



Component processes in contour integration: A direct comparison between snakes and ladders in a detection and a shape discrimination task



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ABSTRACT

In contour integration, a relevant question is whether snakes and ladders are processed similarly. Higher presentation time thresholds for ladders in detection tasks indicate this is not the case. However, in a detection task only processing differences at the level of element linking and possibly contour localization might be picked up, while differences at the shape encoding level cannot be noticed. In this study, we make a direct comparison of detection and shape discrimination tasks to investigate if processing differences in the visual system between snakes and ladders are limited to contour detection or extend to higher level contour processing, like shape encoding. Stimuli consisted of elements that were oriented collinearly (snakes) or orthogonally (ladders) to the contour path and were surrounded by randomly oriented background elements. In two tasks, six experienced subjects either detected the contour when presented with a contour and a completely random stimulus or performed a shape discrimination task when presented with two contours with different curvature. Presentation time was varied in 9 steps between 8 and 492 ms. By applying a generalized linear mixed model we found that differences in snake and ladder processing are not limited to a detection stage but are also apparent at a shape encoding stage.

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1. Introduction

Organizing a visual scene in coherent perceptual units requires perceptual grouping, that is combining elements in meaningful configurations, a process known to follow the principles introduced by Gestalt psychologists such as Wertheimer (1938; for recent reviews, see Wagemans et al., 2012a, 2012b). For instance, neighboring elements can be grouped based on proximity. Also similarity in color, orientation or shape of the elements can facilitate grouping or good continuation of the elements. A substantial part of research on perceptual grouping has focused on contour integration (for a review, see Hess, May, & Dumoulin, 2013). In contour integration, a contour can be grouped according to the Gestalt principle of collinearity by aligning the orientation of elements along a smooth path while keeping the orientation of the background elements random. In the path paradigm introduced by Field, Hayes, and Hess (1993), subjects have to detect a contour in an array of spatially separate Gabor elements. Their paradigm has initiated an elaborate line of research on the underlying

mechanisms of contour integration. In the past twenty years, several studies have shown that detection performance increases with, for instance, decreasing contour length (Field, Hayes, & Hess, 1993), decreasing curvature (Field, Hayes, & Hess, 1993), longer presentation duration (Roelfsema, Scholte, & Spekreijse, 1999), phase similarity (Hess & Dakin, 1999), decreasing inter-element distance (Field, Hayes, & Hess, 1993) and motion drifting elements (Bex, Simmers, & Dakin, 2001). These and other dependencies on stimulus parameters have provided accumulating evidence for a mechanism of contour integration that combines responses of a number of local independent inputs mediated by long-range interactions between cells with similar orientation preferences (for reviews, see Hess, Hayes, & Field, 2003; Hess, May, & Dumoulin, 2013).

An important stimulus characteristic in contour integration is the relative orientation of the elements: contours elements can be aligned with the path of the contour or have an orientation orthogonal to the contour path. These contours are called 'snakes' and 'ladders', respectively, since the labels were introduced by Bex, Simmers, and Dakin (2001). Despite the similar statistical properties of snakes and ladders, several authors have observed a higher sensitivity for snakes than for ladders in a contour detection paradigm with static (Field, Hayes, & Hess, 1993; Ledgeway, Hess, & Geisler, 2005) and with dynamic stimuli (Bex, Simmers, & Dakin, 2001; Ledgeway, Hess, & Geisler, 2005). In addition, differential

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effects of phase manipulation (Bellacosa Marotti, Pavan, & Casco, 2012; Hansen & Hess, 2006), element separation (May & Hess, 2008), spatial arrangement (Bellacosa Marotti, Pavan, & Casco, 2012) and perpendicular context (Dakin & Baruch, 2009; Robol, Casco, & Dakin, 2012) have been observed between snakes and ladders. The observed differences in psychophysical experiments have raised the question whether snakes and ladders are mediated by the same mechanism or whether different mechanisms are involved (e.g., May & Hess, 2007, 2008). A study by Casco et al. (2009) suggested different temporal dynamics for ladders and snakes because they observed a late shift of ERP towards positive values at 275 ms for similarity (which is associated with ladder perception), while collinearity (which is associated with snake perception, see Bellacosa Marotti, Pavan, & Casco, 2012) evoked an earlier positive response between 40 and 179 ms. On the contrary, May and Hess (2007) have not found evidence for different integration speeds of snakes and ladders in a psychophysical experiment. In sum, whether snakes and ladders are processed differently is still unclear.

Statistical properties of natural images have been correlated with snakes and ladder detection (e.g., Elder & Goldberg, 2002). For instance, prevalence of aligned image segments was higher than that of parallel image segments, indicating higher probability of collinear contours compared to parallel contours in natural images (Geisler et al., 2001). The aligned information, which is also present in snakes, can be related to the contours in the images, while the parallel information, which is also present in ladders can be associated with (texture) regions of the same object (Hess, Hayes, & Field, 2003; Ledgeway, Hess, & Geisler, 2005). For instance, an edge at one side of a branch is made up of collinear lines, while there is another parallel edge that marks the boundary of the wooden texture surface of the branch. It has been suggested that there is a relationship between the natural image statistics and the strength of long-range connections between neurons in the visual cortex (Hess, Hayes, & Field, 2003), namely that higher probability in natural images is associated with stronger connections. These connections strengths can in turn be linked to performance differences between snakes and ladders.

At least at the conceptual level, two aspects of contour processing can be distinguished (Loffler, 2008). One aspect concerns the grouping of contour elements belonging to the contour and the segregation of these elements from the background (two processes that often go hand in hand; see Machilsen & Wagemans, 2011; Sassi, Machilsen, & Wagemans, 2012; Sassi et al., 2010; Vancleef et al., 2013). This process is necessary to be able to detect the contour in a field of randomly oriented elements. The type and strength of grouping will differ between snakes and ladders, and between different shapes. For instance, the linking will be faster in shallow curves, where the orientation differences between the elements are smaller, compared to highly curved contours (Hess, Beaudot, & Mullen, 2001). For precise shape judgments, however, this process is probably not sufficient (Loffler, 2008). In a second type of processing, which is focused more on the shape of the contour than its detection, it seems quite likely that an abstraction of the elements is made and the contour is represented as a whole, irrespective of its parts. At that level of representation, characteristics of the contour, like shape, curvature, symmetry or length can be assessed.

These two aspects of contour processing are at stake in detection and (shape) discrimination tasks, respectively: in a detection task subjects have to merely detect the contour, while in a shape discrimination task subjects have to process and identify the shape in addition to detection (Robol, Casco, & Dakin, 2012). In other words, for detection the first type of processing is sufficient, while for shape discrimination both types of processing are necessary. Loffler (2008) also suggested that an imprecise fast feed-forward

collinearity mechanism is involved in detection, while shape discrimination (e.g., curvature discrimination) requires a refine slower mechanism that includes additional lateral and feedback connections. Moreover, Prins, Kingdom, and Hayes (2007) have pointed to the important distinction between a contour detection task and a shape discrimination task. They referred to the processing mechanisms in contour curvature analysis that have been identified by Watt and Andrews (1982): (1) an orthoaxial position system that is sufficient for contour detection, and (2) a slope and position analysis system that extracts curvature and can compare shapes in a shape discrimination task.

Although it has been suggested that both tasks are related to different aspects of contour processing, requiring different component processes and different levels of representation, a direct comparison between tasks has been made thus far in the context of contour integration. This is what our study sets out to do. To recapitulate, snake and ladder perception have mainly been studied in detection paradigms (Field, Hayes, & Hess, 1993) and these studies have shown a better detection for snakes than for ladders following various low-level stimulus manipulations (Bellacosa Marotti, Pavan, & Casco, 2012; Bex, Simmers, & Dakin, 2001; Field, Hayes, & Hess, 1993; Hansen & Hess, 2006; Hess, Ledgeway, & Dakin, 2000; Ledgeway, Hess, & Geisler, 2005; May & Hess, 2007, 2008). Whether encoding of the contour at the second level is still different for snakes and ladder is unclear. Comparing a detection task and a shape discrimination task would indicate if snakes and ladders are still processed differently at the level of shape encoding, or whether the differences are limited to the early processing stages that only play a role in a detection task. Our study aims to address this issue.

A first suggestion that shape encoding differs between snakes and ladders has been provided by Dakin and Baruch (2009), who investigated snake and ladder perception in a shape discrimination task and also found weaker performance for ladders than for snakes. However, because no direct comparison with a detection task was made in that study, it is not clear whether this difference can be completely attributed to an early processing stage like contour detection, or whether the difference is specifically due to different mechanisms at a shape encoding level. In addition, the effect of local orientation (parallel or orthogonal to the contour path) on shape discrimination of – mostly closed – contours and in the absence of background noise has been studied and contrasting results have been observed with different methods. On the one hand Gheorghiu and Kingdom (2008) found evidence for orientation selectivity of shape encoding since shape after-effects were reduced when the adaptor and test stimulus differed in orientation. Also, Levi and Klein (2000) observed an advantage for aligned elements in shape discrimination of closed circles. Another example is the study by Saarinen and Levi (2001) who found an effect of local element orientation on contrast detection thresholds in judging the orientation of a C-shaped figure. On the other hand, Vernier acuity does not seem to be influenced by a collinear or orthogonal orientation of the flankers (Keeble & Hess, 1998; Kooi, De Valois, & Switkes, 1991). In addition, the detection thresholds of radial frequency patterns (RFPs) are influenced in a similar way by parallel and orthogonal masks (Habak et al., 2004). Last, Keeble and Hess (1999) showed that the detection of positional jitter on the contour is not affected by the element orientations in both circles and open contours. Taken together, these findings illustrate that it is unclear whether collinearity has an influence only on detection and not on shape discrimination of contours, as concluded by Keeble and Hess (1999).

The aim of our study, therefore, was to investigate whether shape encoding of contours in a contour curvature discrimination task also differs depending on the nature of the regularity in the element orientation (which differs between snakes and ladders).

Hence, we present subjects with two stimulus types: snakes and ladders, in two tasks: a detection task and a shape discrimination task. A major advantage in comparison to the previous studies is that we compare detection and shape discrimination directly in the same subjects and with the same stimuli (similar to [Meinhardt et al., 2006](#)). This direct comparison enables us to derive more solid conclusions about differential shape encoding of snakes and ladders than the more tentative conclusions from previous studies, as reviewed above. In line with previous findings, we expect lower performance for ladders than for snakes in the detection task. The interesting comparison lies in the difference between snakes and ladder performance in the shape discrimination task. If shape encoding is similar for snakes and ladders, then we expect to find a similar performance difference between snakes and ladders in the detection and the discrimination task. In this case, the advantage of snakes over ladders would be limited to the first level, which is only apparent in the detection task. This would be reflected in a nonsignificant interaction between task and stimulus type. However, if shape encoding of snakes is easier or faster or better than of ladders (in addition to the differences at the first processing stage), then we expect an additional difference between snakes and ladders in the shape discrimination task compared to the detection task, thus a significant interaction between task and stimulus type.

As was explained before, linking of elements not only differs between snakes and ladders but is also affected by the curvature of the shape because linking of the elements is easier with smaller orientation differences between the elements. Therefore, we also expect to find an advantage for contours with a shallow curvature (referred to as “smooth”) compared to a stronger curvature (referred to as “curved”) in the detection task, although this is somewhat tangential to our primary research question about shape encoding.

2. Methods

2.1. Subjects

Six subjects participated in the study. They were 21–38 years old; three were male and three were female. All subjects were experienced psychophysical observers and had normal or corrected-to-normal vision. Three were completely naïve to the goals of the experiments (DB, DS, JB), while the three remaining subjects were not (EG, MS and author KV).

2.2. Stimuli

Stimuli consisted of small Gabor elements placed on a uniform gray background ([Fig. 1](#)). Stimuli of 10 by 10° (231 × 231 pixels at a viewing distance of 50 cm) were generated with the Grouping Elements Rendering Toolbox (GERT, [Demeyer & Machilsen, 2012](#)) for MATLAB (Mathworks). Based on orientation similarities, some elements in the stimulus display could be linked to form a curved contour. In the snake grouping displays, the Gabor elements took an orientation parallel to the local tangent of the curve, resulting in grouping based on collinearity. In the ladder grouping displays, the Gabor elements took an orientation orthogonal to the local tangent of the curve. All background elements were randomly oriented. The contour continued horizontally from the left to the right end of the display and took a sinusoidal shape with a small (0.36°) or large amplitude (0.72°), corresponding to smooth and curved contours, respectively. In either case, the phase of the sine wave was fixed at zero and the frequency at one, resulting in one cycle with a fixed horizontal position. The vertical position of the sine wave was jittered from the central position and over all

stimuli it covered 80% of the display for the large amplitude and 73% of the display for the small amplitude. Positions of elements along the contour and in the background were determined quasi-randomly: positions were restricted by a minimal inter-element distance of 0.55° and a minimal distance from the border of 0.25° for the background elements. Fixing the mean element distance on the contour to 0.6° resulted in the absence of a global and local density cue between the contour elements and the background elements as assessed by the Voronoi method incorporated in the GERT toolbox. The Gabor patches were even-symmetric and constructed by multiplying a cosine luminance grating with a circular Gaussian. The sine wave had a spatial frequency of 3.64 cycles per degree and the Gaussian envelope was characterized by a standard deviation of 0.1° visual angle. The masking stimuli were phase-scrambled versions of the above described stimuli following a circular normal (von Mises) distribution.

2.3. Apparatus and set-up

Subjects were seated in a dark and silent room. They rested their head in a chin-and-forehead rest and viewed the center of the stimuli binocularly from a distance of 50 cm. The stimuli were presented on a color calibrated CRT-monitor (View Sonic Graphics Series G90fB: 17 in., screen resolution 912 by 684 pixels, refresh rate 130 Hz). To guarantee precise luminance control and accurate timing in stimulus presentation and response registration, a Visual Stimulus Generator (ViSaGe, Cambridge Research Systems) graphic card controlled stimulus presentation. The mean luminance of the display was 69 cd/m². Responses were registered by a Cedrus response box (RB-530, Cambridge Research Systems). MATLAB environment (MathWorks) was used to generate stimuli and to operate the ViSaGe.

2.4. Procedure

In all conditions, subjects performed a temporal two-alternative forced-choice task (2AFC). Each trial started with a fixation cross presented for 800 ms. For both stimuli in a trial, we applied backward and forward masking for 300 ms. The duration of the stimulus intervals was manipulated. Stimuli were presented for nine different presentation times: 8 ms, 15 ms, 23 ms, 31 ms, 47 ms, 62 ms, 123 ms, 246 ms, and 492 ms. Pilot experiments revealed that this logarithmic scale with additional points at 23 ms and 47 ms nicely covers the whole range of the psychometric function. In addition to presentation times, we manipulated the task. In the first task, the detection task, one interval contained a target stimulus with a contour (small or large curvature), in the other interval all Gabor elements were randomly oriented, and so no collinearity grouping or linking could take place apart from that created by the random selection of element position and orientation. Subjects had to indicate in which interval the contour appeared. In the second task, the shape discrimination task, subjects discriminated between the small and the large curvature of the contour. They indicated the interval with the stimulus with the larger curvature. We opted for two separate tasks, and not for both a detection and discrimination judgment in a single trial, in order to obtain independent measures and to reduce the cognitive load of the task. These two tasks were combined with our two stimulus types: snakes and ladders, resulting in four conditions: snake detection, ladder detection, snake discrimination, ladder discrimination. While the presentation times varied randomly, trials were blocked for these four conditions to allow subjects to use an optimal encoding mechanism for each condition. The order of the conditions was randomly determined and each condition was preceded by 36 practice trials. The practice trials were followed by 18 blocks of 50 trials for each condition. For each data point, we collected 100

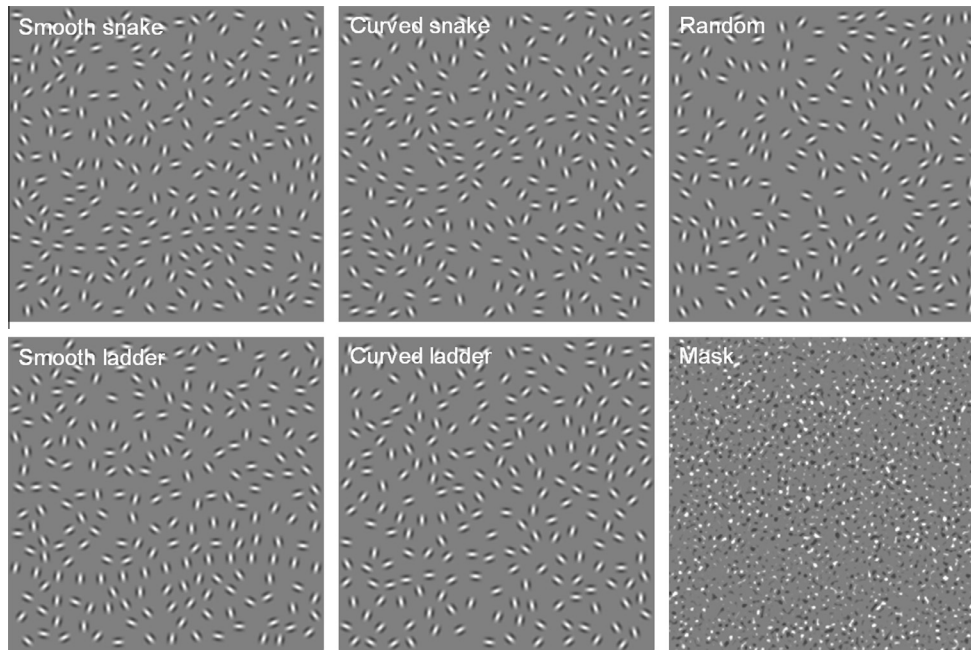


Fig. 1. Example of the stimuli. Gabor elements on the contour could have an orientation that is either parallel (snakes) or orthogonal to the contour path (ladders). Varying curvature resulted in smooth or curved contours. A stimulus with only random oriented Gabor elements was used in the detection task. Every stimulus is forward and backward masked by the mask present in the last column.

measurements resulting in 3600 trials (2 tasks \times 2 stimulus types \times 9 presentation times \times 100 measurements). Subjects could take breaks or stop the session after each block. For most subjects, data were collected in four sessions of about 1.5 h.

3. Results

3.1. Evaluation of data quality in individual analyses

To evaluate the quality of the data, we fitted psychometric functions to the data of each subject individually. For each combination of stimulus type and task a psychometric curve was fitted for each subject using the Psignifit toolbox version 2.5.6 for MATLAB. Fitting methods applied in this toolbox are described in Wichmann and Hill (2001a, 2001b). Data were fitted with three free parameters: alpha, beta and lambda (lapse rate), with lambda constrained by the interval 0–0.05. The guessing rate, gamma, was fixed at .5 proportion correct. We fitted the psychometric curve by a Weibull function. As can be seen in Fig. 2, we observed high correspondence between the data and the fitted psychometric functions. At the shortest presentation times (8–17 ms), subjects performed at chance level for almost all conditions. Performance gradually rose with increasing presentation time and quickly reached 90% correct at 47 ms for the snakes. For ladders, similar performance was reached around 123 ms. Goodness-of-fit was evaluated by deviance measures. For 20 of the 24 psychometric curves, the fitting procedure resulted in good goodness-of-fit statistics (Table 1). In the remaining four psychometric curves, the fits were still acceptable and they were therefore also included in the analyses.

After maximum likelihood fitting, 4999 bootstrap simulations were run to estimate the variability of the fitted parameters and to calculate confidence intervals. Estimated 75% correct thresholds are shown in Fig. 3 and Table 2. As is evident from the graphs, for all subjects snakes were easier to detect and to discriminate than ladders. When averaging over stimulus type, all but one subject showed higher thresholds for shape discrimination than for detection. In addition, the observed threshold difference between snakes

and ladders seems to be larger in the discrimination task than in the detection task for five out of six subjects. Comparison of 82.5% correct threshold showed a similar pattern of results for three out of six subjects, for the other subjects the differences between conditions were in the same direction but reduced.

3.2. Identification of significant effects in the group analyses

To test if our impressions from the individual analyses were supported statistically, we performed a group analysis. Data were analyzed by fitting several generalized linear mixed models (Bolker et al., 2009; Jaeger, 2008) to the group data. Generalized linear mixed models can model binary outcome data (correct/incorrect) that are logistically transformed with a lower asymptote at 50% correct to model the guess rate in the experiment. In addition to general effects of the manipulations, these models offer the advantage of modeling variability between subjects by including random effects. More details on this method and the advantages over ANOVA and fitting psychometric curves are described in Vancleef et al. (2013). Analyses were performed in SAS (SAS Institute Inc.), a software package for statistical computing.

We applied these techniques by including fixed main effects and interaction effects of presentation time, stimulus type (snake or ladder) and task (detection or discrimination) in the model. We allowed the effect of presentation time and the effect of stimulus type to vary over subjects and therefore included random effects of these predictors. In search of a satisfying model, we started with a model including all aforementioned effects and applied a backwards stepwise procedure. This means that we excluded non-significant effects in each step until we obtained a model that only contained significant effects. We evaluated the effect of a predictor in explaining the data by performing a *t*-test. To meet convergence criteria of the iterative parameter estimation procedure and to facilitate interpretation, presentation time was logarithmically transformed. In addition, it was centered on the threshold estimates from the individual analyses averaged over subjects and over conditions. This mean threshold estimate

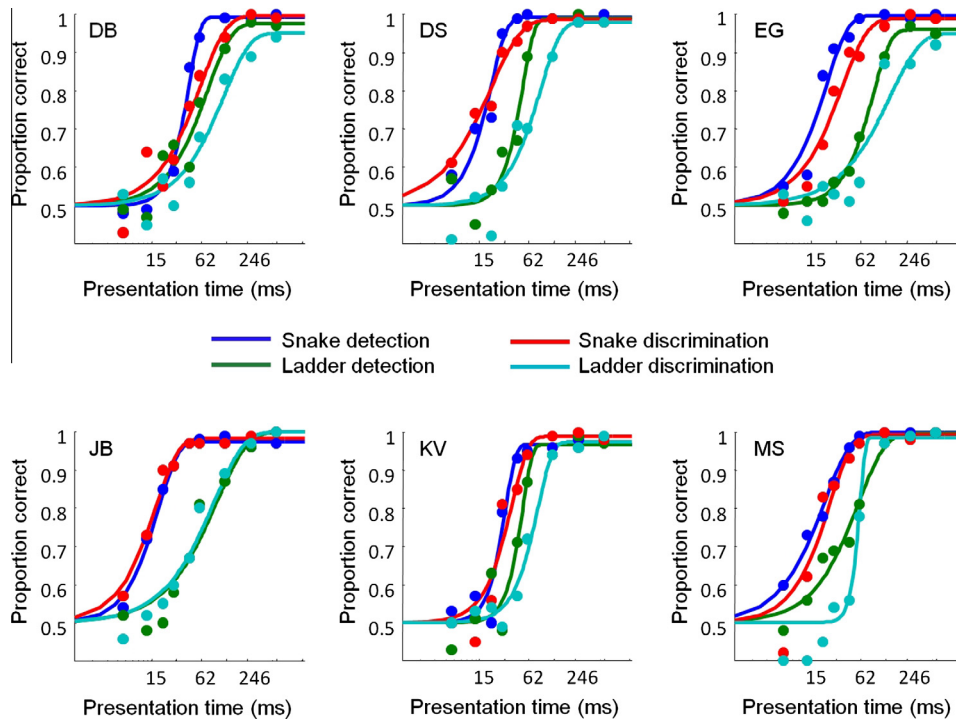


Fig. 2. Psychometric functions for each subject. The data (dots) and psychometric function for the snake detection task are plotted in blue, the ladder detection task in green, the snake discrimination task in red and the ladder discrimination in turquoise. In the detection task data are combined for both low and high curvature contours. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Goodness-of-fit statistics for each subject in all four conditions.

Subjects	Detection				Discrimination			
	Snakes		Ladders		Snakes		Ladders	
	<i>D</i>	<i>p</i>	<i>D</i>	<i>p</i>	<i>D</i>	<i>p</i>	<i>D</i>	<i>p</i>
DB	3.95	.74	8.25	.24	11.01	.08	8	.29
DS	11	.08	9.45	.16	3.13	.85	12.56	.06
EG	10.76	.07	1.06	.98	10.03	.13	18.01	.01
JB	3.09	.83	10.35	.13	8.08	.31	6.14	.43
KV	9.43	.18	13.4	.05	14.51	.02	4.42	.63
MS	0.85	.95	5.11	.52	17.09	.01	13.93	.03

D = deviance, significant *p*-values are in bold.

(47.55 ms) was almost equal to the median presentation time (47 ms) and is therefore suited as center point in our analyses.

In the final model, we observed a significant main effect of presentation time (parameter estimate = 2.09, $SE = 0.14$, $t(4) = 14.83$, $p < .001$): increasing the presentation time resulted in an increase of performance ($OR = 8.10$). In addition, we found a significant main effect of stimulus type (parameter estimate = 1.65, $SE = 0.30$, $t(4) = 5.45$, $p = .006$) and task (parameter estimate = -1.06 , $SE = 0.09$, $t(4) = -12.30$, $p < .001$). This indicated that the odds for a correct answer were about five times larger for snakes than for ladders ($OR = 5.21$), and that the odds for a correct answer in the discrimination task were 65% lower than in the detection task ($OR = 0.35$). Furthermore, we found the predicted two-way interaction between stimulus type and task to be significant (parameter estimate = 0.75, $SE = 0.13$, $t(4) = 5.90$, $p = .004$). To interpret this interaction, we calculated contrasts for each task. This revealed that ladders were much more difficult than snakes in the discrimination task (estimated difference = 2.40, $SE = 0.32$, $t(4) = 7.58$, $p = .002$), while the effect was smaller in the detection task (estimated difference = 1.65, $SE = 0.30$, $t(4) = 5.45$, $p = .006$). Besides the absolute differences, we also compared relative

differences between stimulus types in both tasks and found evidence for a larger ratio difference between snake and ladders in the discrimination task than in the detection task (estimated difference in ratio = -0.79 , $SE = 0.19$, $t(4) = -4.19$, $p = .014$). In addition, we found a better detection for smooth contours than for highly curved contours in the detection task (estimated difference = -0.73 , $SE = 0.09$, $t(4) = -7.92$, $p = .001$). Individual data and model predictions are shown in Fig. 4. From this figure, it is also evident that at a group level comparison of the 75% and the 82.5% correct thresholds between conditions supports the same conclusions as the analysis presented above.

4. Discussion

We examined whether shape encoding of snakes and ladders diverged, in addition to the differences observed at the level of linking and contour detection. Our results provide support for this hypothesis since we found a dissimilar effect of stimulus type (snake or ladder) in the detection and the shape discrimination task. More specifically, we observed a larger difference between snake and ladder performance in the discrimination task than in the detection task. This would suggest that processing differences between snakes and ladders are not limited to the aspect of contour detection that is present in both tasks but that there are additional differences regarding shape encoding that are only apparent in the shape discrimination task. Although our parameter estimates represent performance differences between conditions at a fixed presentation time (namely, the average presentation time threshold), the results could similarly be interpreted as a difference in integration times between conditions at fixed performance levels, in other words, by comparing presentation time thresholds (see also Fig. 4). Therefore, our results suggest different integration times for snakes and ladders at both a detection and a shape discrimination stage. Besides the study's focus on the comparison between tasks, we observed the more obvious advantage

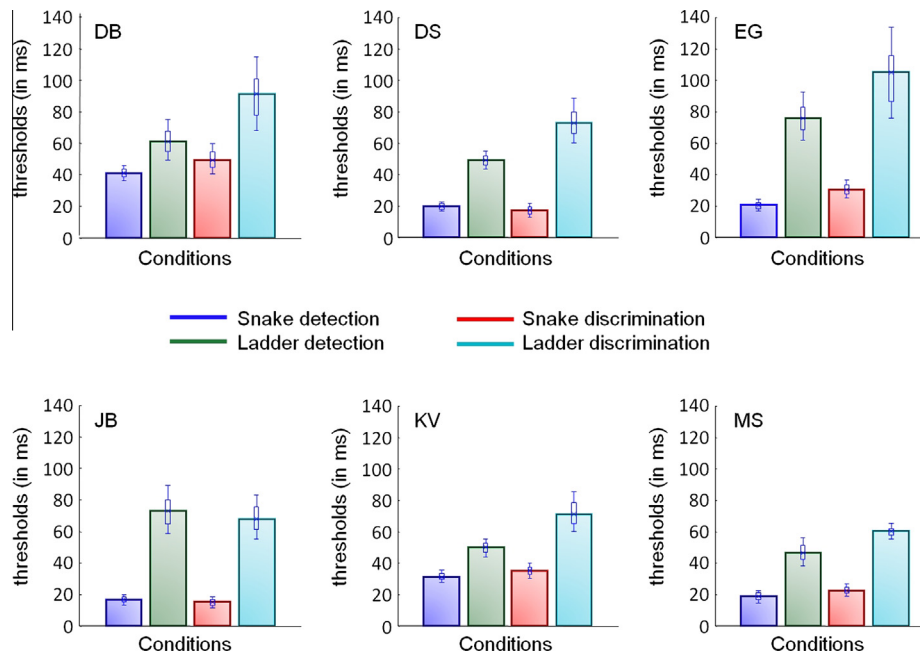


Fig. 3. Estimated thresholds for each subject. Error bars show confidence intervals of one (inner range) and two (outer range) standard deviations for the mean threshold estimate. As in Fig. 2, thresholds for the snake detection task are plotted in blue, the ladder detection task in green, the snake discrimination task in red and the ladder discrimination in turquoise. In the detection task data are combined for both low and high curvature contours. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Threshold estimates and confidence interval for the estimates for each subject in all four conditions.

Subjects	Detection				Discrimination			
	Snakes		Ladders		Snakes		Ladders	
	Th	CI	th	CI	th	CI	Th	CI
DB	41.1	[36.4 45.9]	61.0	[48.7 74.3]	49.2	[40.5 58.8]	91.3	[69.0 115.1]
DS	19.8	[16.6 22.7]	49.1	[43.3 54.7]	17.3	[12.8 21.5]	72.7	[60.0 88.2]
EG	20.5	[16.7 24.2]	75.8	[62.2 92.9]	30.5	[24.9 36.4]	105.2	[75.6 134.8]
JB	16.8	[13.5 20.1]	72.9	[58.5 88.9]	15.3	[11.9 18.5]	68.0	[55.4 83.5]
KV	31.1	[27.7 35.6]	49.8	[44.1 55.1]	35.0	[30.0 40.0]	71.3	[60.3 85.1]
MS	18.6	[14.8 22.3]	46.4	[37.9 55.2]	22.5	[18.5 26.7]	60.1	[54.8 64.8]

th = threshold, CI = 95% confidence interval.

of snakes over ladders in both tasks, and of shape detection over discrimination for both snakes and ladders. Our data also shed light on curvature effects in contour integration. The present study supports the view that contours with a smaller curvature are easier to detect than contours with a larger curvature (Field, Hayes, & Hess, 1993; Geisler et al., 2001; Hess & Dakin, 1997; Ledgeway, Hess, & Geisler, 2005).

The present study confirms previous findings on better performance for snakes than for ladders in a detection task (Bex, Simmers, & Dakin, 2001; Field, Hayes, & Hess, 1993; Hess, Ledgeway, & Dakin, 2000; Ledgeway, Hess, & Geisler, 2005; May & Hess, 2007, 2008) and in a shape discrimination task (Dakin & Baruch, 2009). Therefore, the current findings strengthen the idea that snake perception is mediated by a different mechanism than ladder perception. However, we extended the understanding of snake and ladder perception by comparing snake and ladder perception directly in a detection task and in a discrimination task. Our results indicate that the difference between both is not limited to early processing levels like contour detection, but can be extended to a higher-level shape encoding level as well. However, since previous studies on the effect of local orientation on shape discrimination have shown conflicting results with different methods (Gheorghiu

& Kingdom, 2008; Habak et al., 2004; Keeble & Hess, 1998, 1999; Kooi, De Valois, & Switkes, 1991; Levi & Klein, 2000; Saarinen & Levi, 2001), our results might be limited to the shape discrimination of curved open contours. It is unclear whether the previously reported contrasting observations are related to differences in element separation (as suggested by Levi and Klein (2000)), in tasks (e.g., detection versus shape-after effects), or in a local or global processing level (as suggested by Gheorghiu and Kingdom (2008)). In this respect, our conclusions are limited to the specific stimuli and tasks used here and further research is needed to generalize them to other stimuli and tasks.

A biological explanation for our findings can be found in long-range horizontal connections between orientation selective cells in the primary visual cortex that have been proposed as the biological substrates of snake and ladder perception (Bauer & Heinze, 2002; Ernst et al., 2004; Hess & Field, 1999; Hess, Hayes, & Field, 2003; Kovács, 1999; Ledgeway, Hess, & Geisler, 2005; Li & Gilbert, 2002; Li, Piëch, & Gilbert, 2006). On the one hand, excitatory connections between neighboring cells with similar orientation preference might mediate snake perception (Bauer & Heinze, 2002; Ernst et al., 2004; Hess & Field, 1999; Kapadia, 1999; Kapadia, Westheimer, & Gilbert, 2000; Kovács, 1999; Ledgeway,

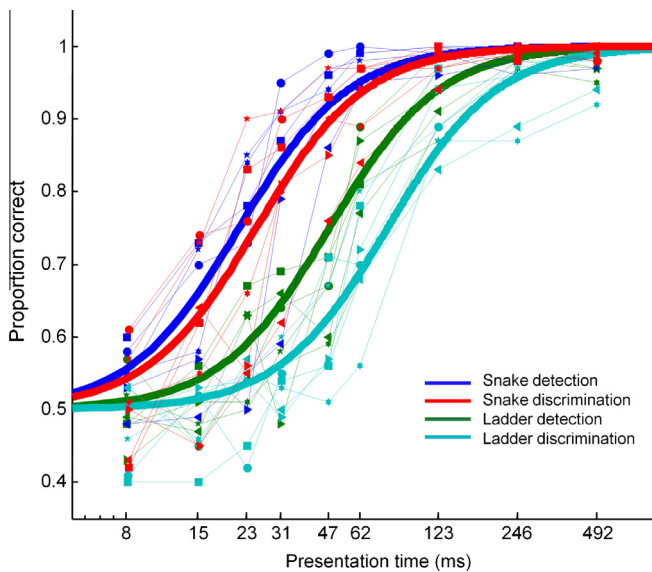


Fig. 4. Individual data and model predictions. Thin lines show the performance at an individual level (each symbol represents one subject). Thick lines are the model predictions at a group level. The predicted curves show a smaller difference between snake and ladder detection (blue versus green curve) than between snake and ladder discrimination (red versus turquoise). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Hess, & Geisler, 2005; Li & Gilbert, 2002; Li, Piëch, & Gilbert, 2006; Piccini et al., 2003). On the other hand, the underlying neural processes are less clear for ladders. For instance, Bosking et al. (1997) found evidence for weaker orthogonal connections that can mediate ladder perception. This might explain the better performance in snakes compared to ladders. Another biological substrate for ladder perception could be inhibitory trans-axial connections, as was suggested by Ledgeway, Hess, and Geisler (2005). These proposed neural correlates of ladder and snake perception are situated in early visual areas and are involved in early processing stages. Curvature tuning however is attributed to V2 and V4 in which neurons respond to simple geometric shapes, angles and curves (Anzai, Peng, & Van Essen, 2007; Hedg e & Van Essen, 2000; Hess, May, & Dumoulin, 2013; Ito & Komatsu, 2004; Pasupathy & Connor, 1999). The results of the present study suggest that also contour integration at higher levels for shape encoding like V2 and V4 proceeds differently for snakes and ladders. Hence, our psychophysical results can provide inspiration for studies on biological substrates of contour integration to broaden towards higher level aspects of contour integration.

Our results might also have implications for models of contour integration. Although several models have been proposed to describe the mechanism of snake perception (e.g., Ernst et al., 2012; Field, Hayes, & Hess, 1993; Hess & Dakin, 1997; Hess & Field, 1999; Li, 1998; Ursino & La Cara, 2004; VanRullen, Delorme, & Thorpe, 2001; Watt, Ledgeway, & Dakin, 2008), only few can also explain ladder perception (Dakin & Baruch, 2009; May & Hess, 2008; Yen & Finkel, 1998). First, the basic units in the association field model of Yen and Finkel (1998) are orientation selective filters that are interconnected by long-range horizontal connections. Competing excitatory connections are situated along (co-axial) and parallel (trans-axial) to the orientation axis of the filter to support snake and ladder perception, respectively. The second model that explains both snake and ladder perception is a filter-overlap model by May and Hess (2008). Their model incorporates two orthogonal filter stages with a rectification in between to account for both snake and ladder detection. Third, the filter-overlap model

of Dakin and Baruch (2009) that was designed for snakes, can be extended to account for ladder perception by including broader orientation bandwidth Gabor filters at their two filtering stages and allow the filters of the first stage to overlap in order to model selective advantage for snakes. In their model, snakes are represented as an increased activity at the contour location, while ladders are represented as a decrement in local contour energy. Unfortunately, none of these three models allow to distinguish between outputs that are relevant in a detection task and those that are relevant in a shape discrimination task, so no predictions could be made based on the models. As a consequence, our findings highlight the need to extend the focus of model building from low level contour encoding at V1 to higher level aspects of contour integration like shape encoding. From our study, it is unclear whether this should be a different shape encoding mechanism for snakes and ladders or whether the existing differences at low levels of encoding might be exaggerated in later stages (e.g., weaker signals, less detailed representation of the underlying curve). Possibly, the observed snake and ladder differences in the shape discrimination task have resulted from a non-linear processing stage that amplified existing differences in the detection stage. Although our study has shown the existence of differences in shape encoding of snakes and ladders, follow-up studies should focus on the nature of this difference and on the mechanisms underlying it.

In summary, by comparing performance in a detection and a shape discrimination task, this study showed that different processing of ladders and snakes is not limited to contour detection but is also apparent at the level of shape encoding. Further research in contour integration on models and biological substrates would benefit from extending their focus to higher level influences on contour integration like shape encoding.

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