribute conditions, luminance motion or disparity-defined micropatterns were alternated with unoriented blobs composed of randomly distributed dots. An example of stimuli where only luminance-defined orientations were used and all other micropatterns were unoriented can be seen by viewing one of the frames with no fusion.

randomly assigned to define the randomly oriented edge in each noise micropattern. In preliminary investigations, single attribute stimuli were created by simply turning one of the attributes off by erasing all micropatterns whose edges were created by that attribute, both in the target and noise patterns. It was found however that positional cues were salient in such stimuli since they contained only half the number of micropatterns as in the corresponding inter-attribute stimuli, so that paths could be detected from the positional cues alone. Therefore and for reasons described below, the single attribute paths were created by replacing all micropatterns of the other attribute with non-oriented micropatterns leaving only four micropatterns aligned along the path interleaved with non-oriented blobs of randomly displaced dots (as seen in any of the images in Fig. 8 without fusion). The intervening unoriented blobs could act as a mask that interferes with the path formation rather than a neutral stimulus that does not affect path formation. However, for any hypothetical attribute specific channel, similar masking is provided in the single attribute as in the inter-attribute conditions. For an attribute specific channel, the blobs carrying edges in attributes that are unnoticed for that channel (illustrated in Fig. 9a) are equivalent to the intervening noise elements in the single attribute conditions (illustrated in Fig. 9b). Thus, probability summation analysis from the outputs of hypothetical independent channels can be used since the inter-attribute and single attribute stimuli are similar in the ‘eyes’ of attribute-specific channels.

4.2. Procedure

The same procedure was used in Experiment 3 as in Experiment 1. The author L.P. and one naive observer P.J. participated in the experiment. The percent correct responses were calculated from 50 trials in each stimulus condition.

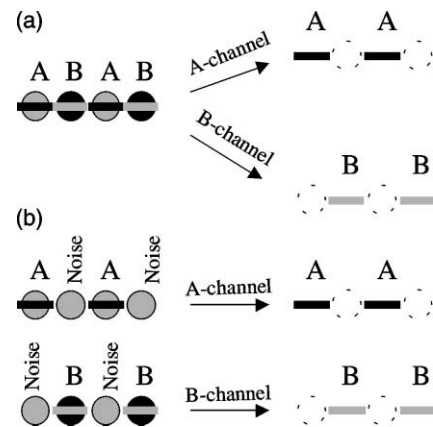


Fig. 9. (a) Leftmost: Aligned path elements of two attributes, A and B, alternating along a straight path are displayed schematically. Rightmost: If such paths are detected by attribute specific independent channels, and if attributes A and B alternate along the path, then the A-channel notice only the edges composed of the A elements and the B-channel notice only the edges composed of the B elements. The other intervening micropatterns will at most provide noise to the channels, here displayed with dotted circles. (b) This means that the same output from attribute specific channels are expected if the A or B attribute is replaced with unoriented noise elements.

4.3. Results and discussion

If it is assumed that the path linking process is attribute specific and takes place in independent channels then the theoretically best possible performance is obtained by probability summation. Two such hypothetical channels are activated when aligned edges of alternating attributes are used along the path as shown in Fig. 9a. The output from either channel alone can be measured by turning the input to the other channel off (Fig. 9b), as was done in the single attribute conditions. The results from Experiment 3 are shown in Fig. 10 and reveal a clear synergism in the path linking process. Linking is efficiently performed between aligned edges alternately created by contrasts in different attributes along the path.

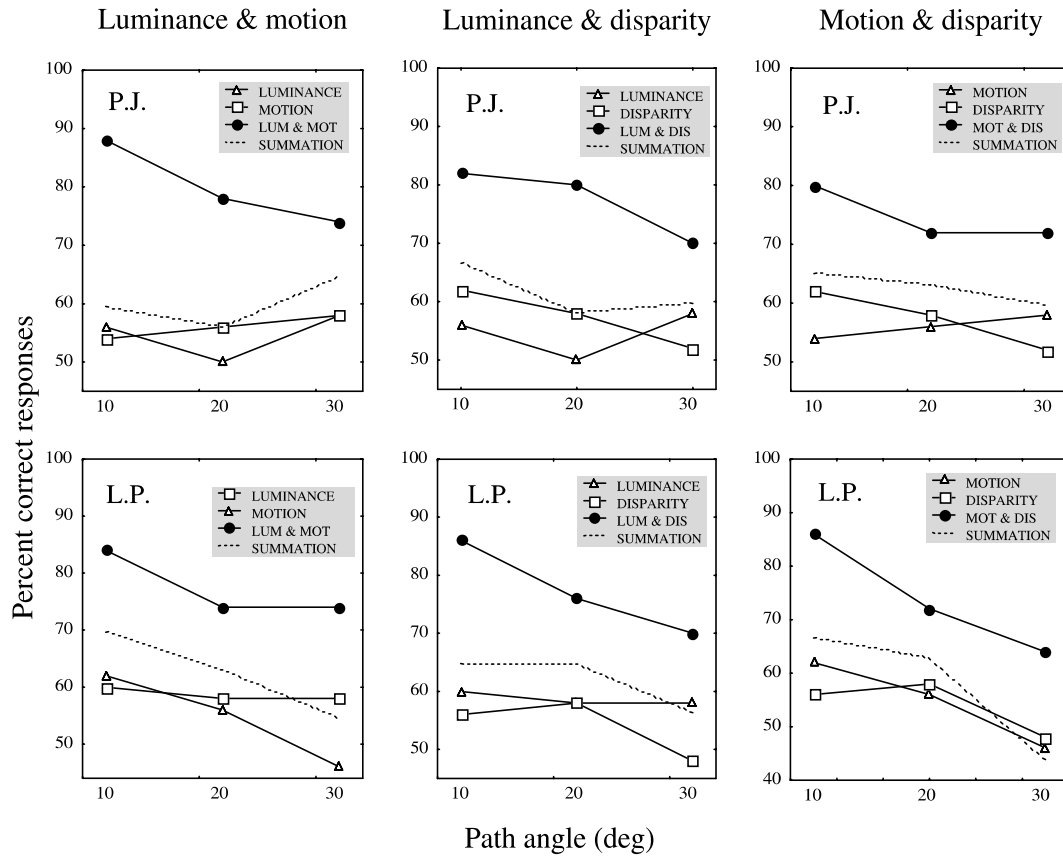


Fig. 10. The percent correct path detection as a function of path-angle obtained from Experiment 3 for observer L.P. and P.J. Eight path elements created by either luminance, motion or disparity edges created the paths. Filled circles show the results obtained when pairs of attributes alternated along the path. The unfilled squares and triangles show the results obtained in conditions where only one of the attributes were used to create the path and oriented noise elements, and all other elements were unoriented blobs of dots. The dotted lines show the expected probability summation performance in the inter-attribute conditions as calculated from the results obtained in the single attribute conditions with one of the attributes turned off. Actual performance exceeds the performance predicted by probability summation.

The performance is much better than predicted by probability summation as calculated from the results obtained in the single attribute conditions with Eq. (2). So, facilitation of path detection occurs when aligned edges in different attributes are added to different locations along the path. This should be contrasted with the results of Experiments 1 and 2 where no facilitation was found when edges in different attributes were added to the same locations along the path. A possible interpretation of the results is that the path linking process has access to all path elements located at different positions along the path, irrespectively of the attributes (luminance, motion, and disparity contrasts) that defines the path elements. This means that the independent channel hypothesis can be dismissed. These results are contrary to the degradation in performance obtained when colour polarity or contrast alternates along the target path, suggesting colour polarity and contrast selective path linking (McIlhagga & Mullen, 1996).

In the single attribute conditions in Experiment 1 paths were created with eight path elements of the same attribute along the path, while the single attribute paths

in Experiment 3 were created with four path elements interleaved with noise. If the linking process is completely attribute invariant then the percent correct responses in the inter-attribute conditions in Experiment 3 should be between the results obtained from the corresponding single attribute conditions in Experiment 1, with the same number of path elements. Therefore, a comparison was made between the results obtained from single attribute conditions in Experiment 1 and the inter-attribute conditions, with the two corresponding attributes interleaved along the path, in Experiment 3. Comparison with these results obtained for L.P., who participated in both these conditions, reveal an attribute specific component. Path detection was degraded when four path elements of one attribute were interleaved with four path elements of the other attribute (Experiment 3), compared to the two conditions when the corresponding same attributes with eight elements was used along the path (Experiment 1) (Fig. 11). So, the linking process must be able to tell the difference between conditions where alternating attributes and the same attribute is used along the path and cannot be completely attribute

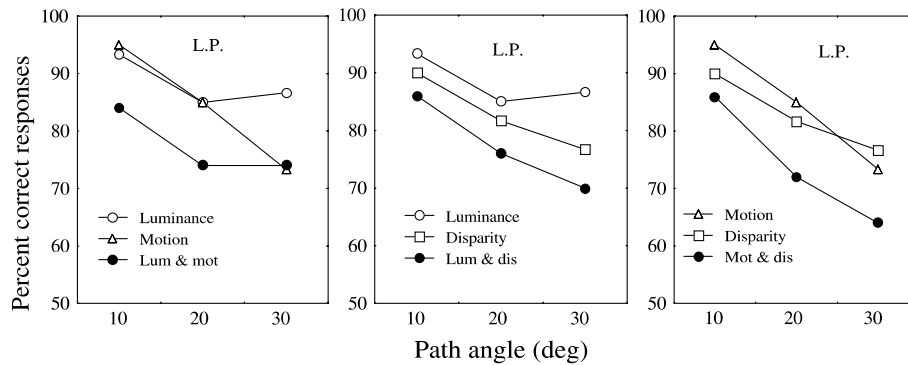


Fig. 11. The results from Experiment 1 (single attribute conditions, unfilled markers) and Experiment 3 (corresponding inter-attribute conditions, filled circles) for L.P. Path detection performance was better when the path elements were created by the same attributes along the path than when they alternated between two attributes along the path. This result demonstrates an attribute specific component in the path linking process.

blind. This suggests the existence of an attribute specific component in the path linking process.

5. General discussion

Experiments 1 and 2 shows that the same rules, limiting the path formation, were used irrespectively of the attributes used to create paths. Increased path angle or element orientation range resulted in similar decrease in performance across the attributes. Closed paths as opposed to open paths have previously been shown to facilitate path detection when luminance contrasts has been used to create the path elements. Experiment 2 showed that this closure effect was attribute invariant for paths created by elements of luminance, motion, and disparity edges. Previous path detection experiments have shown that the loss in performance in contour linking tasks cannot be accounted for by decreased contrast when colour or luminance are used to define the edge elements (Mullen et al., 2000). Likewise, the results of Experiments 1 and 2 showed that adding superimposed edges created in the different attributes did not improve the performance in path detection. In the eyes of the path linking process, suprathreshold edge elements have a specific orientation irrespectively of the contrast or the number of attributes used in conjunction to create the path elements as long as the sampling density is the same. Experiment 3 showed that when the attributes (luminance, motion, and disparity) used to create the oriented micropatterns alternate along the path, its detection is much better than predicted by probability summation of independent channels, derived from conditions when one of the attributes were replaced with unoriented elements. This suggests an attribute invariant component in the path linking process, although it is not complete since performance is better when the same attribute is used along the whole path as in Experiment 1. Interestingly, this is contrary to the results obtained when equiluminant aligned path ele-

ments created by red–green or blue–yellow colour contrasts alternate along the path, then path detection becomes severely degraded compared to when the same colour contrast is used (McIlhagga & Mullen, 1996). This implies that for the path linking process, edges in luminance, motion and disparity are more closely related than colour edges of different colour contrasts.

The results may only apply to foveally presented stimuli since foveal path detection seems to differ from parafoveal path detection when luminance-defined path elements are considered (Hess & Dakin, 1999). In foveal vision there seem to be a linking process operating that connect the activity of orientation sub units. The impoverished performance when presenting the path parafoveally cannot be accounted for by the reduced acuity associated with such presentations. Instead it seems that parafoveal path integration is mediated by the summed activity of cells with the same preferred orientation. Contour linking in peripheral field, beyond 10° of eccentricity, can be accounted for without linking interactions between the segments, simple filtering will suffice (Hess & Dakin, 1999). Thus, it might be that contextual path linking processes are missing in parafoveal regions.

A single filter theory, or a theory with specialised curvature detectors explaining the human performance in foveal path finding tasks would lead to a combinatorial explosion of the number of required filters (Hess & Field, 1999). An alternative solution is that paths are represented by distributed cell activity in the brain. This raises the question of how the brain ‘knows’ which cell activities belong together? Field et al. (1993) proposed an *association field* describing the parameters of an integration field limiting the binding of contours across visual space (Fig. 12). Integration of the activity of cells having non-overlapping receptive fields with similar orientation preferences occurs within this association field and extends across large distances along the main axis of the filters. The parameter space limiting the association field is akin to the rules proposed by Kellman and Shipley (1991) describing the constraints for illu-

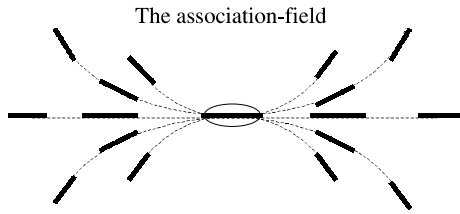


Fig. 12. A schematic illustration of the association field (Field et al., 1993) that specifies the rules limiting perceptual interpolation of oriented elements across visual space. The line segments display possible edge elements in the visual scene. The middle target segment within the oval might be linked with any of the flanking elements as long as at least one segment, aligned with the target, is present in both lobes are aligned and not too distant. The lengths of the flanking bars denote the coupling strength with the middle segment, as can be seen it decreases with distance and curvature. The association field has its neural counterpart in the excitatory connections between orientation selective neurons in primary visual cortex. It also has a counterpart in the statistics of edge occurrences in natural images.

sory contour formation. Similar connections structure has been used in many computational contour completion and contour enhancement models (e.g., Braun, Niebur, Schuster, & Koch, 1994; Grossberg & Mingolla, 1985; Zucker, Dobbins, & Iverson, 1989). The association field also account for the closure effect since orientation selective cells are interconnected along closed loops so activity from closed contours lead to reverberating activity around the loop of interconnected cells (Pettet et al., 1998).

The association field may have its neural underpinning in lateral connections between orientation selective neurons. Existing lateral connections between orientation columns with similar orientation preferences support this idea (e.g., Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Gilbert & Wiesel, 1979; Malach, Amir, Harel, & Grinvald, 1993; Rockland & Lund, 1982). These connections seem to extend a greater distance along the orientation axis than orthogonal to it (Bosking et al., 1997). These results are in line with the psychophysical results from the path detection paradigm. They are also in line with the near threshold facilitation studies of targets that occur when they are superimposed on illusory contours induced by either luminance (Dresp & Bonnet, 1995; Poom, 2001a), texture, motion, or disparity cues (Poom, 2001b). Furthermore, the statistical analysis of the properties of luminance contours in natural images show that edge co-occurrences in such images follow rules that are very similar to the rules of edge linking derived from psychophysical examinations of path detection (Geisler, Perry, Super, & Gallogly, 2001).

To be accounted for by the two-stage model of global contour formation, the possibility that inter-attribute illusory contours and inter-attribute path linking occur in early visual areas require the existence of attribute invariant edge detecting mechanisms. The tilt illusion has been used as a tool for gathering psychophysical

evidence for such attribute invariant edge detecting mechanisms in cortical areas V1 and/or V2 (Poom, 2000). Neurophysiological and psychophysical results taken together provide evidence that the tilt repulsion effect is mediated by lateral inhibition of orientation selective cells in cortical area V1 and/or V2 (e.g., Wenderoth & Johnstone, 1987). This illusion occurs irrespectively whether the inducing grating and test bar is created by luminance, motion or disparity contrasts, and it also occurs when different attributes are used to create the inducer and the test bar, suggesting attribute invariant orientation detection in these areas (Poom, 2000). Rivest and Cavanagh (1995) also found integration of edge information at a common site in an edge localisation paradigm. Further evidence for attribute invariance in early visual areas comes from neurophysiological results showing that cells signalling edge orientation and polarity (i.e., border ownership) in random-dot stereograms exist in area V2 (von der Heydt, Zhou, & Friedman, 2000). At least some of these cells also code the border ownership for luminance-defined edges that is part of a figure (Zhou, Friedman, & von der Heydt, 2000). It is also known that cells in primate visual cortex respond to the orientation of edges created by luminance and relative motion (Marcar et al., 1992), and cells in area V1 respond to stereoscopic edges (e.g., Poggio & Poggio, 1984) and signal partially occluded edges (Sugita, 1999). Contextual modulation of the responses of cells in these areas has also been shown since neuronal activity induced by illusory contours has been found in early cortical areas such as V2 (von der Heydt, Peterhans, & Baumgartner, 1984), and V1 (Seghier et al., 2000; Sheth, Sharma, Rao, & Sur, 1996).

Previous studies have revealed a luminance-contrast sign dependent component in the path linking process (Field et al., 1997), and failure of the linking when aligned path elements are created by alternating colour contrasts or polarity along the path (McIlhagga & Mullen, 1996). The motion contrast and depth contrast in the stimuli used here was of the same sign along the motion and disparity-defined paths in all experiments and coherent unidirectional motion was used for the motion-defined elements. This raises questions to be addressed in future studies, namely if the path linking process is sensitive to the sign of depth, motion contrast, and motion direction reversals along the path? Such sensitivity would make ecological sense since parts of the same object usually moves coherently and are located at the same depths.

6. Concluding remarks

Correlated retinal image properties steer the development of the visual brain. Retinal activity tends to be correlated along edges and such edges are common in

natural images. Therefore, based on natural environmental stimulation, edge detectors develop driven by the Hebbian learning rule ‘cells that fire together wire together’. Edges that belong to the rim of objects as opposed to edges intrinsic to objects such as surface texture may often be defined by contrasts in several attributes such as luminance, motion, and disparity. Therefore it is probable that, driven by Hebbian learning rules, cells develop that are selectively sensitive to the orientation of edges irrespectively of the attribute that define the edge, i.e. attribute invariant edge detectors. Similarly, ecological constraints cause edges in images to be roughly aligned (Geisler et al., 2001). This constraint makes cells with roughly aligned orientation preferences to be more strongly coupled than cells with other orientation preferences. Such developmental mechanisms may drive the neural substrate to be sensitive to contextual modulations in the image and mediate the pop out of global features as described by the Gestalt laws and the association field proposed by Field et al. (1993). Thus it seems likely that the development of the neural underpinning of the association field may be driven by correlated natural-image properties binding attribute-invariant edge detectors that have roughly aligned orientation preferences.

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References

- Beck, J., Rosenfeld, A., & Ivry, R. (1989). Line segregation. *Spatial Vision*, 4, 75–101.
- Bocking, W. H., Zhang, Y., Schofield, B., & Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in three shrew striate cortex. *The Journal of Neuroscience*, 17, 2112–2127.
- Braun, J., Niebur, E., Schuster, H. G., & Koch, C. (1994). Perceptual contour completion: a model based on local, anisotropic, fast-adapting interactions between oriented filters. *Society for Neuroscience Abstracts*, 20, 1665.
- Cavanagh, P., & Mather, G. (1990). Motion: the long and short of it. *Spatial Vision*, 4, 103–129.
- Dresp, B., & Bonnet, C. (1995). Subthreshold summation with illusory contours. *Vision Research*, 35, 1071–1078.
- Dresp, B., & Grossberg, S. (1997). Contour integration across polarities and spatial gaps: from local contrast filtering to global grouping. *Vision Research*, 37, 913–924.
- Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: evidence for a local ‘association field’. *Vision Research*, 33, 173–193.
- Field, D. J., Hayes, A., & Hess, R. F. (1997). The role of phase and contrast polarity in contour integration. *Investigative Ophthalmology and Visual Science*, 38(Suppl.), S999.
- Geisler, W. S., Perry, J. S., Super, B. J., & Gallogly, D. P. (2001). Edge co-occurrences in natural images predicts contour grouping performance. *Vision Research*, 41, 711–724.
- Gilbert, C. D., & Wiesel, T. N. (1979). Morphology and intracortical connections of functionally characterised neurons in the cat visual cortex. *Nature*, 280, 120–125.
- Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: boundary completion, illusory figures and neon color spreading. *Psychological Review*, 92, 173–211.
- Heitger, F., & von der Heydt, R. (1993). A computational model of neural contour processing: figure-ground segregation and illusory contours. In *Proceedings of the 4th International Conference on Computer Vision, Berlin*. Los Almitos, CA: IEEE Computer Society Press.
- Hess, R. F., & Dakin, S. C. (1999). Contour integration in the peripheral field. *Vision Research*, 39, 947–959.
- Hess, R. F., & Field, D. J. (1995). Contour integration across depth. *Vision Research*, 35, 1699–1711.
- Hess, R. F., & Field, D. (1999). Integration of contours: new insights. *Trends in Cognitive Sciences*, 3, 480–486.
- Hess, R. F., Hayes, A., & Kingdom, F. A. A. (1997). Integrating contours within and through depth. *Vision Research*, 37, 691–696.
- Julesz, B. (1964). Binocular depth perception without familiarity cues. *Science*, 145, 356–362.
- Kanizsa, G. (1955). Margini quasi-percettivi in campi con stimolazione omogenea. *Rivista di Psicologia*, 49, 7–30. Also translated in: In S. Petry & G. E. Meyer (Eds.), *The perception of illusory contours* (pp. 40–49). New York: Springer.
- Kaplan, G. A. (1969). Kinetic disruption of optical texture: the perception of depth at an edge. *Perception and Psychophysics*, 6, 193–198.
- Kellman, P. J., & Shippley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, 23, 141–221.
- Koffka, K. (1935). *Principles of Gestalt psychology*. New York: Harcourt Brace Jovanovich.
- Kovacs, I., & Julesz, B. (1993). A closed curve is much more than an incomplete one. *Proceedings of the National Society of Sciences USA*, 90, 7495–7497.
- Köhler, W. (1940). *Dynamics in Psychology*. New York: Liveright.
- Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *The Journal of Neuroscience*, 7, 3416–3468.
- Malach, R., Amir, Y., Harel, M., & Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. *Proceedings of the National Academy of Sciences USA*, 90, 10469–10473.
- Marcar, V. L., Raiguel, S. E., Xiao, D., Maes, H., & Orban, G. A. (1992). Do cells in area V2 respond to the orientation of kinetic boundaries. *Society for Neuroscience Abstracts*, 18, 1275.
- Marr, D. (1982). *Vision*. San Fransisco, CA: W.H. Freeman & Co.
- McIlhagga, W. H., & Mullen, K. T. (1996). Contour integration with color and luminance contrast. *Vision Research*, 36, 1265–1279.
- Mullen, K. T., Beaudot, W. H. A., & McIlhagga, W. H. (2000). Contour integration in color vision: a common process for the blue–yellow, red–green and luminance mechanisms? *Vision Research*, 40, 639–655.
- Parent, P., & Sucker, S. W. (1989). Trace inference, curvature consistency and curve detection. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 11, 823–839.
- Pettet, M. W., McKee, S. P., & Grzywacz, N. M. (1998). Constraint on long range interactions mediating contour detection. *Vision Research*, 38, 865–879.
- Poggio, G. F., & Poggio, T. (1984). The analysis of stereopsis. *Annual Review of Neuroscience*, 7, 379–412.

- Poom, L. (2000). Inter-attribute tilt effects and orientation analysis in the visual brain. *Vision Research*, 40, 2711–2722.
- Poom, L. (2001a). Visual inter-attribute contour completion. *Perception*, 30, 855–865.
- Poom, L. (2001b). Visual summation of luminance lines and illusory contours completed between pictorial, motion, and disparity cues. *Vision Research*, 41, 3805–3816.
- Regan, D. (1999). *Human perception of objects: Early visual processing of spatial form defined by luminance, color, texture, motion and binocular disparity*. Sinauer Associates, US.
- Rivest, J., & Cavanagh, P. (1995). Localization of contours defined by more than one attribute. *Vision Research*, 36, 53–66.
- Rockland, K. S., & Lund, J. S. (1982). Widespread periodic intrinsic connections in the tree shrew visual cortex. *Science*, 215, 1532–1534.
- Roskies, A. L. (1999). The binding problem. *Neuron*, 24, 7–9.
- Seghier, M., Dojat, M., Delon-Martin, C., Rubin, C., Warnking, J., Segebarth, C., & Bullier, J. (2000). Moving illusory contours activate primary visual cortex. *Cerebral Cortex*, 10, 663–670.
- Sheth, B. R., Sharma, J., Rao, S. C., & Sur, M. (1996). Orientation maps of subjective contours in visual cortex. *Science*, 274, 2110–2115.
- Smits, J. T. S., Vos, P. G., & van Oeffelen, M. P. (1985). The perception of a dotted line in a noise: a model of good continuation and some experimental results. *Spatial Vision*, 1, 163–177.
- Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. *Nature*, 401, 269–272.
- Uttal, W. R. (1975). *An autocorrelation theory of form perception*. New York: Wiley.
- von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, 224, 1260–1262.
- von der Heydt, R., Zhou, H., & Friedman, H. S. (2000). Representation of stereoscopic edges in monkey visual cortex. *Vision Research*, 40, 1955–1967.
- Wehrhahn, C., & Dresch, B. (1998). Detection facilitation by collinear stimuli in humans: dependence on strength and sign of contrast. *Vision Research*, 38, 423–428.
- Wenderoth, P., & Johnstone, S. (1987). Possible neural substrates for orientation analysis and perception. *Perception*, 16, 693–709.
- Yen, S., & Finkel, L. H. (1998). Extraction of perceptually salient contours by striate cortical networks. *Vision Research*, 38, 719–742.
- Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *The Journal of Neuroscience*, 20, 6594–6611.
- Zipser, K., Lamme, V. A. F., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *The Journal of Neuroscience*, 16, 7376–7389.
- Zucker, S. W., Dobbins, A., & Iverson, L. (1989). Two stages of curve detection suggest two styles of visual computation. *Neural Computation*, 1, 68–81.