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Long-range spatial integration across contrast signs: a probabilistic mechanism ?

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ABSTRACT

It is widely assumed that the integration of orientation contrast across spatial gaps within the long-range regime is not selective to the contrast sign of the individual stimuli. Probabilistic models of perceptual integration, however, suggest that long-range spatial integration should be, if not selective, at least sensitive to local contrast signs. To clarify this issue, we tested predictions of a model based on conditional probabilistic weights of identical and opposite contrast signs in a simple spatial configuration of two co-linear lines. Contrast detection thresholds of the target line presented either by itself (control condition) or simultaneously with the co-linear inducer (test condition) were measured. The contrast sign of targets and inducers was varied so that all four possible combinations of signs were produced in the test conditions: 1) dark target with dark inducer, 2) dark target with bright inducer, 3) bright target with bright inducer and 4) bright target with dark inducer. The contrast intensity (Weber ratio) of dark and bright inducers was identical. The coaxial distance between target and inducer was constant in each of two experiments, testing for two distances that corresponded to an angular separation within the long-range domain of spatial integration as defined previously. It is found that targets and inducers with identical contrast signs produce significantly stronger facilitating effects on detection than stimuli with opposite signs. The data closely match predictions consistent with those of a probabilistic model of line contrast integration across spatial gaps and contrast signs within the long-range regime.

1. INTRODUCTION

It is well established that the contrast detection of dots, line stimuli or Gabor patches (*targets*) is facilitated by the presence of a co-linear line or Gabor patch (*inducers*). Such facilitating interactions between co-linear stimuli in visual contrast integration have been found in psychophysical studies on humans (e.g. Polat & Sagi, 1993; 1994 a, Dresp, 1993, Tzvetanov & Dresp, 2002, Li & Gilbert, 2002) and on the awake monkey (Kapadia, Ito, Gilbert, & Westheimer, 1995). It is assumed that lateral interactions between neurons in primary visual cortex are the physiological substrate of these effects (e.g. Kapadia et al., 1995, Gilbert, 1998, Polat, 1999), which appear to exhibit functional characteristics of visual learning (Polat & Sagi, 1994 b, Dresp, 1998, Adini, Tsodyks & Sagi, 2002, Li & Gilbert, 2002), possibly enabled by structure - specific (i.e. selective) cortical plasticity (e.g. Gilbert, 1998).

1.1. Contrast integration across spatial gaps and contrast signs

The spatial separation of co-linear stimuli and their contrast sign influence facilitating interactions. With coaxial gaps smaller than approximately 20 minutes of visual arc (*arcmin*) between a target and an inducer, stimuli with the same contrast sign produce facilitating interactions; with coaxial gaps larger than 20 arcmin, combinations of stimuli of either contrast sign also produce noticeable contrast detection facilitation (Polat & Sagi, 1993, Morgan & Dresp, 1995; Wehrhahn & Dresp, 1998). Similar observations have been reported from orientation discrimination experiments with co-linear lines and Gabor patches (Brincat & Westheimer, 2000). These findings lend strong support to models which assume the existence of two stages, or functional regimes, of visual spatial integration: a *short-range regime* that is sensitive to local characteristics of visual stimuli such as their contrast signs, and a *long-range regime* that disregards local stimulus properties, such as the sign of contrast, and is sensitive only to the global configuration (e.g. Grossberg & Mingolla, 1985). The long-range regime of visual spatial integration describes a stage of processing that is critical to form and object perception,

since it generates the grouping of contour information across space, the emergent segmentation of features, and the figure-ground segregation of shapes.

Recent work by Tzvetanov & Dresch (2002) suggests that the spatial limit of the long-range regime of integration of two co-linear lines of a given length, presented on plain backgrounds, may extend to a co-axial target-inducer separation of 150 arcmin. Moreover, data from psychophysical experiments by Li & Gilbert (2002), with co-linear line targets and inducers presented on noisy backgrounds, suggest that the spatial limits of long-range integration are situated within a dynamic range of co-linear separations and may depend on training, or visual learning.

1.2. How “insensitive” is long-range spatial integration to the contrast sign of stimuli?

Assessing whether parts belong to one and the same or to different objects in the visual field is one of the major tasks the human perceptual system has to accomplish. While two-stage integration models such as those referred to above use the working hypothesis that local information of contrast sign is irrelevant to visual grouping across larger gaps between stimuli activating the long-range regime of spatial integration, other models assume that whether a given information carried by a stimulus is relevant or not to this integration or grouping process is determined by probabilistic mechanisms.

Feldman (2001) suggested that contour grouping relies on a probabilistic process by which spatial information from co-linear stimuli in the visual field is computed on the basis of likelihood estimates. In his model, spatial integration is defined as a process that makes decisions which, under conditions of uncertainty, are based on conditional probabilities associated with any event that may be critical to the perceptual interpretation of a visual scene or a stimulus. Feldman successfully applied Bayesian probability theory to perceptual judgements as to whether a given configuration of dots may form a smooth contour or not.

Extended to other situations, such as those where such a probabilistic process would have to decide whether two separate lines in the visual field form a contour or not, identical lines with constant spatial separation and the same contrast sign, for example, would be given equal probabilistic weights; objects with otherwise identical properties

and constant separation, but opposite contrast signs, would be given different, conditional probabilistic weights. A probabilistic model would, in this case, imply that spatial contrast integration, or visual grouping, is sensitive to the contrast sign of stimuli.

As mentioned earlier, psychophysical data on facilitating interactions between co-linear targets and inducers in contrast detection tend to support the view that the long-range regime of spatial integration, the one supposed to generate visual grouping and the formation of object contours, is not sensitive to the contrast sign of stimuli. However, phenomenal observation suggests that configurations consisting of stimuli with opposite contrast signs produce less salient visual groups compared with configurations consisting of stimuli with identical sign (Fig 1). Recently, Tzvetanov (2003) found results showing that co-linear targets and inducers with identical contrast signs systematically produce stronger facilitating interactions than stimuli with opposite contrast polarities in a contrast detection task activating the spatial regime of long-range line contrast integration (i.e. coaxial separations larger than 20 arcmin between target and inducer). The differences in thresholds found were small, but systematic for two out of three observers. How insensitive is the long-range regime of spatial integration to the contrast sign of stimuli ? Given that the studies on facilitating long-range spatial interactions mentioned above concern data obtained with relatively small numbers of subjects, generally not more than three or four, it may be possible that a sensitivity to contrast sign exists, but could not be brought to the fore because a much larger sample of observations would have been required to do so.

1.3. Is long-range spatial integration across contrast signs influenced by a probabilistic mechanism ?

If long-range grouping of visual stimuli is sensitive to the contrast sign of stimuli, significant differences in contrast detection thresholds for targets and inducers of identical sign and thresholds for targets and inducers of opposite signs should be found with a sufficiently large number of subjects and observations. The next question to be addressed then, is which kind of mechanism or process would account for such a

sensitivity to contrast sign. As mentioned above, probabilistic mechanisms of visual spatial integration (e.g. Feldman, 2001) qualify as potential candidates.

To find out whether long-range spatial integration across contrast signs is consistent with a probabilistic model, it would have to be shown that facilitating long-range spatial interactions between co-linear targets and inducers can be “probabilistically” predicted. Here, we propose to test a simple model for visual grouping across co-linear space and contrast signs that associates mathematically and functionally plausible, conditional probabilistic weights with two stimuli of either identical or opposite contrast sign. Our study deals with contrast detection experiments designed to measure, or probe, contour integration or grouping. This is achieved by comparing the detection thresholds of line targets presented alone to thresholds of targets presented with a co-linear inducer. The relative facilitation magnitude generated by the presence of the inducer is computed as follows: a detection threshold ratio is obtained by dividing the threshold for the detection of the target presented with the co-linear inducer (d_1) by the threshold for the detection of the target presented without the inducer (d_2). The relative magnitude or amount of spatial facilitation (A) produced by the inducer on the detection of a co-linear target of either sign is obtained by subtracting the detection threshold ratio (R) from 1.

We consider a straightforwardly probabilistic model for a simple spatial configuration of one target and one co-linear inducer of identical length, with constant co-axial separation within the spatial limits previously defined as the long-range regime of integration (e.g. Wehrhahn & Dresch, 1998, Brincat & Westheimer, 2000, Tzvetanov & Dresch, 2002). The wider theoretical background of the model is that of probabilistic theory in general, and that of likelihood ratios, or conditional probabilistic weights, associated with conditions of visual stimulation (e.g. Knill & Richards, 1996), in particular. To generate quantitative predictions, we start by defining a deterministic case of contour grouping where the likelihood that the local elements will produce spatial facilitation, i.e. will group, corresponds to a probability of $p = 1$. With two co-linear lines, such a case would be that of a target and an inducer with equal length and polarity, separated by a spatial gap that is empirically known to produce grouping or spatial facilitation. When no further variations occur in such a configuration, or in the conditions

under which it is presented, its conditional probabilistic weight takes a theoretical, empirically justified, value of $pw = 1$. This conditional probabilistic weight changes when further variations are introduced in the initial spatial configuration, or in the conditions under which it is presented. For example, if half of the spatial configuration defined by the two co-linear lines is given the other sign, the conditional probabilistic weight of the new configuration is reduced to half that of the initial condition. This reduction is, in fact, the mathematical consequence of the assumption that contrast sign influences grouping or spatial facilitation through a probabilistic mechanism, with a likelihood ratio of 1/1 for the integration of a single contour across a single sign, and a likelihood ratio of 1/2 for the integration of a single contour across two signs, all other things, such as spatial separation or inducer contrasts, being equal.

This way of reasoning is novel in the domain of contrast detection studies, where the usual models use summative or multiplicative mechanisms. In fact, if we simply consider the visual brain as a machine that has to make a decision whether to group two lines into a single one or not, it becomes clear that, under conditions of optimal spatial separation, it will readily group two lines of identical polarity into a single line by producing an integrated neural firing pattern coding for that polarity. When these two lines are given opposite polarity, the visual brain has to make a further decision. This consists of choosing, out of two possibilities, the polarity to be coded for by the grouped response given that an integrated firing pattern cannot code for two polarities at the same time. When only half of the configuration that is to be grouped signals for the polarity that will be chosen, then the resulting, integrated firing rate should only be half the initial rate. This would mean that the overall grouping power of the configuration is reduced to half that of the initial configuration with the single sign. This then leads to the hypothesis that the amount of psychophysical spatial facilitation produced by the configuration with two different contrast polarities would be only half that produced by the initial configuration.

The relative magnitude (A) of spatial facilitation produced by a configuration of co-linear targets and inducers depending on its conditional probabilistic weight (pw) is then predicted by

$$A = (I - R) \times pw;$$

the probabilistic weight of a configuration of two stimuli with only one contrast sign is, as explained above, considered to be $pw = 1$. The probabilistic weight of a configuration with two stimuli carrying opposite contrast signs, given that the two stimuli possess equal length and constant separation, corresponds to the weight of the configuration with a single sign divided by two, $pw = 1/2$, as explained above. The relative amount of spatial facilitation generated by a configuration with a single contrast sign is then predicted by

$$A_I = (I - R) \times I$$

and the relative magnitude of spatial facilitation generated by configurations with the two opposite contrast signs by

$$A_2 = A_I \times I/2$$

To test these predictions, we designed a contrast detection experiment where a line target was presented with and without a co-linear line inducer of identical length and with constant co-axial separation. The goal of the study was to clarify whether:

- 1) Long-range spatial integration of colinear lines is sensitive to the contrast sign of the individual stimuli. If such an assumption holds, co-linear lines of identical contrast sign would be expected to produce significantly stronger facilitation than co-linear lines of opposite sign.
- 2) The long-range regime of spatial integration generates constant facilitatory interactions between co-linear targets and inducers (e.g. Tzvetanov & Dresch, 2002). This would lead to the prediction that any effect of contrast sign should be of similar magnitude for any target-inducer separation that falls within the long-range spatial regime.

- 3) The magnitude of the effect of contrast sign on long-range spatial integration in a sufficiently simple spatial configuration is predicted by the average absolute magnitude of spatial facilitation multiplied by a probabilistic weight, as given above.

2. METHODS

We measured contrast detection thresholds of a line target presented foveally for a brief duration on a computer screen, either by itself (control condition) or simultaneously with a co-linear line, the so-called inducer (test condition). The contrast sign of target line and inducer was varied so that all four possible combinations of signs were produced in the test conditions: 1) dark target with dark inducer, 2) dark target with bright inducer, 3) bright target with bright inducer and 4) bright target with dark inducer. The contrast intensity (Weber ratio) of dark and bright inducers was identical. The coaxial distance between target and inducer was constant in each of the two experiments, each corresponding to an angular target-inducer separation within the long-range domain of spatial integration, as defined previously in the literature (e.g. Wehrhahn & Dresch, 1998, Brincat & Westheimer, 2000, Tzvetanov & Dresch, 2002). In a first experiment, we tested all of the 20 observers for a coaxial target-inducer separation of 25 arcmin. To confirm that similar results are obtained at a larger target-inducer separation within the long-range spatial regime, we tested four of these 20 observers for a co-axial target-inducer separation of 80 arcmin.

2.1. Subjects

20 young volunteers with normal or corrected-to-normal vision participated in the first experiment. All subjects were asked to accomplish a given experiment in two successive afternoon sessions. The first afternoon session served as a training session. Four of these 20 observers then participated in the second experiment with the larger

target-inducer separation. This corresponded to two more, successive afternoon sessions for each of these four subjects.

2.2. Training

For training, each observer had to accomplish a full set of test and control conditions, presented in random order, on the first afternoon of a given experiment. This corresponded to 240 trials per experimental condition, with four test conditions and one control for each target polarity, representing a total of 1440 training trials per observer. Individual data from the training session were analyzed to check whether a given observer was able to produce consistent data within a given experimental condition. Observers who failed to produce acceptable psychometric functions, or who found it difficult to concentrate during the task, were not asked to participate in the experimental session the following afternoon.

2.3. Stimuli

The line stimuli were generated by an IBM compatible PC equipped with a graphic card (VGA Trident), and presented on a monochrome computer screen with a 60 Hz frame rate and a resolution of 640x480 pixels. For the measurement of contrast thresholds for the detection of the target line, six different luminance levels were generated by combinations of RGB signals, calibrated with a MINOLTA photometer. In the case of the bright target line, these luminance levels corresponded to 14.2, 14.5, 14.8, 15.1, 15.4 and 15.7 cd/m²; in the case of the dark target line, to 9.8, 9.5, 9.2, 8.9, 8.6 and 8.3 cd/m². The luminance of the background on which the lines were presented was 12 cd/m². The luminance of the co-linear inducer was 16 cd/m² in the case of the dark inducer, and 8 cd/m² in the case of the bright inducer. Target lines and co-linear inducers had an equal angular length of 20 arcmin, an equal width of one arcmin, and were separated by a coaxial gap of 25 arcmin in the first experiment, and by a coaxial gap of 80 arcmin in the second experiment.

2.4. Procedure

A stimulus presentation, or trial, corresponded to two successive stimulus intervals separated by a temporal delay of 200 milliseconds, with the target presented randomly during either the first or the second stimulus interval. The inducer was presented in both stimulus intervals in the test conditions. Targets and inducers were preceded by a brief sound, and presented for about 32 milliseconds in a given stimulus interval. They were presented simultaneously in stimulus intervals containing an inducer and a target. In a given trial block, the six different luminance levels of the target were presented 40 times in a random order according to the method of constant stimuli. A two-alternative temporal forced-choice procedure was employed, where observers had to press one of two possible keys on the computer keyboard to indicate whether they had seen the target in the first or the second of the two successive stimulus intervals. A new trial was initiated 800 milliseconds after a response had been given.

3. RESULTS

The individual data produced by observers in the experimental session on the second afternoon of a given experiment were used for further analysis. In a first step, thresholds for the detection of the target lines in the different conditions described above were determined. Each threshold estimate was based on a total number of 240 (6x40) trials. The percentage, or probability (p), of correct detection of the target line was calculated for each observer and each experimental. These probabilities were transformed ($\ln(p/1 - p)$) to produce linear psychometric functions ($y = ax - b$) of the absolute difference between the luminance of the target line and the luminance of the background. Detection thresholds (x) were calculated on the basis of the parameters of the individual psychometric functions obtained for each experimental condition ($x = (y + b)/a$). The detection threshold here corresponds to $p = 0.75$, which gives $\ln = 1.09$ on the ordinate (y) of the psychometric function.

On the basis of these individual thresholds, the detection threshold ratio (R), comparing the threshold measured with a colinear inducer against the threshold measured in the no-inducer situation in a given experimental condition, was computed. This ratio is obtained by dividing the threshold for the detection of the target presented with the colinear inducer (d_1) by the threshold for the detection of the target presented without the inducer (d_2). The relative amount or magnitude of spatial facilitation (A) produced by an inducer of a given sign on the detection of a co-linear target of a given sign was computed by subtracting the threshold ratios (R) from 1.

3.1. Target-inducer separation of 25 arcmin

Figure 2 shows relative magnitude of facilitation in the four experimental conditions for each of the 20 observers, identified by their initials. The data reveal that, occasionally, a specific configuration of opposite contrast signs may produce a relative amount of facilitation that is similar or identical to the magnitude produced by a configuration of identical sign. However, configurations with a single contrast sign generally tend to produce greater relative magnitudes of facilitation than configurations with the two opposite contrast signs.

The average A produced by a bright inducer on the detection of a bright target is 0.29 with a standard error of 0.013 ($N=20$), and the average A produced by a dark inducer on the detection of a dark target is 0.28 with a standard error of 0.020 ($N=20$). This gives an average relative amount or magnitude of facilitation (A_1) of 0.285 and a standard error of 0.0165 ($N=40$) for configurations consisting of stimuli with identical contrast signs. The average A produced by a bright inducer on the detection of a dark target is 0.14 with a standard error of 0.016 ($N=20$), and the average A produced by a dark inducer on the detection of a bright target is 0.12 with a standard error of 0.014 ($N=20$). This gives an average magnitude of facilitation (A_2) of 0.13 and a standard error of 0.015 ($N=40$) for configurations consisting of targets and inducers with opposite contrast signs.

Figure 3 represents the average relative amount of facilitation plotted for each of the 20 observers and the two combinations of contrast signs in the stimulus configurations. The graph shows that the configurations with a single contrast sign

systematically produce stronger facilitation than the configurations with the two opposite contrast signs. This effect of the contrast sign of the stimuli on the amount of facilitation was found to be statistically significant ($T(1,78) = 9.7598$; $p < .001$)).

3.2. Target-inducer separation of 80 arcmin

Figure 4 shows relative magnitudes of facilitation in the four experimental conditions for each of the four observers, identified by their initials. The data reveal that configurations with a single contrast sign generally tend to produce greater magnitudes of facilitation than configurations with the two opposite contrast signs. The effects are similar to those obtained with a target-inducer separation of 25 arcmin.

The average A produced by a bright inducer on the detection of a bright target is 0.25 with a standard error of 0.017 ($N=4$), and the average A produced by a dark inducer on the detection of a dark target is 0.30 with a standard error of 0.044 ($N=4$). This gives an average relative amount of facilitation (A_1) of 0.275 and a standard error of 0.03 ($N=8$) for configurations consisting of stimuli with identical contrast signs. The average A produced by a bright inducer on the detection of a dark target is 0.14 with a standard error of 0.036 ($N=4$), and the average A produced by a dark inducer on the detection of a bright target is 0.16 with a standard error of 0.035 ($N=4$). This gives an average magnitude of facilitation (A_2) of 0.15 and a standard error of 0.0355 ($N=8$) for configurations consisting of targets and inducers with opposite contrast signs.

Figure 5 shows the average relative magnitude of facilitation for each of the four observers and the two combinations of contrast signs in the stimulus configurations. Again, the configurations with a single contrast sign systematically produce stronger facilitation than the configurations with the two opposite contrast signs. The effect of the contrast sign of the stimuli on the amount of facilitation at a target-inducer separation of 80 arcmin is statistically significant ($T(1,14) = 4.190$; $p < .01$)).

3.3. Probabilistic model

The psychophysical data were compared with the probabilistic model given above for a simple configuration of one line target and one co-linear line inducer of identical size with constant co-axial separation in the long-range regime of spatial integration. In the model, the probabilistic weight (pw) of a target-inducer configuration with a single contrast sign is considered to be maximal ($pw = 1$). This leads to the prediction that the probabilistic weight of a target-inducer configuration with the two, opposite contrast signs would be expected to be half that amount ($pw = 1/2$). The relative amount or magnitude of facilitation (A) multiplied by the conditional probabilistic weight (pw) of the configuration producing that magnitude predicts the effect of the sign of contrast of the stimuli. In the model as given above, the psychophysical result for a target-inducer configuration with the two, opposite contrast signs is predicted by

$$A_2 = A_1 \times 1/2$$

which gives

$$A_2 = 0.285 \times 1/2$$

in the case of the target-inducer separation of 25 arcmin with thresholds from 20 observers. This gives a hypothetical relative magnitude of facilitation of 0.1425 for target- inducer configurations with opposite contrast signs. The theoretical value differs by only 0.0125 from the observed average value, given above, for this condition. Such a difference represents less than the standard error for the condition with targets and inducers with opposite contrast signs. The model, therefore, produces statistically reliable predictions of the psychophysical observations. The dotted horizontal line in the graph shown in Figure 3 indicates the predicted A_2 for targets and inducers of opposite contrast sign, the straight horizontal line indicates the average A_2 as observed in the experiment.

The prediction for a target-inducer configuration with opposite contrast signs and a target-inducer separation of 80 arcmin is

$$A_2 = 0.275 \times 1/2$$

This gives a hypothetical relative magnitude of facilitation of 0.1375 for target-inducer configurations with opposite signs. This theoretical value differs by 0.0125 from the observed average value, given above, for this condition. The difference between prediction and data obtained with four observers for a target-inducer separation of 80 arcmin represents less than the standard error, given above, for the condition with targets and inducers with opposite contrast signs. The probabilistic model, again, is shown to produce statistically reliable predictions. The dotted horizontal line in the graph represented by Figure 5 indicates the predicted A_2 for targets and inducers of opposite contrast sign, the straight horizontal line indicates the average A_2 as observed in the experiment.

4. DISCUSSION

Our observations unambiguously show that long-range spatial integration of visual information across co-linear space and contrast signs is sensitive to the contrast sign of stimuli. They therefore clarify that, provided a sufficiently large number of observations is collected with a sufficiently large sample of trained observers, co-linear targets and inducers of identical contrast sign are found to generate significantly stronger long-range spatial facilitation in a line contrast detection task than stimuli with opposite contrast signs, although thresholds in the two conditions can be similar or identical for a given individual in a given experiment. In addition, our observations confirm that any combination of contrast signs produces exclusively facilitating interactions between co-linear targets and inducers for target-inducer separations within the limits of the long-range spatial regime of integration. Therefore, they are basically consistent with earlier conclusions from similar experiments, conducted with considerably smaller numbers of observers, that long-range spatial integration is not selective to the contrast sign of co-linear stimuli (e.g. Dresp & Grossberg, 1997; Wehrhahn & Dresp, 1998; Dresp, 1999; Brincat & Westheimer, 2000). However, our data clarify that “non-selectivity” to contrast

sign does not imply “insensitivity”. They thus reveal an important, new aspect of long-range spatial interactions which has theoretical implications with regard to certain two-stage models which claim that the second stage of visual spatial integration, also referred to as the grouping stage or the long-range spatial regime, disregards the contrast signs of the individual stimuli of a spatial configuration (e.g. Prazdny, 1983; Grossberg & Mingolla, 1985).

4.1. Implications for two-stage models of spatial grouping

Two-stage models of grouping, such as that suggested by Grossberg & Mingolla (1985), claim that the short-range, or first stage of processing of visual spatial information, is selective to local stimulus properties such as their contrast sign, whereas the long-range, or second stage of integration, which operates across larger spatial gaps, would be selective to configurational properties only. This theoretical assumption seemed justified by the argument that, in order to achieve coherent global percepts, long-range grouping needs to eliminate local contrast signs via some kind of summative mechanism (e.g. Prazdny, 1983; Grossberg & Mingolla, 1985; Reid & Shapley, 1988). Such a rationale is supported by evidence that contour grouping operates efficiently across opposite contrast signs (e.g. Field, Hayes, & Hess, 1993), and that various phenomena of perceptual interpolation, including the one seen in figures with illusory contours, are as strong in spatial configurations of opposite contrast signs as in configurations of a single sign (e.g. Prazdny, 1983; 1985, Dresch, Bonnet, & Salvano-Pardieu, 1996). However, although the assumption of a non-selectivity of long-range grouping to local contrast signs does clearly hold, the claim that information of contrast polarity is completely irrelevant (e.g. Brincat & Westheimer, 2000), or eliminated by summative mechanisms (Grossberg & Mingolla, 1985) at that stage of processing, cannot be sustained in the light of our present findings. The fact that a simple spatial configuration of two identical co-linear lines with opposite contrast signs is shown to have half the weight of that of two identical lines of the same sign in the genesis of facilitating interactions is consistent with a probabilistic mechanism of spatial integration across contrast signs. Such a mechanism would preserve the relative weight of a given contrast sign at the long-range stage of

integration rather than completely eliminate differences in polarity. This is consistent with a probabilistic theory of contour vision, like that suggested by Feldman (2001), which is based on Bayesian probability theory applied to visual perception (e.g. Knill & Richards, 1996).

4.2. Probabilistic contour integration

Feldman (2001) argued that a probabilistic theory of contour integration requires an explicit model, in terms of appropriate likelihood functions or probabilistic weights, of the alternative grouping hypotheses that are possible for a given configuration. He proposed conditional likelihood functions that successfully predict explicit grouping of individual dots into a smooth contour, or which grouping interpretation is likely to be chosen by a human observer when a dot configuration is ambiguous, and can be grouped into either a single or two distinct virtual lines. The model we propose here is consistent with such a probabilistic approach, but applies to a different kind of perceptual task. In spatial contrast integration studies, which are designed to study visual grouping across co-linear space (e.g. Polat & Sagi, 1993; 1994 a, b, Dresch, 1993, Tzvetanov & Dresch, 2002), observers are not asked to judge how co-linear elements would group, but their grouping potential is inferred from the magnitudes of facilitating spatial interactions between co-linear elements. Here, for the simplest possible configuration of two co-linear lines, we apply a simple probabilistic combination rule with mathematically coherent probabilistic weights attached to configurations of identical and opposite contrast signs. These probabilistic weights successfully predict the magnitude of facilitating spatial interactions between co-linear lines with opposite contrast signs in comparison with facilitating interactions between lines of identical sign. Such local spatial interactions have been identified as probes for the neurophysiological substrates of contour grouping (e.g. Kapadia et al., 1995). They involve visual cortical plasticity, as shown recently in the studies by Adini et al. (2002) and Li & Gilbert (2002).

4.3. The spatial boundaries of long-range contour integration and the influence of visual plasticity

The present findings, by revealing similar magnitudes of spatial facilitation for coaxial target inducer separations of 25 and 80 arcmin, suggest that the effect of contrast sign on local contour interactions is likely to be constant across the spatial regime of long-range integration. Findings from earlier studies (e.g. Brincat & Westheimer, 2000, Tzvetanov & Dresp, 2002) suggested that the spatial limits of the long-range regime of integration of two co-linear lines extend between coaxial separations of 20 and 150 arcmin. Recently, Li & Gilbert (2002) presented local contour configurations consisting of co-linear line segments embedded in a context of randomly oriented lines. Their results show that the detectability of a contour configuration presented in global noise is determined by interactions between the relative number of co-linear lines and their co-axial separation. These findings further reveal the complexity of contextual effects on contour integration, which not only depends on the local characteristics of the contour elements as such, but also on the visual information by which they are surrounded. Moreover, the absolute critical spacing between co-linear lines was shown to increase with decreasing surround noise density. This important finding highlights the role of top-down influences on early mechanisms of visual integration. Top-down influences are suitable candidates to account for apparently controversial psychophysical data related to the spatial limits of long-range facilitating interactions.

There is general agreement on the fact that co-linear facilitatory interactions drop off as the spatial separation between target and inducer increases, but it has remained unclear whether they drop off abruptly, or decrease gradually, and whether the long-range spatial regime has clear upper and lower boundaries. While data by Polat & Sagi (1994) or Kapadia et al. (1995) show gradually decreasing detection facilitation with increasing spatial separation between co-linear stimuli, Tzvetanov & Dresp (2002) have shown that spatial interactions between a low contrast inducing line and a co-linear target line show gradually decreasing detection facilitation between co-linear separations of 5 and 25 arcminutes and a plateau effect of constant facilitation with an abrupt drop back to control detection levels between co-linear separations of 140 and 160 arcminutes. The

four subjects in that condition were all widely experienced psychophysical observers and, in addition, highly trained in that specific study task, i.e. had spent a whole year in the lab working on the project, which meant that they often spent several hours per day repeating measurements over relatively long periods. Results from another condition with three unexperienced observers, who were minimally trained for the study task, showed that a high-contrast inducer produced gradually increasing facilitation between co-linear separations of 5 and 25 arcminutes and a plateau effect of constant facilitation with a much more gradual return to control detection levels between co-linear separations of 80 and 170 arcminutes. These observations not only show that the contrast intensity of an inducer critically influences co-linear facilitation/masking, as previously demonstrated also by Polat & Sagi (1994 a), but they furthermore suggest an influence of individual visual experience, or training levels, on long-range interactions. The abrupt change from constant long-range facilitation to control threshold levels seen in the four highly trained and experienced observers in Tzvetanov & Dresp's (2002) study could be explained by a specific training effect where the long-range regime of facilitating interactions is pushed to its upper limit, and the mechanism then responds in an "all or nothing" manner to stimuli beyond that limit. This interpretation is supported by further data from Tzvetanov (2003), but requires additional control experiments to be fully validated. If such an explanation holds, however, this would mean that training not only reinforces contextual effects on grouping at a given, constant spatial separation (e.g. Dresp, 1998), but also modifies the spatial boundaries of long-range integration.

Visual learning has been reported to influence the upper spatial limit of long-range integration across co-linear space (e.g. Polat & Sagi, 1994 b). It specifically seems to enable local contour detection across increasingly larger co-axial gaps, up to a limit defined by a co-axial separation of about two degrees of visual angle between co-linear lines (Li & Gilbert, 2002), or possibly more, depending on noise density, or the number of distracting context elements in a display. This would be consistent with functional properties of cortical interactions in V1 (e.g. Grossberg & Raizada, 2000), which exhibit plasticity. Cortical plasticity, by enabling the visual system to adapt quickly to new stimulations, would fulfill an important ecological role in the development of specific visual skills and visual experience in general.

We conclude that multiple stages of processing influence spatial mechanisms of visual integration across gaps and contrast polarities. Such an integration preserves the relative weight of a local contrast sign, possibly at any separation between individual stimuli within the long-range spatial domain at a given, individual level of training. The process or mechanism by which this is achieved appears to obey, as the results of our study would suggest, a probabilistic principle when the simplest possible local configuration of two co-linear lines is presented to human observers on a plain background. Feldman (2001) pointed out that probabilistic mechanisms represent a “rational strategy for perception”. The present data encourage us to suggest that probabilistic processing, as a functional property of the brain, may influence any stage of neuro-cognitive processing where critical decisions about a visual stimulus are to be made.

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FIGURE CAPTIONS

Figure 1

The human perceptual system groups local contour signals across spatial gaps and contrast signs to achieve figure-ground segregation of objects and shapes. However, shapes with contours of a single contrast sign (upper half) may appear more salient than shapes with contours of alternating contrast signs (lower half).

Figure 2

Relative magnitude or amount of facilitation produced by target-inducer configurations of two co-linear lines with a coaxial separation of 25 arcmin for each of the 20 observers tested. Even though, for a given observer, a configuration with the two opposite contrast signs (bright vs dark) may produce a facilitating effect that is similar to that produced by a configuration with a single sign (see data of observers AF, AM, and EL), the latter are shown to produce generally stronger facilitating effects.

Figure 3

Average relative magnitude of facilitation for each of the 20 observers as a function of the two main combinations of contrast signs. The effect of contrast sign shown here is statistically significant, as revealed by a T-test (see RESULTS).

Figure 4

Relative magnitude of facilitation produced by configurations with a target-inducer separation of 80 arcmin for each of the 4 observers tested. Again, the configurations with a single sign are shown to produce generally stronger facilitating effects.

Figure 5

Average relative magnitude of facilitation for each of the 4 observers, tested with a target-inducer separation of 80 arcmin, as a function of the two main combinations of contrast signs. The effect of contrast sign is statistically significant, as revealed by a T-test (see RESULTS).

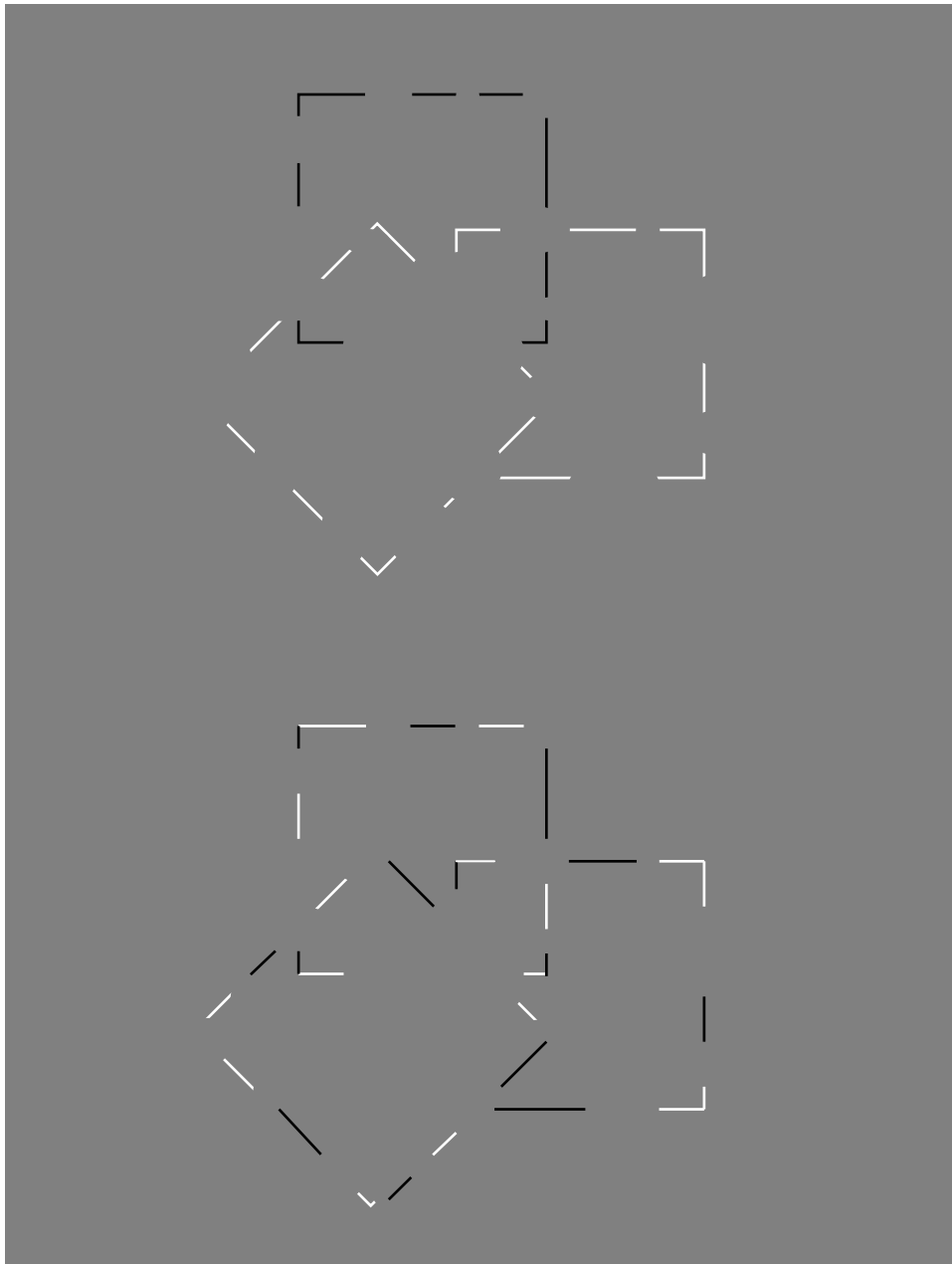


Figure 1

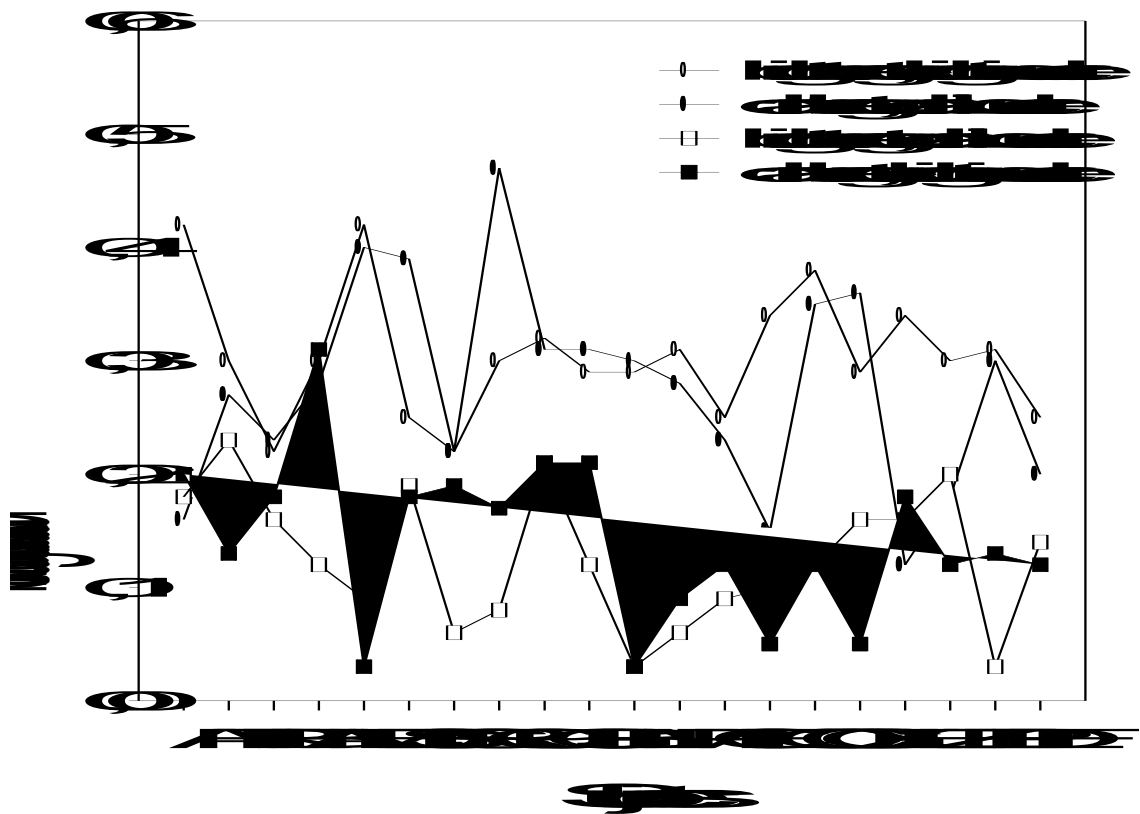


Figure 2

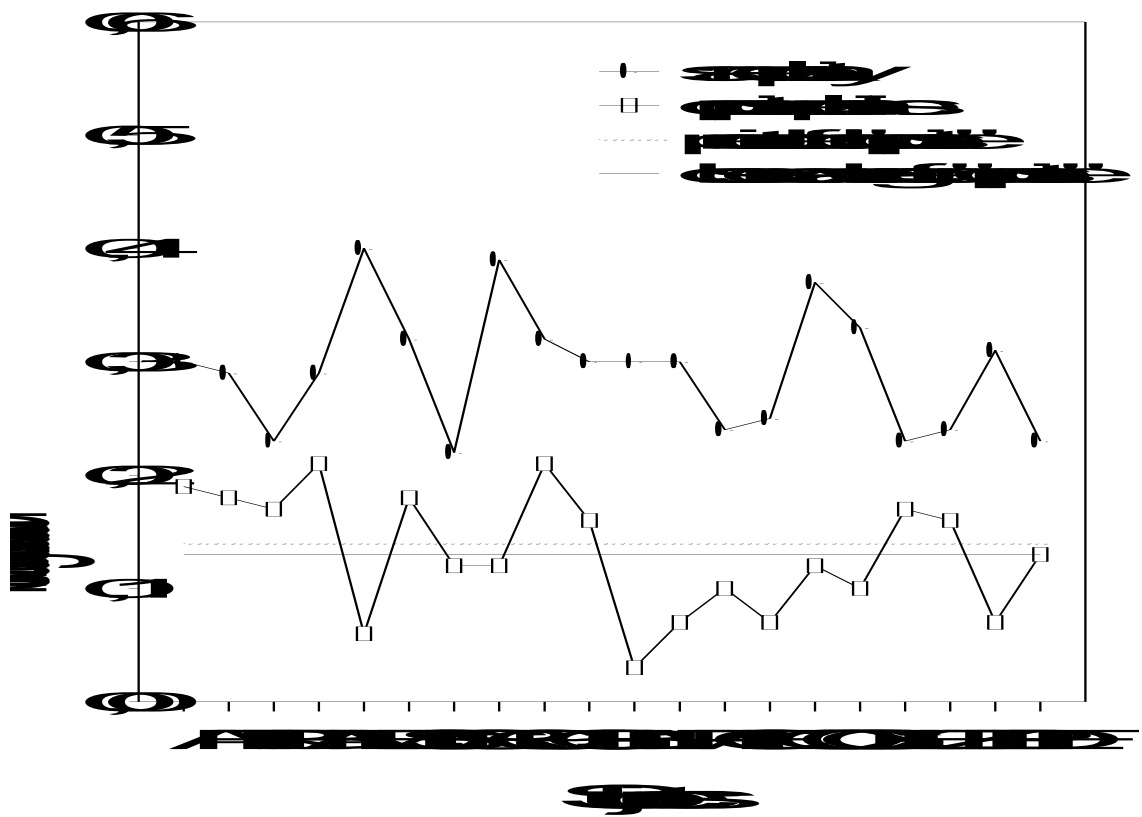


Figure 3

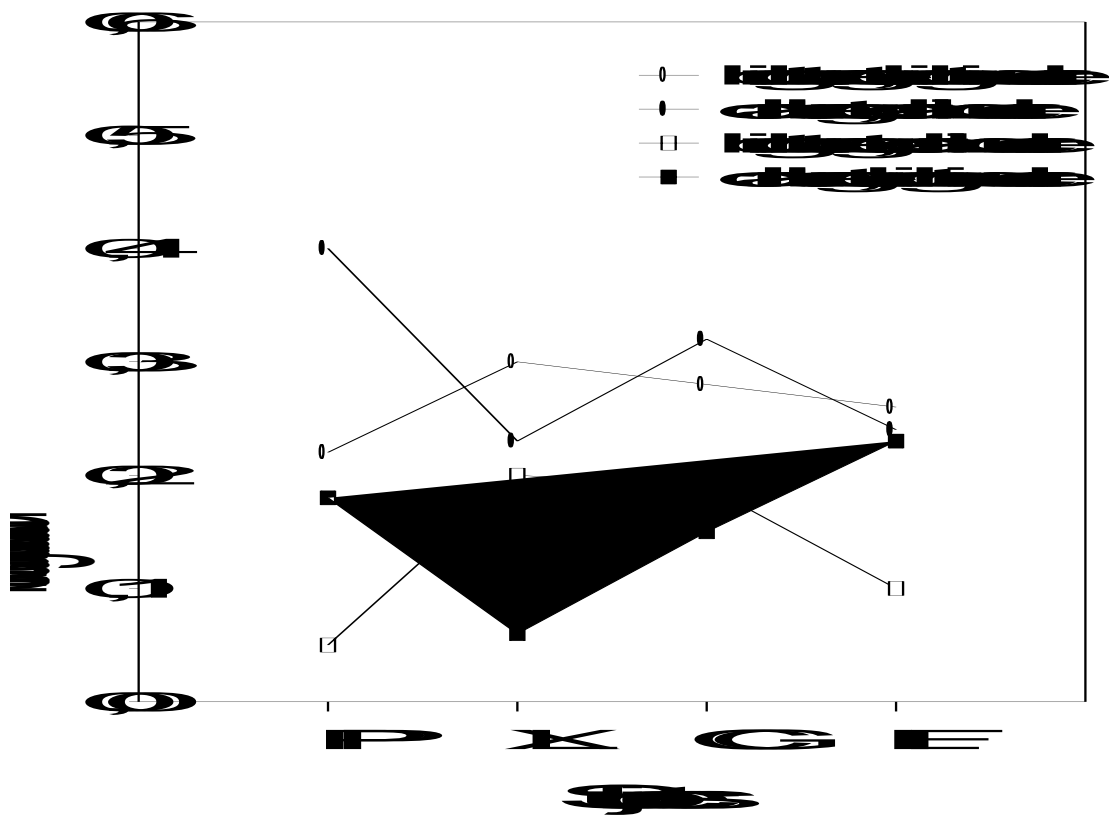


Figure 4

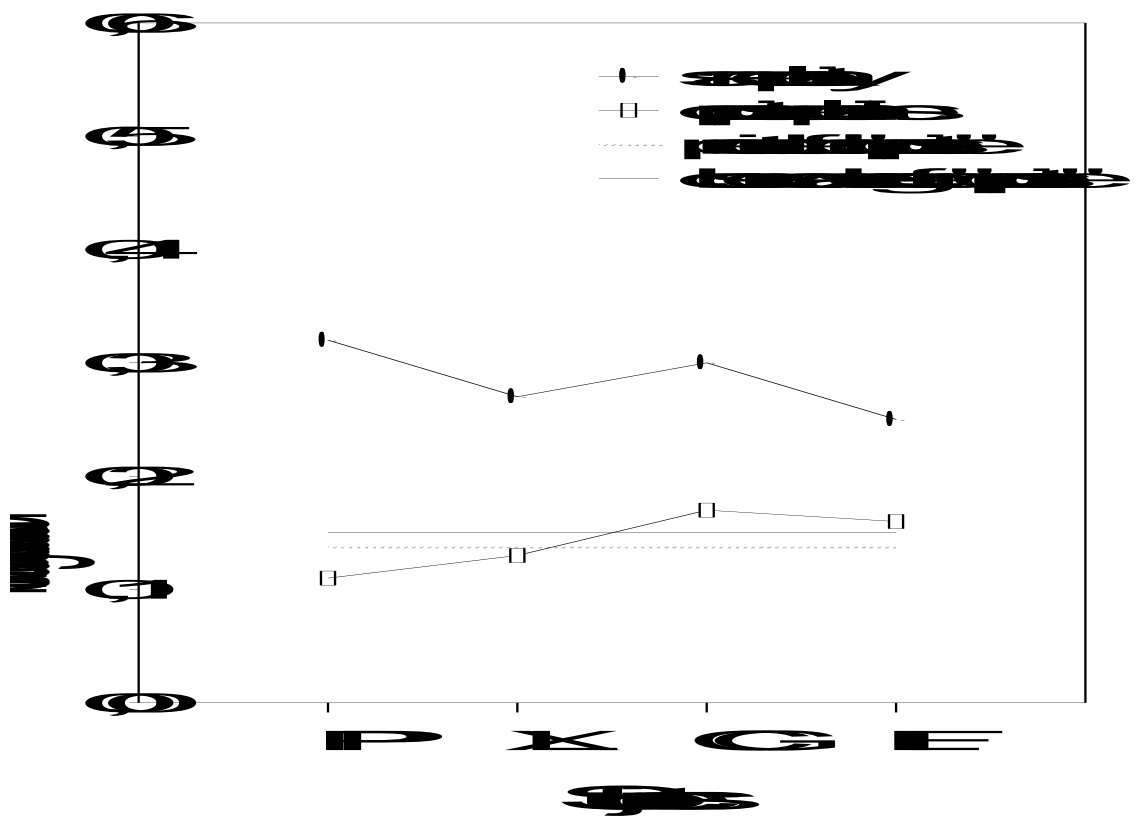


Figure 5