

# Global orientation estimation in noisy conditions

Nadejda Bocheva\*, Simeon Stefanov, Miroslava Stefanova, and Bilyana Genova

Department of Sensory Neurobiology, Institute of Neurobiology, Bulgarian Academy of Sciences, Sofia, Bulgaria,

\*Email: [nadya@percept.bas.bg](mailto:nadya@percept.bas.bg)

The present paper studies the perceived orientation of line patterns with variable elongation, line length, orientation jitter, and presentation time. It evaluates whether the internal noise and sampling efficiency evaluated by equivalent noise paradigm (Pelli 1981) depend on the spatial configuration and temporal characteristics of the stimulation. The evaluated internal noise was compared to the results of double-pass noise estimation. In addition, the eye movements of the participants during active exploration of the line patterns were recorded and analyzed with respect to the stimulus characteristics. The results indicate the presence of late internal noise and show that the internal noise and sampling efficiency strongly depend on the elongation, duration and line length of the patterns. The response time increases with the orientation jitter and with the variability in line length of the patterns. It is longer also near the reference orientation for the low levels of added external noise. These results contradict some of the major assumptions of the variance-summation model and question its applicability in characterizing the perceived orientation of multi-element patterns.

Key words: vision, orientation perception, equivalent noise paradigm, elongation, response time, double-pass

## INTRODUCTION

To understand the neural mechanisms and processes involved in different visual tasks a well-spread procedure is to evaluate the visual performance in noise (Doshier and Lu 1998, 1999, Gold et al. 2000, Pelli and Farell 1999). This approach is also used to study the abilities of the visual system to determine different statistical properties of an image like the mean orientation or motion direction of multi-element patterns (Dakin 2001, Beaudot and Mullen 2006, Dakin et al. 2009, Solomon 2010, Tibber et al. 2014, Dakin et al. 2005, Bocheva et al. 2013) or their orientation variance (Solomon 2010). One such methodology is labelled equivalent noise paradigm (e.g. Pelli 1981) and relies on the changes in performance depending on the relative amounts of the added external and internal noise. When the added external noise is much less than the internal noise, the variability in the responses is determined predominately by the internal noise while at large values it depends mainly on the amount of exter-

nal noise. The effect of these two sources of noise – internal and external, on the orientation discrimination thresholds are considered additive and the model is labelled variance-summation model (e.g. Beaudot and Mullen 2006) or averaging paradigm (Allard and Cavanagh 2012). The results are described using two measures – an estimate of additive internal noise possibly related to the tuning characteristics of the neurons sensitive to orientation/motion and an estimate of the number of samples used in the evaluation of the global orientation in conditions of added external noise. When the number of samples used in the evaluation is larger, the observers pooled information in the stimulus more efficiently, thus the effective sample size is proportional to the sampling efficiency (Solomon 2010). This approach in describing the processes involved in estimating the statistical properties of the images like mean orientation, mean direction or mean variance in orientation is equivalent to the so-called linear amplifier model (Pelli 1981). It assumes that the internal noise in the visual system occurs early, it is additive and does not depend on signal strength.

Some researchers (Solomon 2010), however, considered also the possibility that the internal noise occurs not only in the early stages of visual information pro-

Correspondence should be addressed to N. Bocheva  
Email: [nadya@percept.bas.bg](mailto:nadya@percept.bas.bg)

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Table I

Experiment	Hypothesis tested
Experiment 1	The spatial configuration of the patterns affected their perceived orientation. Two sources of information – the mean orientation of the line segments and the global orientation specified by the overall shape of the patterns affected the perceived global orientation.
Experiment 2	Line length variability affects the performance independently of pattern elongation.
Experiment 3	Temporal integration is involved in global orientation estimation. In conditions of time pressure its effect is reduced.

cessing, but at the later stages as well and tried to evaluate the separate contribution of early and late noise on task performance. Likewise, Dakin (2001) suggested that the internal noise represents not only the sampling uncertainty related to local orientation estimation, but also the uncertainty associated with the decision process. The variance-summation model as used in studying mean orientation perception could hardly separate these two options. The inability to distinguish the position of the additive internal noise in the processes involved in visual task performance is discussed, for example, by Lu and Doshier (2008) for other observer's models that include not only additive internal noise, but also multiplicative noise and non-linear transduction function.

Another issue related to using the equivalent noise method was raised recently by Allard and Cavanagh (2012). These authors questioned one of the assumptions of the equivalent noise paradigm: the independence of sampling efficiency from the levels of external noise (low or high). Their data suggest that the ratio of the discrimination thresholds for single and multiple elements at low noise differs from that at high noise. Also, the size and number of elements had a different effect on discrimination performance at low and high noise levels. Allard and Cavanagh argued that at low noise averaging the information provided by the elements was either unneeded or required fewer resources, which violates the assumption of constant sampling efficiency at all levels of noise. The authors also suggested that the precision of orientation estimates was not the same at low and high noise levels and fine discriminations took place only at low levels of noise. Thus, these considerations imply that the processing strategy at low and high levels of noise may differ. However, changes in sampling efficiency with the lev-

els of external noise may be due not to strategy modification, but to the presence of multiplicative noise in estimating the mean orientation of the patterns (e.g. Burgess and Colborne 1988).

Beaudot and Mullen (2006) also presented arguments against the interpretation of orientation discrimination performance in terms of additive internal noise and sampling efficiency even though the variance-summation model described well the behavioral data of their own and other studies. They argued that orientation sensitive detectors did not show monotonic responses to orientation, their response variability was better described by multiplicative (Geisler and Albrecht 1995) rather than additive noise and the variance summation model did not account for the circular nature of orientation information.

In summary, the overview of the studies using equivalent noise paradigm for examining mean orientation discrimination implies that while this methodology is appropriate for describing the experimental data, the interpretation of the results still needs further study and clarification. In the present study, we attempted to evaluate the contribution of decision mechanisms in mean orientation discrimination. To achieve this goal we used long presentation times that allow the integration of sensory information over time and compared the performance with conditions when the observers chose when to stop processing the stimulus and initiate response. To disentangle the relationship between accuracy and response time, we used two different instructions: in the first the participants were allowed to use as much time as they needed without requiring speeded responses; in the second we stressed both on accuracy and speed. Most previous studies used short fixed presentation time 100 ms (Dakin 2001); 150 ms (Dakin et al. 2009, Solomon 2010);

200 ms (Allard and Cavanagh 2012); 400 ms (Tibber et al. 2014 for children) and, to our knowledge, none has studied the response time for orientation discrimination in noisy conditions.

We also reasoned that the self-determined stimulus presentation would make the stimuli equivalent in difficulty; the temporal accumulation of information would be completed and this would provide better characterization and separation of the sensory processes involved in orientation discrimination and the processes of decision making. We assumed that in these conditions the decision uncertainty would be reduced with no effect on sampling efficiency.

In addition, we studied the effect of stimulus elongation on the parameters of the equivalent noise model. We assumed that this stimulus characteristic would have no effect on the performance if the limiting factor in noiseless conditions is only the precision of local orientation estimates. However, it might affect the decision uncertainty by creating a conflict between the average orientation of the line elements forming the stimulus pattern and the overall orientation of the pattern outline i.e. by the orientation information determined by the positions of the pattern elements. For non-elongated patterns this information is ambiguous, while for elongated patterns it is related to the first principal axis of multi-element patterns (dot clusters, Yakimoff 1981; Glass patterns, Lansky et al. 1989) or multi-part 2D shapes (Cohen and Singh 2006). Pattern elongation was expected to influence the estimates of internal noise, leaving the sampling efficiency unchanged since the results of Dakin (2001) indicated that the number of samples was independent of the spatial arrangement and depended entirely on the number of pattern elements.

Lastly, we varied the length of the line elements reasoning that increasing line length would improve the precision of local orientation. Thus, we again expected that this manipulation would affect the estimate of the additive internal noise in variance-summation model. However, it might have some effect on the sampling efficiency as well if the number of samples pooled to estimate the mean orientation of the patterns is determined by area of fixed size.

To further evaluate what limits the performance in determining the mean orientation of line patterns we used a double-pass procedure (e.g. Burgess and Colborne 1988) presenting the same stimuli and added noise in different experiments. Using the consistency

of the responses in the double-passes allows estimating the contribution of different noise sources in mean orientation estimation.

The hypotheses tested in the study in the different experiments are presented in a tabular form below. In all experiments we tested the effect of mean line orientation, orientation jitter, and pattern elongation on task performance.

Our results show that the bias and discrimination thresholds strongly depend on the elongation of the patterns and the line length of the elements. The two parameters of the variance-summation model also change with these stimulus characteristics. Moreover, the response time needed to perform the task varies with the noise level and the line length. Significant interactions are observed between the noise level and the deviation of the mean line orientation from the reference orientation and between the noise level and elongation of the patterns. We conclude that the averaging process operating in estimating mean pattern orientation depends on the spatial and temporal characteristics of the patterns and relating the internal noise only to the precision of the local estimates for orientation may be too simplistic.

## GENERAL METHODS

### Subjects

Five subjects, aged 33–60 years participated in all experiments. All of them had normal or corrected to normal vision and were naïve to the purposes of the study.

### Stimuli

Ten random dot patterns of 50 points were generated. Each pattern was rotated at random angle in the range 0–360°. Every dot in the patterns served as end-point of a line segment with length 0.8° visual angle in experiments 1 and 3a or in the range of 0.8–1.2° visual angle in experiments 2 and 3b. The line width was equal to 0.1° visual angle in all experiments. The orientation of the segments was randomly selected from a normal distribution with a predefined mean value and standard deviation. Nine different mean orientations from the vertical were used:  $-10^\circ$ ,  $-7.5^\circ$ ,  $-5.0^\circ$ ,  $-2.5^\circ$ ,  $0^\circ$ ,  $2.5^\circ$ ,  $5.0^\circ$ ,  $7.5^\circ$  and  $10^\circ$ . The spread of the orientation distributions (the noise level) was  $4^\circ$ ,  $11^\circ$ ,  $18^\circ$ ,  $25^\circ$  and

32°. In the choice of the noise levels we have taken into account the data of Maloney et al. (1987) and Dakin (1997) that the noise level affects the performance in orientation discrimination tasks if it is larger than 7.8–8.0°.

The overall stimulus set contained 450 unique stimuli with different global orientation, elongation and with different orientation flow created by the line segments. Examples of the stimuli used in experiments 1 and 3a are given in Figs 1A, 1B. Fig. 1C presents an example of the stimuli in experiments 2 and 3b.

### Procedure

The subject sat in a well-lit room at a distance of 60 cm from the computer screen. A single stimulus was presented at the center of the screen in a circular aperture with diameter of 22° visual angle and luminance of 0.2 cd/m<sup>2</sup>; the area outside the aperture was white with luminance of 90.0 cd/m<sup>2</sup>. The lines were white with luminance of 90.0 cd/m<sup>2</sup>. The stimuli were presented on a computer screen (21" Dell Trinitron with Nvidia Quadro 900XGL graphic board) using Psychtoolbox (Brainard 1997, Pelli 1997). The refresh rate of the monitor was 85 Hz, and the resolution was set to 1280×1024 pixels. The observation was binocular.

The subject's task was a binary forced-choice: to determine whether the pattern was tilted clockwise or anticlockwise to the implicit vertical standard. The observers used the mouse buttons to indicate their responses.

Two different stimulus durations were used in experiments 1 and 2: 1.67 s and duration, determined

by the Subject. These two conditions were presented in separate blocks. The order of stimulus presentation in the two conditions was the same. This allows applying to the data the double-pass consistency test (Burgess and Colborne 1988). In experiment 3 the Subjects were asked to perform speeded responses.

The eye movements during stimulus presentation in experiment 1 were recorded with Tobii glasses (Tobii Tech) with temporal resolution of 30 Hz and spatial resolution of 0.5° visual angle.

### Statistical analyses

All statistical analyses in the study were performed using R (R Core Team 2014). We performed generalized mixed effects regression with probit or Poisson link functions and linear mixed effects models using lme4 (Bates et al. 2014). The package phia (De Rosario Martinez 2013) was used to analyze interactions in the fitted models and to represent in more compact way the significance of the main and interaction terms. In generalized mixed effects regression models, only the mean line orientation of the patterns was used as a regressor, while the other experimental variables: the noise level, the stimulus duration and the group (elongated or non-elongated) and their interactions were considered as fixed categorical factors.

In analyses of temporal data we used mixed effects linear ANOVA on the log-transformed values. In this way, we tried to circumvent the violation of the non-normality of temporal data. In these analyses the mean orientation of the patterns was also considered categorical factor.

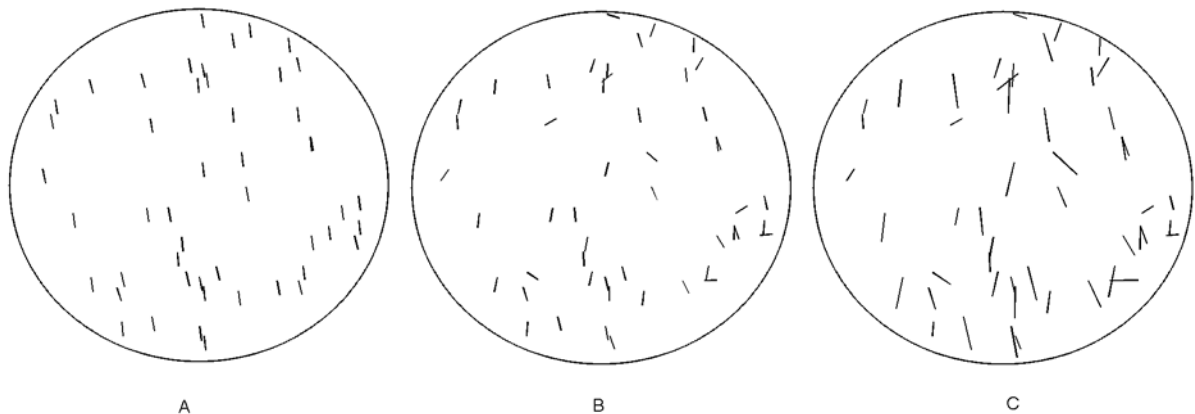


Fig. 1. Examples of stimuli used in the study. (A) Equal line length pattern with a noise level of 4°. (B) Equal line length pattern with a noise level of 32°. (C) Pattern with variable length with a noise level of 32°.

Mixed effect models are an analytical approach suitable for the analysis of grouped data, like in repeated measures. It relies on the assumption that the same functional relation describes the individual responses, but its parameters vary among the individuals. It allows also testing different covariate structures and accounts for multiple sources of heterogeneity in data through the inclusion of random effects in the models (Hall and Clutter 2004).

To select the model that best represent the effects we used the likelihood ratio test (Agresti 2002) to compare models with different fixed or random effects. All claims in the text that a model describes best the data are based on the likelihood ratio test. Model overfitting was tested by a function provided by Bolker (2010).

As a measure of elongation we used the F-test of equality of variances (Johnson et al. 1995) applied to the maximal and minimal variances of the coordinates of the pattern elements, estimated as eigenvalues of the covariance matrix of the coordinates of the line segments. Patterns, for which the maximal and minimal variances of the coordinates differed significantly with  $P < 0.05$  were regarded as elongated, while the rest were regarded as non-elongated. The pattern elongation was assumed to modify the reliability of the global orientation of the outline shape. The global orientation of the outline shape was not varied systematically, but by a random rotation of the patterns in the process of their generation. For this reason we regarded it as a factor whose effect was introducing additional noise in the process of orientation estimation or in the process of decision making. We assumed that for more elongated patterns the global orientation of the outline shape would affect more these processes. As it was not certain at what level of task performance the global orientation of the outline shape modified the perceived orientation, we used the pattern elongation not as a continuous regressor, but divided the patterns on statistical grounds as elongated or non-elongated based on the difference of the maximal and minimal variance of the coordinates of the line segments.

To evaluate the parameters of the variance summation model we used a non-parametric bootstrap procedure (Efron and Tibshirani 1993) and nlme package (Pinheiro et al. 2014) to fit the model to the bootstrapped estimates for the discrimination thresholds and to estimate the 95% of the parameters. One thousand samples were used for the bootstrapping in all experiments.

Further details for the statistical analyses will be given in the results section of the experiments.

## Experiment 1

### Introduction

The aim of experiment 1 was to evaluate whether the elongation of the patterns might affect the perceived orientation of line patterns. The hypothesis was that two sources of information – the global orientation specified by the overall shape of the patterns and the mean orientation of the line segments affected the perceived global orientation and that the weight of each of these sources depended on their reliability.

### Method

#### *Stimuli*

The stimulus set consisted of 450 multi-element patterns generated as described in the General methods section. Each stimulus had 50 lines of equal length ( $0.8^\circ$  visual angle  $\times$   $0.1^\circ$  visual angle).

#### *Procedure*

A single-interval binary classification method was used. The stimuli were presented once for a fixed duration of 1.67 s (142 frames at 85 Hz refresh rate) and once – for duration determined by the subjects. No time pressure was given to the participants. These two conditions were presented in different blocks in counter-balanced order in two different days.

The eye movements of the subjects were recorded by means of Tobii glasses.

### Results

#### *Effect of overall pattern elongation on task performance*

To evaluate the effect of the experimental factors on the perceived orientation of the patterns we performed general linear mixed effects probit regression on the responses “more tilted to the left”.

The results suggest that the data could be modelled best when the mean line orientation, the noise level and their interaction, as well as the interaction of the

noise level and the elongation factor, were included as fixed effects in the mixed model probit regression. In addition, the random factors included a random intercept by subject. The stimulus presentation time: fixed or self-determined had no significant effect on the performance at  $p=0.05$  ( $\chi^2_1=1.16$ ,  $P=0.28$ ). As expected, the mean line orientation significantly affected the performance ( $\chi^2_1=938.52$ ,  $P<0.05$ ). The main effect of elongation was also significant ( $\chi^2_1=13.46$ ,  $P<0.05$ ). The mean line orientation had a different effect at the different noise levels suggesting that the steepness of the psychometric functions varied with the change in the orientation jitter (Fig. 2,  $\chi^2_4=128.07$ ,  $P<0.05$ ). The effect of the noise level ( $\chi^2_4=43.16$ ,  $P<0.05$ ) and its interaction with the elongation ( $\chi^2_4=47.97$ ,  $P<0.05$ ) implies changes in the response bias with the change of these stimulus characteristics.

Visual inspection of the residual plots did not reveal any obvious deviations from normality or homoscedasticity.

Taking into account the significant interactions between the noise level and both the elongation and the mean line orientation of the patterns, separate mixed probit regression analyses of the effect of mean line orientation and noise level were performed for the elongated and non-elongated patterns in order to obtain estimates of the discrimination thresholds.

Fig. 3A represents the mean thresholds for each noise level for elongated and non-elongated patterns. They were obtained as the slope of the estimated psychometric functions. The error bars were estimated using a bootstrap procedure. The figure clearly shows that the discrimination thresholds were affected significantly by the noise level and the thresholds were higher for the elongated patterns.

The bias of the psychometric functions was determined as the negative ratio of the intercepts and slope of the probit regression for each noise level and elongation group (Fig. 4A). The 95% confidence intervals were estimated from the bootstrapped values. The results suggest that the bias was larger for the elongated patterns and that it increased with the increase in orientation jitter.

#### *Parameters of the variance summation model*

A nonlinear regression model of the type:

$$\sigma_{th} = \sqrt{\frac{\sigma_{int}^2 + \sigma_{ext}^2}{N}} \quad (1)$$

was fitted to the discrimination thresholds for the elongated and non-elongated patterns. In (1)  $\sigma_{th}$  refers to the discrimination threshold,  $\sigma_{int}$  and  $\sigma_{ext}$  are respectively the internal and the external noise and  $N$  is the number of samples pooled to determine the global orientation

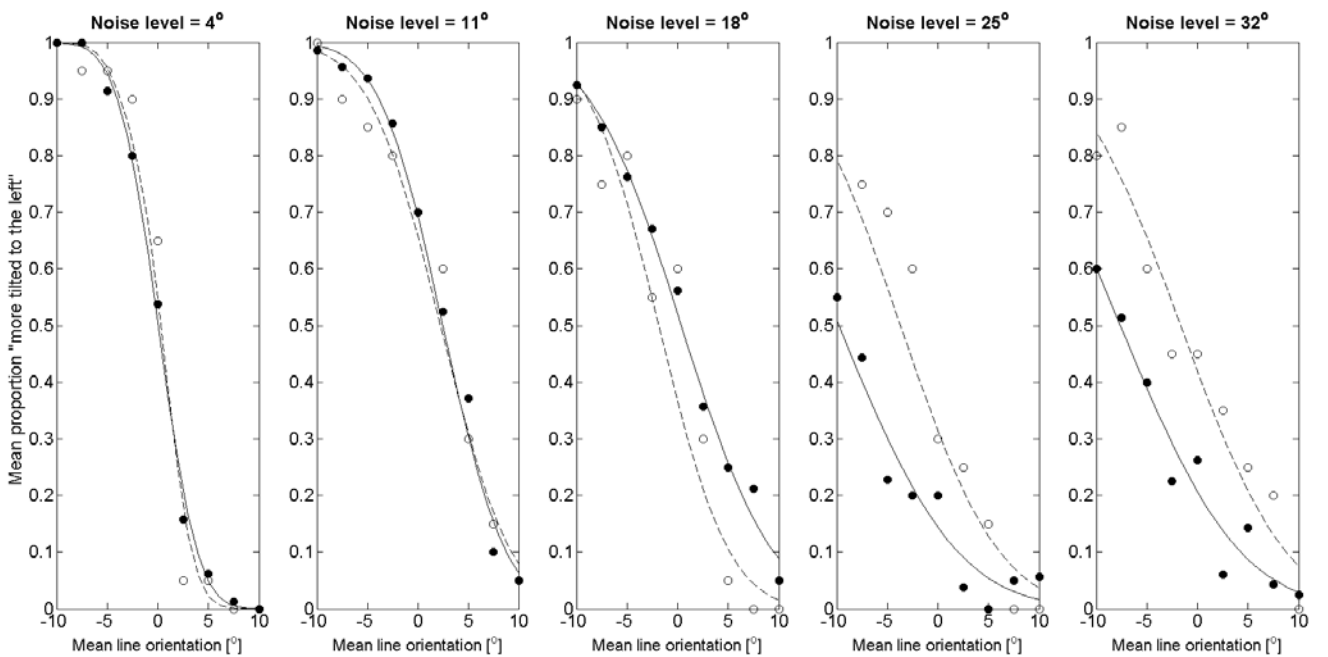


Fig. 2. The averaged proportion “patterns more tilted to the left” as a function of mean line orientation, noise level and pattern elongation. The fitted psychometric functions are also shown.

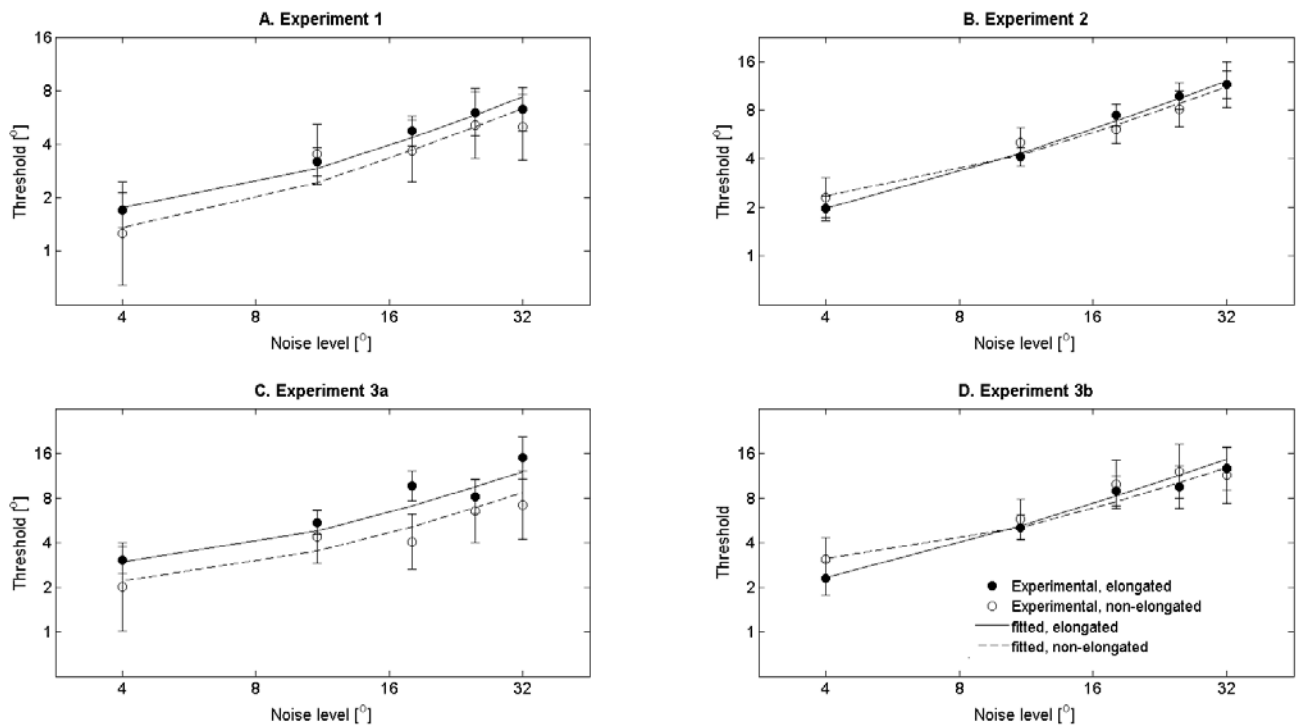


Fig. 3. (A–D) The averaged discrimination thresholds obtained for different noise levels for the elongated and non-elongated patterns in experiment 1–3. The error bars show the 95% confidence intervals for the estimates. The curves represent the variance summation model fitted to the discrimination thresholds.

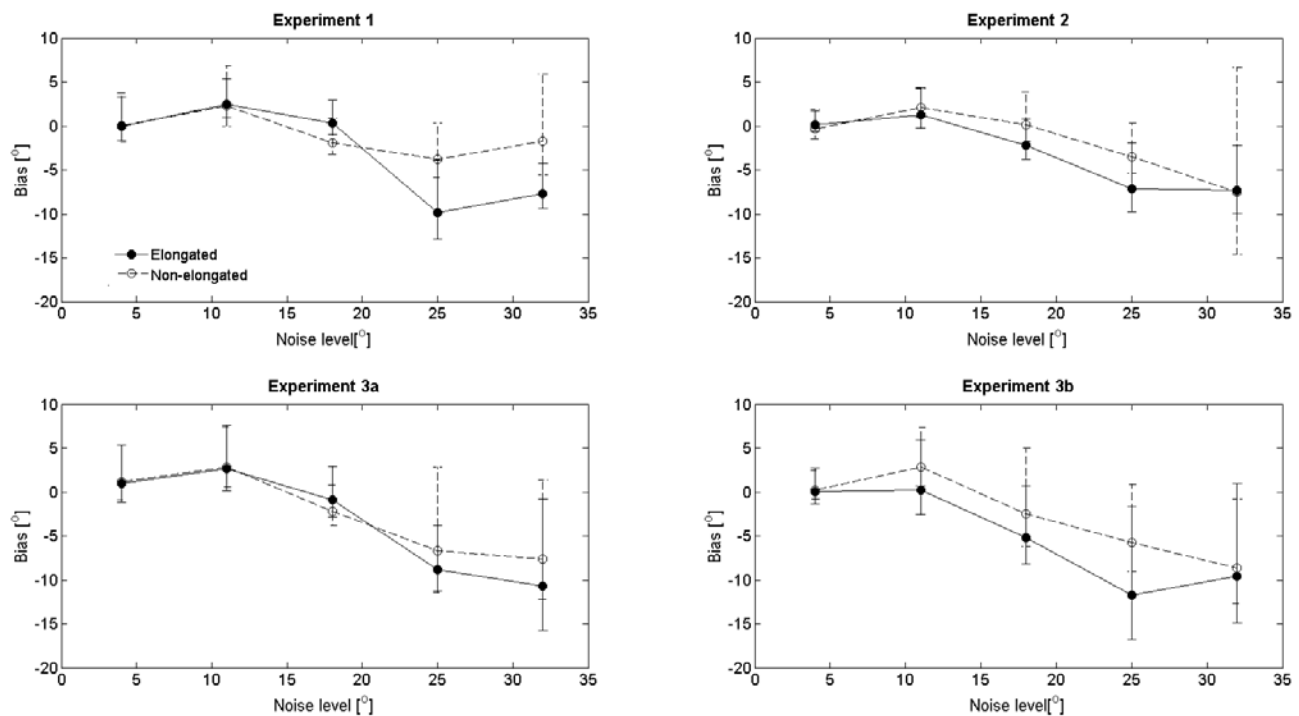


Fig. 4. (A–D) The averaged bias in estimating the mean pattern orientation for different levels of noise and elongation for experiment 1–3. The error bars show the 95% confidence intervals of the estimates.

of the line segments. This form of the variance summation model regards the internal noise as occurring early, before integration of the information provided by the local detectors of orientation.

The model was fitted to the bootstrapped estimates for the discrimination thresholds with the pattern elongation used as a grouping factor. To ensure that the model parameters were positive numbers they were represented with logarithms. The confidence intervals of the model parameters were determined using *confint* function from R package MASS (Venables and Ripley 2002). The estimated additive internal noise was  $6.74^\circ$  [ $6.59$ – $6.88^\circ$ ] for the elongated patterns and  $5.68^\circ$  [ $5.55$ – $5.82^\circ$ ] for the non-elongated patterns. The number of samples used to perform the task was: 9 [ $8.94$ ,  $8.80$ – $9.08$ ] and 12 [ $11.87$ ,  $11.69$ – $12.05$ ]. The values in the brackets give the mean value of the effective number of samples without rounding and their 95% confidence intervals. These results suggest significantly higher sampling efficiency for the non-elongated patterns. The fitted curves based on the variance summation model are also shown in Fig. 3A. It is clear that the model describes well the effect of added external noise on the discrimination thresholds for both types of patterns – elongated and non-elongated.

### *Effect of the stimulus characteristics on response time in self-paced condition*

The time needed to perform the task greatly varied among the observers: two of them (subjects 1 and 2) needed less time than in the fixed duration condition in almost 85% of the stimulus presentations, subject 3 needed less time in 81% of the stimulus presentations, while subjects 4 and 5 required longer time in almost half of the stimuli. The mean response time of the subjects was: 1.34, 1.07, 1.42, 1.67 and 2.52 s for subjects 1–5.

To evaluate whether the experimental factors affect the response time, a mixed effect linear ANOVA was performed on the log-transformed response times. As fixed effects, we entered the mean orientation of the line segments, the noise level, the elongation of the patterns and their interactions. As random effects, we had random intercepts for subjects and by-subject and by-condition random slopes. The results indicated a significant effect of the noise level ( $F_{4,2046}=29.56$ ,  $P<0.05$ ) as more time was needed to perform the task when the noise level increases. The mean line orientation also showed a significant effect ( $F_{8,2046}=6.54$ ,  $P<0.05$ ). In addition, the interaction between the mean orientation of the line segments and the noise level was

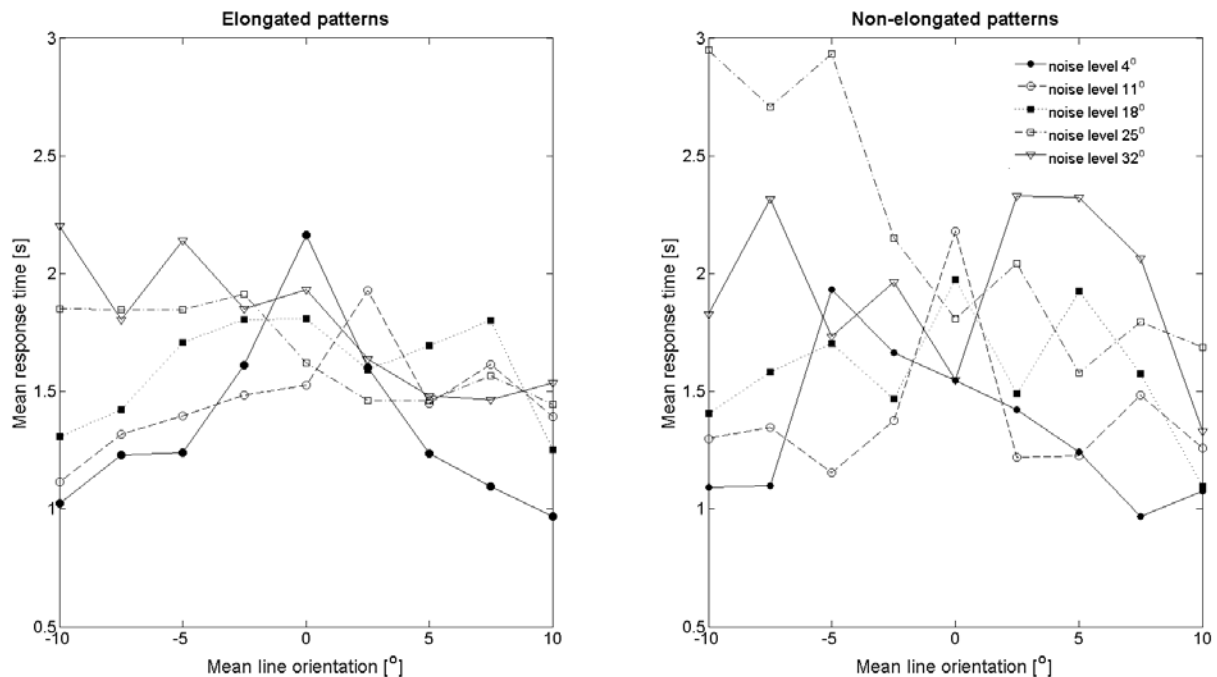


Fig. 5. The average response time needed to determine the mean pattern orientation for different noise levels and mean line orientation for the elongated and non-elongated patterns.



also significant ( $F_{32,2046}=2.57$ ,  $P<0.05$ ). More time was needed to determine the orientation of the patterns when the mean line orientation was close to vertical, but this effect was reduced when the noise level was increased. The interaction of noise level and group (elongated vs. non-elongated) was also significant ( $F_{4,2076.5}=3.82$ ,  $P<0.05$ ). The response time increased more for non-elongated patterns than for the elongated ones when the noise level increased (see Fig. 5).

The effect of experimental factors on response time might be considered as an indication that task difficulty varied across the different conditions. Our experimental setup does not allow estimation of a response time at a fixed level of precision in task performance.

#### *Effect of stimulus characteristics on eye movement parameters*

The mean number of fixations in all experimental conditions was 3.45. To evaluate the effects of the experimental factors we applied a general linear mixed model to the data using Poisson distribution as a link function. The mean orientation of the line segments (based on circular statistics and taken as covariate), the stimulus duration: fixed or self-determined, the noise

level, the elongation of the patterns and their interaction were considered as fixed factors. Models with random intercepts and slopes were tested. The results showed significant effect of the stimulus duration and significant interaction between the stimulus duration and the noise level. The interaction term represented the higher number of fixations in the self-determined condition for the highest levels of noise. In addition, the elongation of the patterns led to higher number of fixations at high noise levels in the self-determined condition. No other factors or interactions were significant at  $P=0.05$ .

The mean duration of fixations for all experimental conditions was 375 ms. The mixed generalized linear model applied to the log-transformed values that best described the data involved as fixed factor the noise level, the elongation of the patterns and the stimulus duration and a random intercept by subjects. The mean duration of fixations decreased with the noise level. There was a significant interaction between the elongation of the patterns, the noise level and the stimulus duration ( $F_{8,3335}=1.97$ ,  $P<0.01$ ). The mean duration of fixations was higher for the elongated patterns for the fixed stimulus duration at low levels of noise while for self-determined duration the non-elongated patterns were fixated longer at low levels of noise.

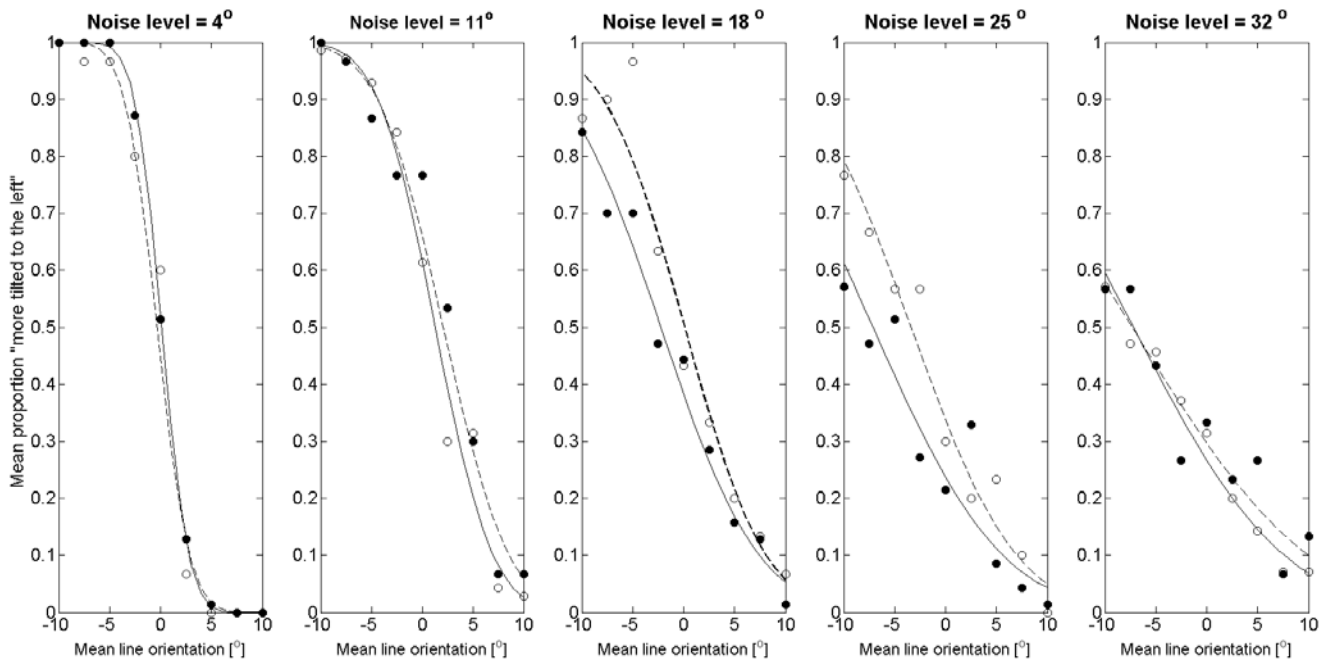


Fig. 6. The averaged proportion “patterns more tilted to the left” for patterns of unequal line length as a function of mean line orientation, noise level and pattern elongation. The fitted psychometric functions are also shown.

## Discussion

The results of experiment 1 suggest that the elongation of the patterns significantly affects the performance of the subjects. In the variance-summation model, this effect is represented by higher values of the additive internal noise and with lower sampling efficiency for elongated patterns. A potential explanation for these findings could be that for elongated patterns there are two sources of orientation information with varying reliability. One of them is related to the average orientation of the line segments; the other is related to the overall shape orientation and is based on positional information of the elements in the pattern. With the increase of the orientation jitter the reliability of the information provided by line segments decreases and the average orientation of the line segments becomes less salient. So, the observers based their estimates either on the information from both cues of global orientation or on the more reliable of the two. As a result, the internal noise increases and is less related to the precision of local orientation of the line segments. The effective sample size is also reduced as the orientation of less line segments contribute to the estimate of global pattern orientation. Hence, the bias of the estimates at high levels of noise increases as the psychometric functions are estimated with respect to

the mean line orientation while in conditions of uncertainty the performance may be less related to it.

This suggestion is supported by differences in the observed bias for the elongated and non-elongated patterns and by the greater increase in response time for non-elongated patterns than for the elongated ones when the noise level increased.

The findings of experiment 1 also suggest that task difficulty evaluated by the response time in a self-paced condition was not equivalent. It was higher when the noise level was high, and depended also on the closeness of the mean line orientation to the reference vertical orientation at low noise conditions. This implies that for short stimulus presentation times the decision uncertainty in evaluating the mean pattern orientation would not be the same. This inference is further confirmed by the longer fixation duration in these conditions. The relationship between response time and the stimulus parameters will be further discussed when comparing the results of experiments 1–3.

## Experiment 2

Experiment 1 suggests that the spatial configuration affected the perceived global orientation of line patterns and changed the internal noise and the sampling

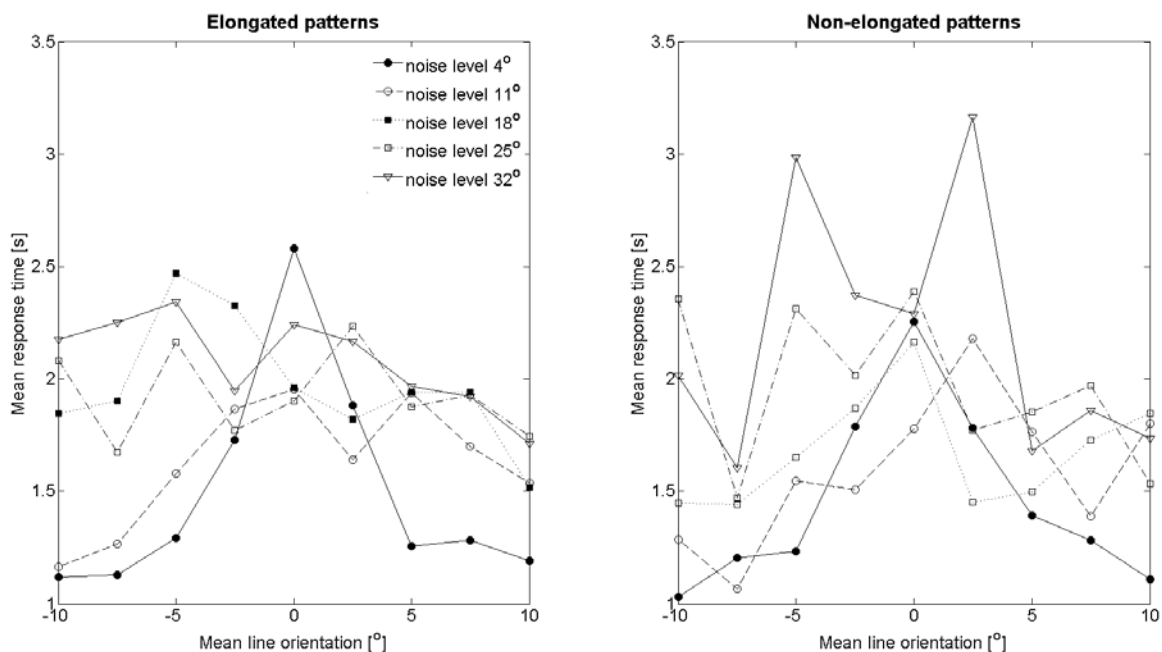


Fig. 7. The mean response time in the self-determined duration condition obtained in experiment 2 as a function of mean line length, noise level and pattern elongation.

efficiency in the variance-summation model. We have presented a potential explanation why the pattern elongation led to lower sensitivity to the average pattern orientation. To further test this hypothesis, in experi-

ment 2 we tried to keep the overall shape of the patterns similar to that in experiment 1, but used a variable length of the line segments in the inner region. The line length was equal or longer than that used in

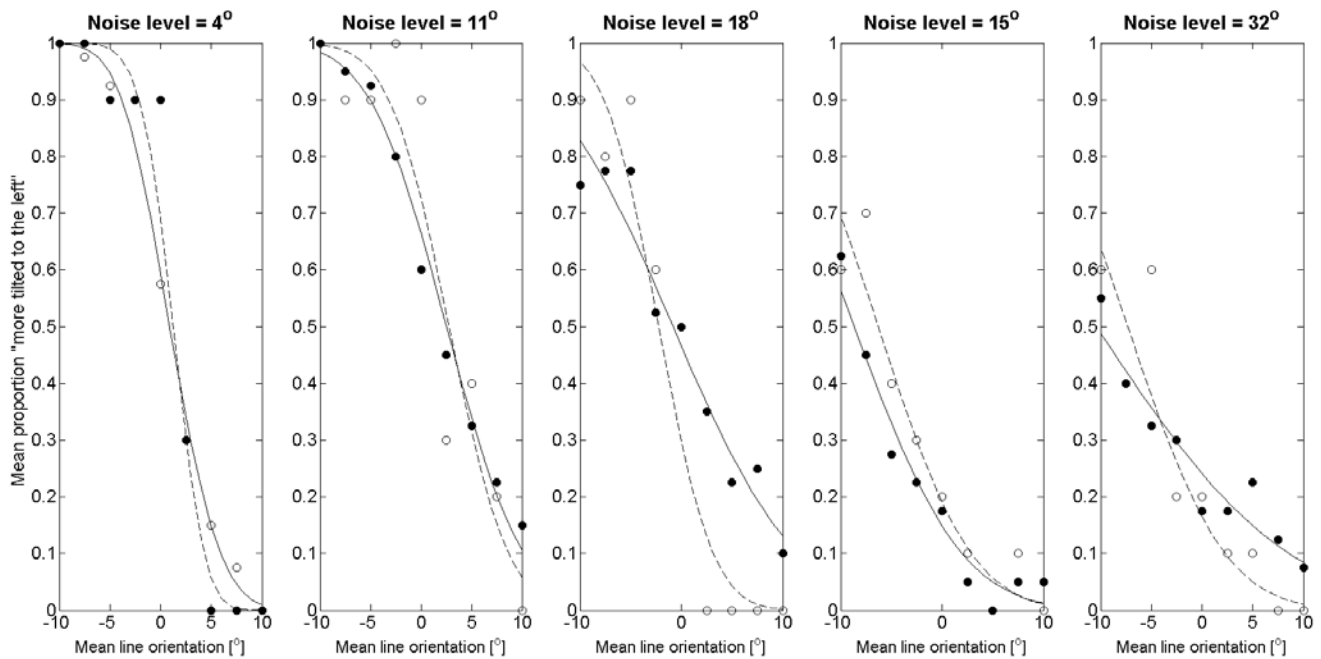


Fig. 8. The mean proportion of responses “more tilted to the left” for patterns of equal length for different mean line orientation, noise level and pattern elongation obtained in experiment 3a. The fitted psychometric functions are also shown.

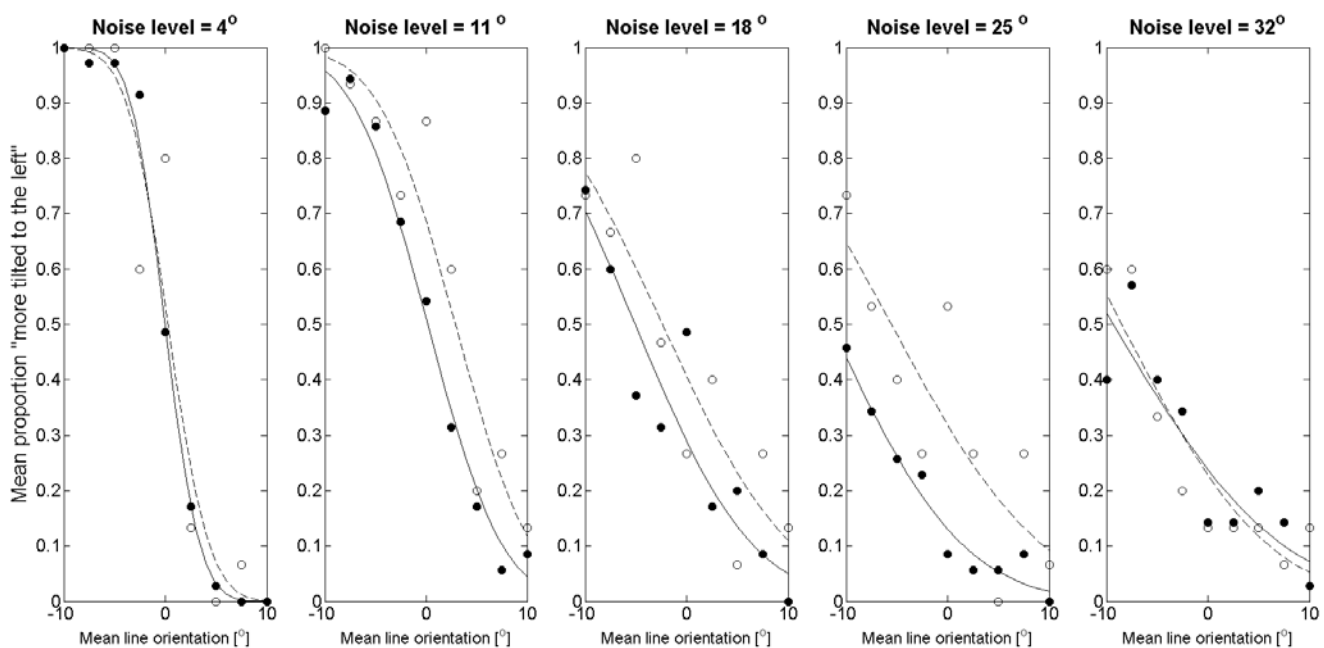


Fig. 9. The mean proportion of responses “more tilted to the left” for patterns of unequal length for different mean line orientation, noise level and pattern elongation obtained in experiment 3b. The fitted psychometric functions are also shown.

experiment 1. This manipulation could improve the precision of local orientation estimates and thus, reduce the early internal noise. The potential occurrence of crowding effects in the periphery of the stimuli was greatly reduced by keeping the length variation only to the interior of the patterns. However, the increase in line length might also affect the effective number of samples used to estimate the mean orientation of the patterns if a fixed area of the stimulus is used for pooling information. It is also possible that the variable line length of the segments may increase the attentional load in task performance changing the sampling efficiency (e.g. Dakin et al. 2009). Nevertheless, it should be independent of pattern elongation in either case.

## Methods

### *Stimuli*

The same set of dot patterns was used to create the stimuli. The covariance ellipse of dot coordinates was determined and for the dots inside it, the line length of the segments was randomly selected in the range  $0.8\text{--}1.2^\circ$  visual angle. For the dots outside the covariance ellipse the line length was set to  $0.8^\circ$  visual angle as in experiment 1. The same values of mean orientation and noise levels as in experiment 1 were used.

### *Procedure*

The procedure was the same as in experiment 1 with the only exception that eye movements were not recorded. Two different stimulus presentation times were used: 1.67 s and duration, determined by the subjects. These presentation times were applied in separate blocks. The experiment contained two series of two blocks performed in a different order on two consecutive days.

## Results

### Effect of stimulus parameters on task performance

The responses “pattern more tilted to the left” were analyzed using a general linear mixed effects probit regression. The results suggested that the model that best fitted the responses included as fixed effects the mean orientation of the line segments, the noise level, and the elongation of the patterns. The duration of the

stimuli – fixed or self-determined had no significant effect on the performance ( $\chi^2_1=0.10$ ,  $P=0.76$ ) and no significant interaction between the stimulus duration and the other factors was observed at  $P=0.05$ . All main effects were significant at  $P=0.05$  ( $\chi^2_1=868.24$  for mean line orientation;  $\chi^2_4=33.99$  – for noise level and  $\chi^2_1=13.06$  – for elongation group). There was significant interaction between the noise level and the mean line orientation ( $\chi^2_4=197.93$ ,  $P<0.05$ ) suggesting different steepness of the psychometric function for different levels of orientation jitter (Fig. 6). The interaction between the noise level and the elongation factor was also significant at  $P<0.05$  ( $\chi^2_4=10.41$ ). The random effects included in the model comprise a random slope for noise by subject.

### *Parameters of the variance summation model*

The estimation of the parameters of the variance summation model follows the same steps as described for experiment 1. The mean slope of the probit regressions at the different noise levels is presented in Fig. 3B together with the fitted curve based on equation (1). The elongation of the patterns was included as a group factor in the non-linear model. The estimated internal noise is:  $3.34^\circ$  [ $3.22\text{--}3.45^\circ$ ] for elongated and  $5.64^\circ$  [ $5.51\text{--}5.76^\circ$ ] – for the non-elongated patterns, while the sampling efficiency represented by the number of samples pooled to determine the over-all orientation of the patterns was 7 [ $7.06$ ,  $6.97\text{--}7.16$ ] vs. 9 [ $8.40\text{--}8.64$ ]. Again, the numbers in brackets show the non-rounded values and the 95% confidence intervals of the effective sample size. The values of these parameters are higher than in experiment 1 suggesting more efficient exploration of the local orientation information.

The bias of the estimates was determined by the negative *ratio* of intercept and slope in the psychometric functions (Fig. 4B). For both types of patterns the bias increased with the increase of the orientation jitter. It was larger for the elongated patterns.

### *Effect of stimulus parameters on the time to perform the task*

In this experiment subjects 1–5 needed less time than the fixed duration of 1.67 s in 48.7%, 62.7%, 78.0%, 58.0%, and 27.7% of cases. The mean response time for each of the subjects was 2.23 s, 1.72 s, 1.34 s, 1.66 s, and 2.34 s, respectively. The increase in

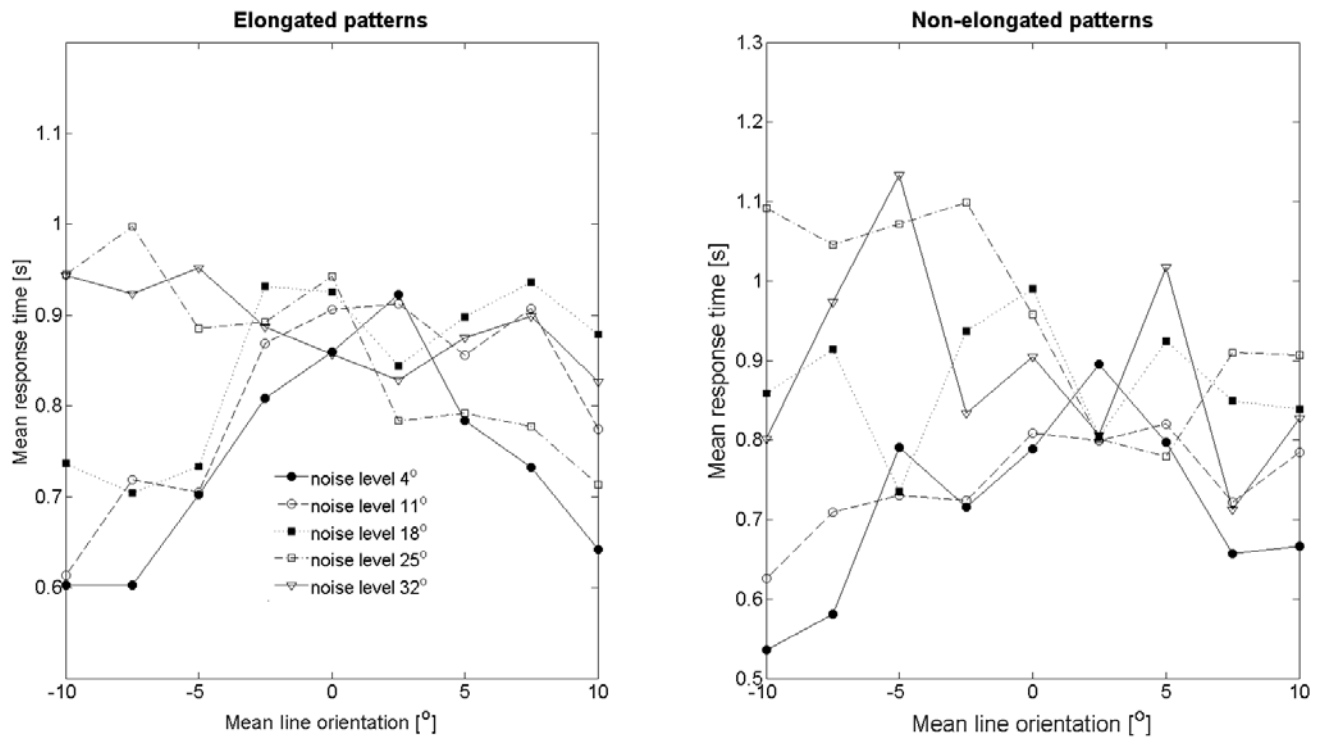


Fig. 10. The mean response time for discrimination thresholds for elongated and non-elongated patterns with equal line length at different noise levels and mean line orientation in experiment 3a.

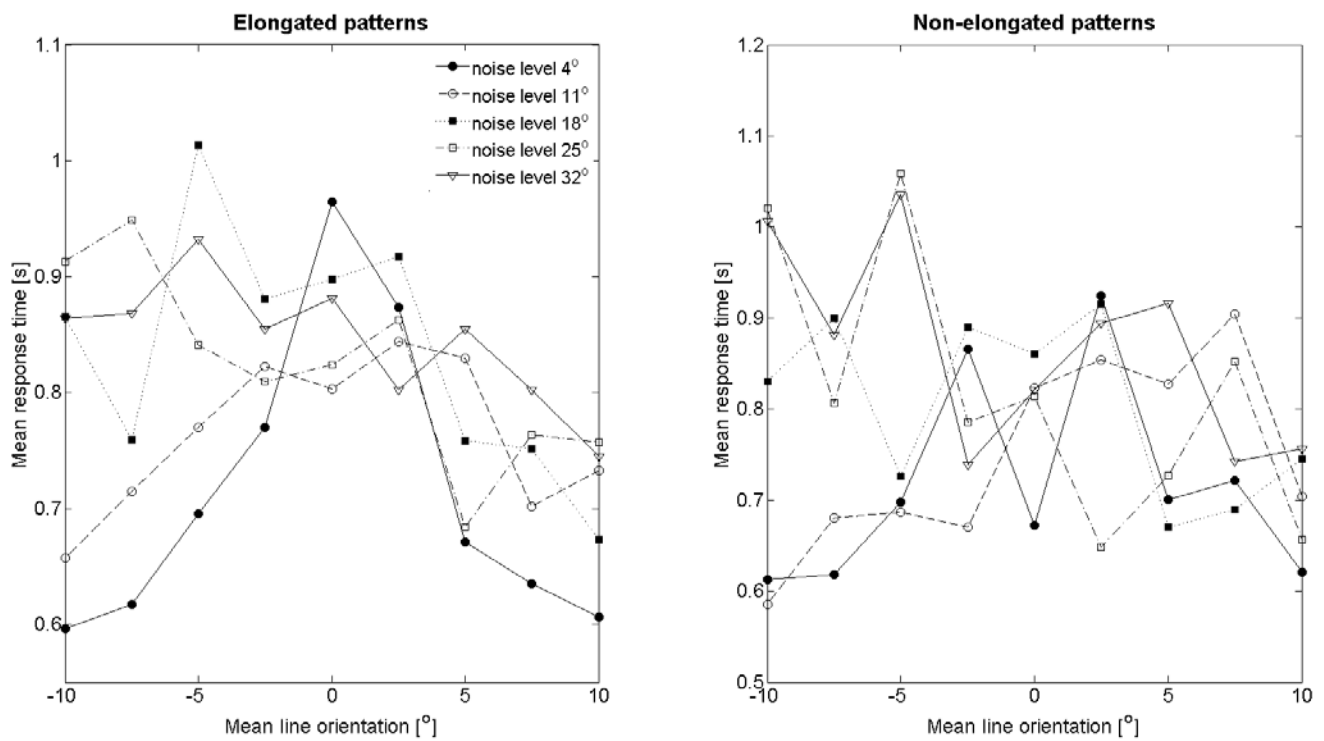


Fig. 11. The mean response time for discrimination thresholds for elongated and non-elongated patterns with unequal line length at different noise levels and mean line orientation in experiment 3b.

response time for some of the Subjects could be interpreted as indication that when the line length varied, the task of determining mean pattern orientation was more difficult.

To evaluate how the response time depended on the experimental factors we performed a linear mixed effects analysis on the log-transformed values. The results suggested that the model that best described the data included only random intercept by subject and shows significant effects of the noise level ( $F_{4,2195}=43.88$ ,  $P<0.05$ ), the mean line orientation ( $F_{8,2195}=15.59$ ,  $P<0.05$ ) and an interaction between the mean line orientation and the noise level ( $F_{32,2195}=3.35$ ,  $P<0.05$ ). The response time increased with the increase in the noise level, depended non-monotonically on the mean line orientation being maximal when it was close to vertical at low noise levels, and depended less on mean line orientation for higher values of noise (see Fig. 7). However, the elongation of the pattern did not significantly ( $P=0.05$ ) influenced the time needed to respond.

## Discussion

The results of experiment 2 confirmed the expectation that manipulating the line length of the segments in the pattern would affect the task performance. However, changing the variability of the line segments reduced the additive internal noise only for the elongated patterns while it was expected to have effect for both types of patterns due to the higher precision of local orientation estimation for longer lines. A possible explanation for these findings might be that increasing the line length leads to more crossings between the line segments and the local information about orientation was based on both the orientation of the single, uncrossed segments and on the angle between the crossing ones. Such hypothesis implies higher bias for both types of patterns. Indeed, the results suggest an increase in the bias and its variability for the non-elongated patterns. It is also possible that the lateral interactions between the local orientation filters reduce their sensitivity. It is unclear, however, why the esti-

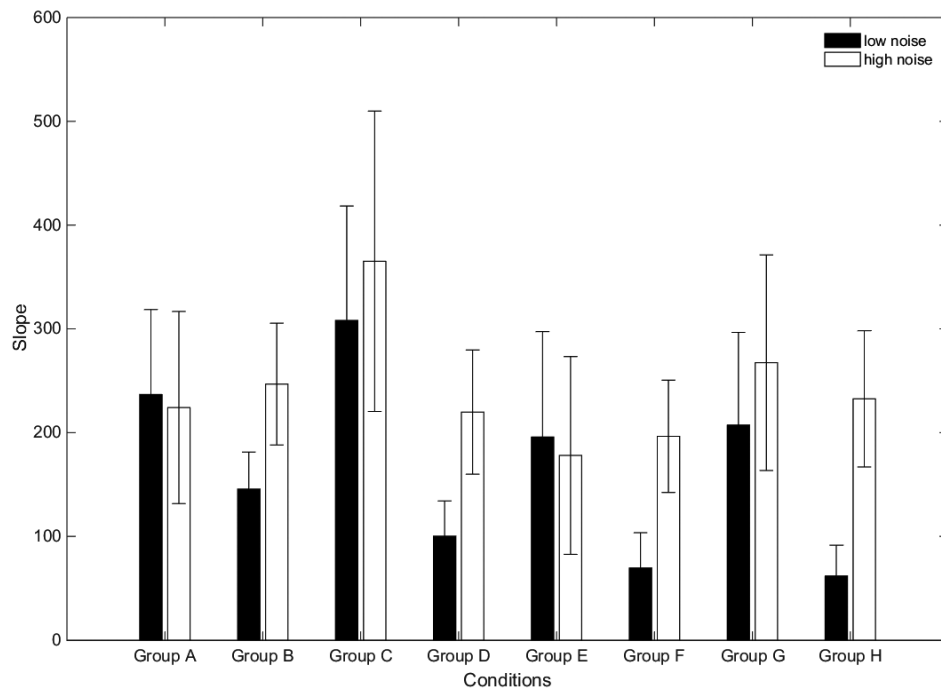


Fig. 12. Slope of the linear fit between percent correct responses and the percent agreement obtained at different presentation times and for patterns of different elongation and line length. Group A: non-speeded condition, elongated patterns, equal line length. Group B: speeded condition, elongated patterns, equal line length. Group C: non-speeded condition, elongated patterns, unequal line length. Group D: speeded condition, elongated patterns, unequal line length. Group E: non-speeded condition, non-elongated patterns, equal line length. Group F: speeded condition, non-elongated patterns, equal line length. Group G: non-speeded condition, non-elongated patterns, unequal line length. Group H: speeded condition, non-elongated patterns, unequal line length.

mated internal noise was reduced so significantly for the elongated patterns. This might be related to the greater density of points inside the patterns that facilitates the use of positional information in estimating the global orientation based on the principal axis.

The decrease in the effective sample size might be a result of using a limited area for integration of local information, and thus, to the lower number of segments entering it when the line length of the segments was increased or to the higher attentional load for patterns of variable length as compared to those of equal length. Again, it is unclear why this would have unequal effects on elongated and non-elongated patterns. One possibility would be that the encoding of overall shape information based on positional information used for principle axis encoding and of the average line orientation have different time course and the observed effects show the contribution not only of spatial integration, but of temporal integration as well.

### Experiment 3

In experiment 3, we asked the participants to make speeded responses to the stimuli of experiment 1 and 2 in order to better understand the role of temporal integration in orientation estimation. This manipulation of instruction aimed to reduce the potential role of temporal integration of local orientation information.

#### Methods

##### *Stimuli*

The same stimuli used in experiment 1 and 2 were used.

##### *Procedure*

The experiment was divided into two parts performed on different days. Each part had two blocks. In one of them (experiment 3a) all line elements had equal length similar to experiment 1, while in the second (experiment 3b), the line length in the interior of the patterns was variable and larger than in experiment 1 and the stimuli were the same as those used in experiment 2. The order of the two parts was counter-balanced over subjects. The instruction to the subjects was to indicate whether the patterns seemed more tilted to the right or to the left of the vertical trying to

perform the task as fast as possible while being accurate.

#### Results

##### *Effect of stimulus parameters on task performance*

The proportion of responses “more tilted to the left” were analyzed separately for experiment 3a and experiment 3b. A mixed effects general linear probit regression was applied to the data. The results showed that for patterns of equal line length (experiment 3a) the best model included intercept varying among differently elongated groups and random variation of slope and intercept among subjects within groups of different elongation, while the fixed effects include the mean line orientation, the noise level, and their interaction. The elongation of the patterns had no significant effect on the performance ( $\chi^2_1=0.41$ ,  $P=0.52$ ). The mean line orientation ( $\chi^2_1=437.36$ ,  $P<0.05$ ) and the noise level ( $\chi^2_4=47.16$ ,  $P<0.05$ ) as well as their interaction ( $\chi^2_4=81.68$ ,  $P<0.05$ ) significantly affected the performance suggesting changes in bias and sensitivity depending on the orientation jitter.

For patterns with unequal length (experiment 3b) the random effects included random slope and intercept by subject; the fixed effects included the effect of mean line orientation, the noise level, the interaction between the noise level and the mean line orientation and the interaction of noise level and elongation. All main effects and interactions were significant at  $P=0.05$  ( $\chi^2_1=90.72$  – for mean line orientation;  $\chi^2_4=156.37$  – for the noise level;  $\chi^2_1=20.46$  – for the elongation group;  $\chi^2_4=93.31$  – for the interaction of the mean line orientation and the noise level, and  $\chi^2_4=11.54$  – for the interaction of the noise level and the elongation group). The effect of mean line orientation and noise level on the proportion “more tilted to the left” for elongated and non-elongated patterns with equal and unequal line lengths are presented in Figs 8 and 9.

The results of experiment 3 suggest greater individual differences between the participants. It is possible that under time pressure they used different strategies.

##### *Parameters of the variance summation model*

The same analyses as in experiment 1 were used to estimate the slope values of the psychometric function

as a measure of the mean discrimination thresholds and their 95% confidence intervals at different noise levels. The bias and its 95% confidence intervals were estimated by the negative ratio of the intercept and slope of the psychometric functions. The results for elongated and non-elongated patterns with equal and unequal line length are given in Figs 3C, 3D and 4C, 4D.

A non-linear regression was used to evaluate the parameters of the variance summation model (equation 1) based on the bootstrapped estimates of the discrimination thresholds. The elongation of the patterns was used as a grouping variable. The additive internal noise for patterns with equal length was estimated to be  $6.23^\circ$  [5.98–6.48°] for elongated patterns, and  $8.38^\circ$  [8.08–8.68°] – for non-elongated patterns, while for variable line length the corresponding estimates were:  $3.95^\circ$  [3.77–4.13°] and  $6.14^\circ$  [5.94–6.35°]. The effective number of samples for patterns with equal line length was 6 [5.76, 5.60–5.92] for elongated and 19 [18.81, 18.25–19.37] – for non-elongated patterns in experiment 3a and 6 [5.89, 5.77–6.02] for elongated and 5 [5.40, 5.28–5.52] in experiment 3b.

The fitted curves representing the variance summation model are presented in Figs 3C and 3D for patterns of equal or variable length.

#### *Effect of stimulus parameters on the time to perform the task*

The mean response time for subjects 1–5 in experiment 3a was: 1.03, 0.88, 0.67, 0.53 and 1.02 s, while for experiment 3b it was: 0.95, 0.75, 0.72, 0.57 and 0.99 s. If we assume that the motor component of the response is about 200–250 ms, the results suggest that on average the subjects needed much more time to perform the task than usually used in orientation discrimination studies applying the equivalent noise paradigm.

A linear mixed-effects model with factors: mean line orientation, noise level and elongation, as well as their interactions was separately performed on the log-transformed values of the response time for patterns of equal or variable line length. For patterns of equal line length, the results suggest significant main effects of the noise level ( $F_{4,2201}=24.91$ ,  $P<0.05$ ), the mean line orientation ( $F_{8,2155}=6.31$ ,  $P<0.05$ ) and significant interaction between the mean line orientation and the noise level ( $F_{32,2201}=4.83$ ,  $P<0.05$ ). As in previous experiments, the response time

increased with the noise level and was non-monotonic function of the mean line length being highest when the average orientation of the line segments was close to vertical. The effect of the mean line orientation on the response time was reduced at high noise levels.

The response time for unequal pattern length also depended on the noise level ( $F_{4,2155}=18.06$ ,  $P<0.05$ ), the mean line orientation ( $F_{8,2155}=7.47$ ,  $P<0.05$ ) and the interaction between these two factors ( $F_{8,2155}=3.90$ ,  $P<0.05$ ). The interaction between the noise level, the mean line orientation and the elongation of the patterns was also significant ( $F_{8,2155}=1.64$ ,  $P<0.05$ ).

In both analyses, the random factors include random intercept and all factors were considered categorical. The results for the response time are illustrated in Figs 10 and 11.

#### Discussion

The results suggest that when the instruction required speeded responses, the performance of the observers deteriorates. For the elongated patterns, the effective sample size is reduced while the internal noise changed little. For the non-elongated patterns, the variability of the line length of the segments led to significant differences in the parameters of the variance-summation model. When the patterns had equal line length both the internal noise and the sampling efficiency increased significantly. However, when the line length varied, the internal noise increased to a lesser extent, but the sampling efficiency decreased. The serious increase in the sampling efficiency for non-elongated patterns with equal line length could be due to the presence of multiplicative noise or to a change in the response strategy.

The instruction for speeded responses did not change the effect of the stimulus parameters on the response time. As in experiments 1 and 2, the response time depended most on the mean line orientation and the noise level. Longer responses were obtained for patterns with mean orientation close to the vertical when the noise level is low and for high levels of external noise.

To understand better the results of the study, we performed additional analyses, comparing directly the results of all experiments and using other approaches like consistency measures of the responses in double-pass procedure.



### Comparison of the results

#### *Effect of stimulus parameters and stimulus duration on task performance*

To evaluate the effect of stimulus spatial and temporal parameters on task performance the proportion of responses “more tilted to the left” from experiments 1–3 were combined. The stimulus duration was coded as a factor with three different values: fixed duration, self-determined duration with no time pressure and self-determined duration with time pressure (experiment 3). The line length was also coded as a factor with two levels: equal and unequal. The other fixed effects included in the analysis were the noise level, the mean line orientation (and used as a regressor) and the elongation of the patterns. Mixed-effects probit regression was performed. The model that best described the data included a random slope parameter determined by the mean line orientation and a random intercept by subject. The main effect of mean line orientation ( $\chi^2_1=2741.59$ ,  $P<0.05$ ) and of the noise level were significant ( $\chi^2_4=971.47$ ,  $P<0.05$ ). The main effects of line length ( $\chi^2_1=8.73$ ,  $P<0.05$ ), stimulus duration ( $\chi^2_2=14.52$ ,  $P<0.05$ ) and the elongation ( $\chi^2_1=37.02$ ,  $P<0.05$ ) were also significant. The interactions between the noise level and the mean line orientation ( $\chi^2_4=483.95$ ), between the noise level and the pattern elongation ( $\chi^2_4=22.50$ ) and between the noise level and the line length ( $\chi^2_4=34.80$ ) were significant ( $P<0.05$ ). These results indicate that the slope of the psychometric functions depends on the noise level and the location of these functions is different at different noise levels for patterns of different elongation and stimulus duration. The steepness of the psychometric functions depended also on the stimulus duration since the interaction between the mean line orientation and the stimulus duration was also significant ( $\chi^2_4=33.27$ ,  $P<0.05$ ).

The interaction between the noise level, the mean line orientation and the line length of the patterns was also significantly different at  $P<0.05$  ( $\chi^2_4=19.33$ ). Hence, the slope of the psychometric function changes differently at different noise level depending on whether all segments have equal length or the line length varies. The triple interaction between the noise level, the pattern elongation and the line length (equal or unequal) were also significant ( $\chi^2_4=30.51$ ,  $P<0.05$ ).

### Consistency measures

Given that the stimuli with fixed and self-determined duration in experiments 1–3 were the same but differed only in duration allowed us to treat the data in these experiments as double-passes and to use the consistency of the responses to evaluate the internal noise in task performance. Usually, the proportion of response agreement with double-pass experiments is plotted against the proportion correct responses (e.g. Burgess and Colborne 1988, Lu and Doshier 2008).

As in our experiments the number of stimulus presentations was relatively low, we estimated the percent correct responses and the percent agreement combining the data of all subjects comparing the dependence of percent correct on percent agreement between the data in the fixed and non-speeded conditions in experiments 1 and 2 and between these data and the speeded conditions for patterns with equal or unequal line length, obtained in experiment 3 for low noise level ( $4^\circ$ ) and for high noise level ( $32^\circ$ ). The comparison of the slope at low noise levels may indicate the contribution of late noise, while the comparison at high noise levels may allow to separate the effects of multiplicative noise and the changes in sampling efficiency (e.g. Gold 2001).

The relation given by Gold (2001) was used for the fits (equation 2).

$$p_c = k_{I/E} \log_{10}(p_a) + 100 \quad (2)$$

In this equation  $p_c$  corresponds to the percent correct responses,  $p_a$  – to the percent of equal responses (percent of agreement) in the two passes with the same stimuli and  $k_{I/E}$  is the slope related to the *ratio* of the internal to external noise. The lower the slope, the larger the ratio of the internal to external noise.

An analysis of covariance was performed to evaluate whether the slope parameter in equation (2) depended on the condition: non-speeded *vs.* speeded, the elongation of the patterns and the line length of the segments: equal or variable at low and high levels of external noise. The results suggested that at high levels of external noise all regression lines represented by equation (2) had equal slope of 226.45 [200.74–252.16]. When the external noise is low, the length of the lines had negligible effect on the slope parameter, though there is a trend for lower internal noise for patterns of variable length for the non-speeded condition. The condition and the elongation of the patterns signifi-

cantly affected the slope of the regression line at low levels of external noise. The estimated slopes and their 95% confidence intervals are presented in Fig. 12.

As indicated by Gold (2001), a change in slope and correspondingly, in internal-to-external noise ratio at low external noise levels suggests the presence of late noise. Our data show drastic increase in this noise for speeded responses and unequal effect on the elongated and non-elongated patterns. The presence of late noise could be regarded as indication that diverse early mechanisms contribute to global orientation estimation and they differ in their stochastic properties. The lack of significant difference in slopes at high levels of noise rules out the presence of internal noise depending on the stimulus strength (multiplicative noise). Similar conclusions could be made for both types of patterns for the non-speeded conditions. Still, this conclusion should be taken with caution as our estimate is based on relatively small samples and the individual differences between the participants are neglected. As shown by Hasan and others (2012), the precision of the double pass procedure depends on the number of trials and of the observers and is less than 10–15%.

Effect of stimulus parameters on the response time

The response time needed to perform the task may represent the stimulus strength and task difficulty, the time needed for encoding of information and its accumulation and other characteristics of the process of making decisions. For example, Ratcliff (1978) proposed a diffusion model to describe the decision making between two alternatives. He proposed that when a choice was difficult, more accumulated information was needed before initiating a response. The task difficulty was described by a parameter named drift rate  $\nu$ . The model also included a parameter that describes the bias  $z_r$ , i.e. whether there was a difference in the amount of accumulated information for the two alternatives. Another parameter (boundary separation  $a$ ) describes whether the participants preferred accuracy instead of speed of responding; it is a measure of conservatism and can be manipulated by the instruction to the participants. Additionally, the diffusion model includes a parameter  $T_0$  that is considered unrelated to the decision process and combines the time associated with the motor components of the response, as well as the time associated with the encoding processes. Another parameter describes the noise process linked to the decision-making. However, this parameter is not independent of the other model parameters; same

response times could be obtained either by scaling all other parameters or by scaling the noise amplitude by the same amount. More elaborate variants of the diffusion model describe also the inter-trial variability of  $z_r$ ,  $\nu$  and  $T_0$ . We did not consider these variants as increasing the number of the parameters would not be appropriate for the sample size we had. Moreover, the inclusion of additional parameters would provide little additional insight in interpreting and understanding the task performance in our study.

To estimate the parameters of the diffusion model we used fast-dm (Voss and Voss 2007, 2008). The model parameters were estimated separately for each experimental condition i.e. for each level of noise, mean line orientation, line length variation and stimulus duration (low- and high-time pressure) for the elongated and the non-elongated patterns. The responses of all subjects were combined as we were interested mostly in the overall effect of the experimental manipulations on the parameters of the diffusion model. The estimated parameters were analyzed using ANOVA with factors: mean line orientation, noise level, time pressure, elongation and line length. The results of the analyses showed that the bias parameter  $z_r$  depended on the mean line orientation ( $F_{8,347}=4.29$ ,  $P<0.05$ ) and it changed depending on the line length ( $F_{8,347}=5.30$ ,  $P<0.05$ ). The bias parameter was lowest when the mean line orientation was close to the vertical and increases with its deviation from vertical. Furthermore, it was larger for patterns of variable length.

The boundary separation  $a$  depended significantly on the mean line orientation ( $F_{8,349}=2.07$ ,  $P<0.05$ ) being larger when it had positive values; on the line length ( $F_{1,349}=6.09$ ,  $P<0.05$ ), and on the level of time pressure ( $F_{1,349}=307.46$ ,  $P<0.05$ ). Under time pressure, the boundary separation was less while it increased for patterns of variable length.

The drift rate  $\nu$  depended significantly on the mean line orientation ( $F_{8,345}=18.30$ ,  $P<0.05$ ), being slower when the mean line orientation was close to the vertical. It also decreased with the increase of noise level ( $F_{4,345}=8.40$ ,  $P<0.05$ ), suggesting an increase in task difficulty with the increase of orientation jitter. For speeded responses, the drift rate was significantly higher than for non-speeded ones ( $F_{1,345}=31.82$ ,  $P<0.05$ ). There was also some tendency for higher drift rate for patterns of variable line length ( $F_{1,345}=2.78$ ,  $P=0.09$ ).

The non-decisional time  $T_0$  depended on the degree of time pressure ( $F_{1,352}=224.64$ ,  $P<0.05$ ), the line length

variability ( $F_{1,352}=6.60$ ,  $P<0.05$ ), the elongation of the patterns ( $F_{1,352}=14.56$ ,  $P<0.05$ ) and the noise level ( $F_{4,352}=4.12$ ,  $P<0.05$ ). It was shorter under time pressure and for non-elongated patterns, whereas it increased with the noise level and was higher for patterns with variable line length. As this parameter of the diffusion model is related to encoding and non-decisional effects, this finding might be considered as an indication that the processes of encoding orientation information differ depending on the elongation of the patterns or that different early mechanisms contribute to the global pattern orientation of the elongated patterns.

The analyses also suggest that when the orientation jitter is high the responses were more biased and the task difficulty was higher. This may suggest different attentional load at low and high noise levels.

## GENERAL DISCUSSION

The ability of the visual system to evaluate the statistical properties of multi-element patterns has significant importance in tasks like figure-ground segregation of textured patterns, detection of visual contours, object recognition or in the determination of surface spatial layout. The present study shows:

1) increased bias in a global orientation estimation at high uncertainty levels due to higher orientation jitter in the patterns;

2) dependence of the bias on the pattern elongation, line length variation, and time pressure for the response;

3) different estimates of the additive internal noise depending on the pattern elongation, line length variability and stimulus time presentation; Indications for the presence of late internal noise in global orientation estimation from the consistency measures in double pass procedure;

4) changes in sampling efficiency depending on pattern elongation, line length variability, and stimulus time presentation;

5) changes in response time depending on the averaged pattern orientation, noise level, line length variability and time pressure.

The increase in bias with stimulus uncertainty was observed in other studies on orientation discrimination (e.g. Tomassini et al. 2010, Girshick et al. 2011). Girshick and others (2011) interpreted the superior discrimination performance at low noise levels near the cardinal directions as indication for differences in the

amplitude of internal noise in different orientations. Girshick and others (2011) considered different sources of non-uniformity in local estimation of orientation in addition to differences in tuning curves for cardinal directions like the disproportional representation of these orientations in V1, variations in gain, baseline firing rate or correlations in responses. In our experiments the mean line orientation was close to one of the cardinal directions – the vertical, but the orientation jitter changes the range of orientations in the patterns and thus, would increase the non-uniformity in the discrimination precision implying that the internal noise could not be considered the same in low and high noise conditions. Tomassini and others (2010) showed that in conditions of uncertainty the visual system gives higher weight to orientations close to the cardinal directions as these orientations are predominant in the natural environment. The different weight given to elements with different orientation as well as the potential differences in the amplitude of internal noise at different orientation would suggest that the internal noise depends on the orientation jitter and thus, violates one of the main assumptions of the variance summation model – for constant levels of internal noise. It would suggest the presence of stimulus-dependent noise. While we failed to confirm this expectation comparing the slopes of the dependence between the percent agreement and the percent correct responses obtained with the double-pass procedure, we cannot rule out this possibility due to the relatively low sensitivity of double-pass estimates (e.g. Hasan et al. 2012), the low number of responses used in the estimation and the neglect of individual differences between the subjects.

Our data show that the bias depended not only on the level of noise, but also on the pattern elongation. On general, the bias was less for non-elongated patterns than for elongated ones and it differed depending on the stimulus uncertainty and pattern elongation. In these cases the bias was negative. This is strange – more common would be to have higher variability of the estimates, but not a signed bias. The negative bias implies that the patterns appeared more tilted to the left. The different effect of pattern elongation on response bias and its sign might suggest that in conditions of uncertainty or time pressure the visual system may use another source of orientation information related to the axis of object shape and based on positional information. Indeed, the average orientation of the principal axis of the patterns turned out to be

33.66°. The possibility of using other source of information at high uncertainty, however, suggests a change in strategy at high noise levels, a hypothesis already raised by Allard and Cavanagh (2012).

The difference in task performance at high and low noise levels is supported also by the interaction between the noise level and elongation of the patterns observed in the analysis of the effects of the experimental factors on the psychometric function. The results suggest that elongation of the patterns play a significant role mainly in conditions of high uncertainty. It might be that in these conditions the observers' strategy changes and is affected by the global orientation of the overall shape related to their first principal axis. However, we have not explored in detail this issue. It might be that the two global orientation estimates – the one, based on the positional information, represented by the first principal axis and the other – based on averaging the local orientations in the pattern are combined depending on their reliability. Further experiments are needed to provide better understanding of these effects.

The elongation of the patterns affected differently the estimates of the internal noise and effective sample size – a result, which disagrees with the general interpretation of the variance-summation model. The internal noise in averaging orientation or motion direction tasks is usually related to the precision of each local estimate, while the sampling efficiency is considered limited only by the global sample size (e.g. Dakin 2001, Dakin et al. 2009). Our results, however, show a different effect of the temporal and spatial stimulus attributes on the perceived global orientation. For non-elongated patterns, the speeded responses introduced higher levels of internal noise and a significant change in performance depending on the length and/or length variability of the pattern segments. The induction of higher additive internal noise for the non-elongated patterns was confirmed also by the slope estimates of the dependence between the percent correct responses and the response consistency at low noise levels. For the elongated patterns the presentation time had less effect on the performance, it affected mainly the efficiency of using orientation information as estimated by the variance-summation model. The estimated internal additive noise was reduced when the length of the segments was longer and variable. This result was observed both in speeded and in non-speeded conditions and revealed both in the estimated internal noise

and as a trend in the consistency measures of the double-pass procedure at low noise level for the non-speeded responses. Our expectation was that changes in segment length would improve the local orientation estimation and thus, would reduce the additive internal noise for all patterns, irrespective of their elongation. Since the findings of the double-pass procedure suggest the presence of late additive internal noise in averaging the pattern orientation, the reduction of the internal noise might be related to changes in this noise component. The presence of late internal noise and the effect of the stimulus presentation time in our experimental conditions may reflect the dynamics of perceptual decision processes in human brain in conditions of uncertainty and the integration of sensory evidence over time. They could be related to the differences in the strength of the sensory signals and the task difficulty.

Most of the existing studies on global orientation perception use short presentation times (e.g. Dakin 2001, Dakin et al. 2009, Solomon 2010, Allard and Cavanagh 2012, Tibber et al. 2014). Jones et al. (2003) studied the effect of presentation time on orientation discrimination of local and global noisy stimuli and showed that reducing the presentation time from 1 s to 100 ms had insignificant effect on discrimination thresholds. In a complementary study, Anderson et al. (2007) showed that the presence of multiple independent samples over time improved the sensitivity to orientation discrimination. The presentation time used in our study was longer than 1 s in experiments 1 and 2 and was reduced in experiment 3, but its amount was determined by the needs of the observers to perform the task. As our data show, in non-speeded conditions the observers performed 3–4 saccades and the number of saccades increased with orientation uncertainty. Therefore, it might be assumed that due to the eye movements the number of independent samples for orientation discrimination increased. This suggests that in our experimental conditions temporal integration played a significant role and might explain the higher estimates of the effective sample size obtained in our study. In some conditions, they exceed the squared root of the pattern elements – a typical estimate of effective sample size in averaging orientation tasks (e.g. Dakin et al. 2009). However, it could not explain the extreme increase in the effective sample size for non-elongated patterns with equal length obtained for speeded responses. Dakin and others

(2005) proposed that the effective sample size might be related to a system operating on a population of neural responses corrupted by multiplicative noise. Hence, it might be that this multiplicative (Poisson) noise varies with the spatial and temporal characteristics of the patterns.

## CONCLUSIONS

Taken together, the results of the present study show that while a variance-summation model fits well the dependence of the discrimination thresholds on the orientation jitter added to the patterns, the interpretation of its parameters as related to the precision of local orientation estimates and inefficient pooling of this information is too simplistic. The effects of the spatial and temporal factors on the perceived global orientation in the present study imply the involvement of other limiting or contributing factors. Potential contribution to the performance could have lateral interactions in evaluating local orientations; different precision of the local orientation estimates; the integration of segments into contours and the effect of spatial alignment and contextual effects on this process; the global orientation of the shape of the patterns represented by their first principal axis; different effects of uncertainty on perceptual decision making, etc. Understanding the processes involved in estimating the global orientation perception in noisy conditions is important as the equivalent noise methodology is used to describe the deficiency in different age groups (e.g. Bocheva et al. 2013, Manning et al. 2014) or clinical populations (Neveu et al. 2009, Tibber et al. 2014). Our study indicates that further studies are needed to better understand the processes of fine orientation estimation in noisy conditions.

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