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Temporal dynamics of different cases of bi-stable figure–ground perception

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ABSTRACT

Segmentation of a visual scene in "figure" and "ground" is essential for perception of the three-dimensional layout of a scene. In cases of bi-stable perception, two distinct figure–ground interpretations alternate over time. We were interested in the temporal dynamics of these alternations, in particular when the same image is presented repeatedly, with short blank periods in-between. Surprisingly, we found that the intermittent presentation of Rubin's classical "face-or-vase" figure, which is frequently taken as a standard case of bi-stable figure–ground perception, often evoked perceptual switches during the short presentations and stabilization was not prominent. Interestingly, bi-stable perception of Kanizsa's anomalous transparency figure did strongly stabilize across blanks. We also found stabilization for the Necker cube, which we used for comparison. The degree of stabilization (and the lack of it) varied across stimuli and across individuals. Our results indicate, against common expectation, that the stabilization phenomenon cannot be generally evoked by intermittent presentation. We argue that top-down feedback factors such as familiarity, semantics, expectation, and perceptual bias contribute to the complex processes underlying the temporal dynamics of bi-stable figure–ground perception.

1. Introduction

Perceptual organization, such as the stratification of segmented areas into "figure" and "ground", reflects the global configuration of a visual scene, inevitably involving the processing of the context. How do the computational mechanisms in the visual system capture the context? This is one of the central topics in vision research. It has been suggested that top-down feedback projections play an important role in figure–ground organization (Craft et al., 2007; Jehee, Lamme, & Roelfsema, 2007; Kogo & van Ee, 2015; Kogo & Wagemans, 2013; Lamme & Roelfsema, 2000; Peterson, 1999; Poort et al., 2012; Qiu, Sugihara, & von der Heydt, 2007; Self et al., 2012; Stanley & Rubin, 2005; Vecera & O'Reilly, 1998, 2000). In a feedback system, global configurations can dynamically alter the response properties of neurons in lower levels of the cortical hierarchy of visual processing, and hence the whole system can become context sensitive.

A way to investigate the mechanisms underlying the context-sensitive aspects of perceptual organization is the use of images that create bi-stable perception in which the perceptual interpretations of the image keep alternating over time, while the physical input image is kept constant. One of the most famous images to induce perceptual bi-stability involving figure–ground organization is Rubin's "face-or-vase" illusory image (FV, Fig. 1A, Rubin, 1921): The perceptual interpretation keeps alternating between "two faces" on the sides and a "vase" in the center, while the competing area is perceived as a part of the background. Because the perceptual switch in this case is specifically linked to the reversal of the figure–ground organization, we call this phenomenon "bi-stable figure–ground organization" in this paper.

Concerning bi-stable perception in general, several factors are thought to be involved in its temporal dynamics. Perceptual switching has been commonly explained by adaptation of neurons ("fatigue") that represent the current dominant percept in combination with a mutual inhibition circuit (e.g., Huguet, Rinzel, & Hupé, 2014; Kogo, Galli, & Wagemans, 2011; Nawrot & Blake, 1991; Noest et al., 2007; Wilson, 2003). A recent study revealed a gradual adaptation process underlying the dominant percept that eventually leads to the switch (Alais et al., 2010). Kang and Blake (2010) investigated the effect of adaptation on percept durations with a newly developed "online adaptation" paradigm. In addition, a series of recent studies revealed history effects in the temporal dynamics of bi-stable perception. Van Ee (2009) reported that a significant serial correlation—that is, a cumulative history effect

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in the sequence of alternating percepts—is present for a range of bi-stable stimuli. Pastukhov and Braun (2011) demonstrated a cumulative effect of past perceptual experiences (see also, Pastukhov & Braun, 2013; Pastukhov, Lissner, & Braun, 2014; see Pearson & Brascamp, 2008, for review).

To investigate the temporal dynamics and the underlying mechanisms of bi-stable perception, the intermittent presentation paradigm has become a key paradigm (Brascamp et al., 2010; De Jong et al., 2014; Leopold et al., 2002; Maier et al., 2003; Orbach, Ehrlich, & Heath, 1963; Sterzer & Rees, 2008). Presenting a bi-stable image intermittently (i.e., using brief repetitive presentations of the same image with blank periods in-between) often causes reduced alternation frequencies. More specifically, it has been shown that the dominant percept in one cycle survives to the next cycle more often than chance level, which is critically depending on the length of the blank period (Klink et al., 2008; Kornmeier et al., 2007; Pastukhov & Braun, 2013). (The brief presentation period in each cycle of the intermittent presentation is generally called "ON period", and the blank period is called "OFF period" in this paper.) How the ON and OFF periods influence the temporal properties of bi-stable perception must be a direct reflection of the underlying dynamics. Indeed, it has been reported for a range of exposure durations that previously perceived interpretations dominate at the onset of ambiguous sensory information, whereas alternative interpretations dominate prolonged viewing (De Jong, Knapen, & van Ee, 2012). De Jong, Kourtzi, and van Ee (2012) recorded fMRI activity and observed that the mere repetition of the stimulus evoked an entirely different pattern of activity modulations than the repetition of a particular perceptual interpretation of the stimulus. De Jong et al. (2014) used event-related electroencephalography to record the fast dynamics of neural activity shortly after stimulus onset and showed that the number of previous occurrences of a certain percept modulated early posterior brain activity starting as early as 50 ms after stimulus onset. They argued that the memory effect depended on previous perception rather than previous visual input. The short latency and posterior scalp location of the effect suggest that perceptual history modified bottom-up stimulus processing in early visual cortex.

Returning to bi-stable figure–ground perception, the DISC model ("Differentiation-Integration for Surface Completion"; Kogo et al., 2010) employs "border-ownership" (BOWN) as a cardinal factor in determining percept dominance (Kogo, Galli, & Wagemans, 2011). BOWN indicates that a borderline occurs because one surface is on top of the other and that the borderline is an edge of the closer surface. It has been shown that a subset of neurons at the early stages of the visual cortex have response properties that are sensitive to BOWN (Zhou, Friedman, & von der Heydt, 2000). Hence, BOWN seems to be involved in the computation of figure–ground organization in the visual system. The switch between the two percepts in the bi-stable perception of FV corresponds to the switch of the ownership of the two central borderlines and, therefore, it is possible that the competition of the ownership at each location of the boundaries by BOWN-sensitive neurons play a role.

We reported (Kogo, Galli, & Wagemans, 2011) that bi-stable figure–ground perception can be reproduced by implementing the following factors in the model: (1) Top-down feedback projection from a depth map to BOWN computation, (2) adaptation of feedback, and (3) recovery of adaptation. This two-layered hierarchical feedback model produced the stabilization effect in response to intermittent presentation of FV as follows. While the balance of the mutually inhibiting BOWN neurons is shifted by the feedback signals in the direction in favor of the current percept, the feedback signals adapt during image presentation. This adaptation recovers during the following blank period. If the blank interval is short, the recovery is partial while, if it is long enough, the adaptation recovers fully. The extent of this recovery influences the response at the next cycle of the presentation. If the adaptation recovers more, the probability to reproduce the same percept in the next cycle is higher because of the retaining shift in the balance of the mutually inhibiting BOWN neurons. And if the recovery is less, the probability to reproduce the same percept is lower. Hence, the stabilization effect is explained as the result of the shifted balance in the mutually inhibiting BOWN neurons and the recovery of adaptation.

However, intrinsic biases of individuals need to be considered when stabilization effect is measured experimentally. At the very beginning of exposure, the probability of perceiving one of the two percepts may not be at chance level: it is possible that a participant has a bias to perceive one of the two percepts more often than the other percept. This is called "onset bias". Note that the

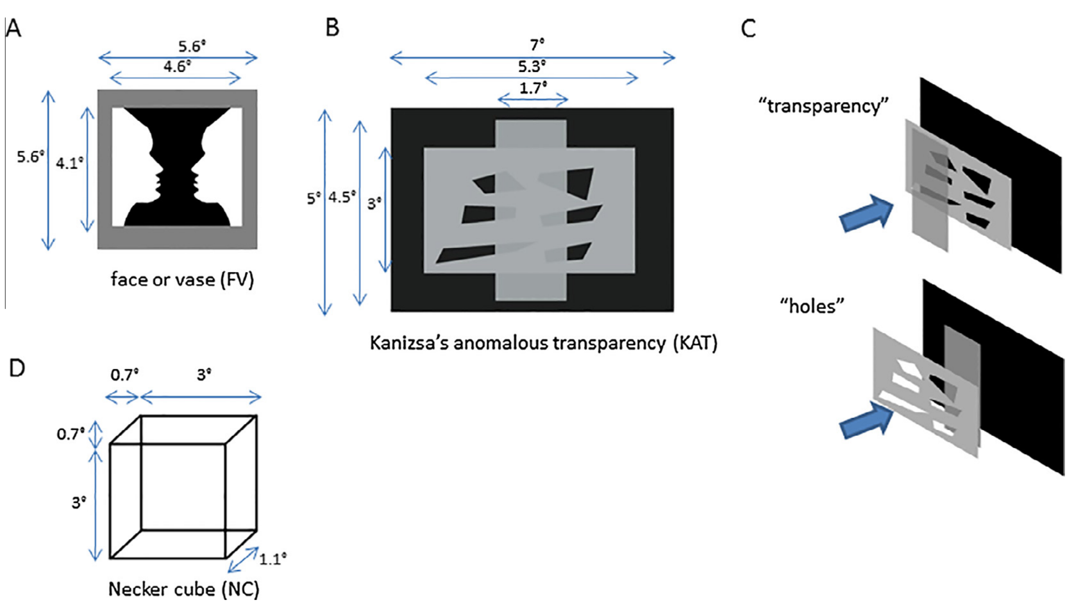

Fig. 1. The three visual stimuli that create bi-stable perception, used in the present study. (A) Face-or-vase (FV). (B) Kanizsa's anomalous transparency (KAT). (C) The two alternating perceptual interpretations generated by the KAT stimulus: either a transparent gray frontal plane is being perceived to float in front of a gray plane with polygons, or a gray plane with holes in it is being perceived to float in front of a vertically elongated gray plane. (D) Necker cube (NC).

average percept durations for individual percepts during continuous presentation may also differ. This bias is called "sustained bias" and it should be distinguished from onset bias (see Carter & Cavanagh, 2007; Stanley et al., 2011). While no biases in both sustained and onset rivalries were incorporated in our model simulation, the onset bias may contribute to the reappearance of the same percept at the onset of each cycle in the experimental data. An apparent stabilization effect is, then, due to the combination of the true stabilization effect and the onset bias. Hence, the stabilization effect *on top of the onset bias* has to be extracted from the experimental data (see Section 2 for how to separate the stabilization effect from the onset bias).

Nevertheless, the prediction by the model of a stabilization effect in response to FV is consistent with the previous behavioral reports with various bi-stable images such as structure-from-motion, quartet dots, Necker cube, binocular rivalry, and motion-induced blindness (Leopold et al., 2002; Orbach, Ehrlich, & Heath, 1963). However, no behavioral data have been reported on the effect of intermittent presentations on typical bi-stable *figure–ground* perception such as FV. If the stabilization phenomenon is not observed in cases of bi-stable figure–ground perception, it suggests the involvement of further, more complex factors than those implemented in the model. We addressed this question by applying the intermittent presentation paradigm to three different images that give rise to bi-stable perception related to figure–ground, depth order, and 3D structure, which are all essential aspects of perceptual organization. More generally, this study will provide crucial information to better understand the mechanisms underlying perceptual organization in the hierarchically organized visual system.

In this study, we included two images in addition to the FV image. First, Fig. 1B shows another image that gives rise to bi-stable figure–ground perception, called Kanizsa's anomalous transparency (KAT, modified from Kanizsa, 1979), which is not widely known. By looking at the image, the majority (but not all) of naive observers first report that the central vertical rectangle (in transparent gray) is on top of the larger (lighter) rectangle that has the six arbitrary shaped polygons ("transparent", Fig. 1C top). However, another perceptual interpretation is possible. In the second perceptual interpretation, the large rectangle is the closest surface to the viewer that has six holes with the arbitrary shapes, through which parts of the vertical rectangle behind it are seen ("holes", Fig. 1C bottom). Once the two possible perceptual interpretations are pointed out to them, participants report automatic switches between the two perceptual interpretations. In contrast to FV, the perceptual switch in KAT is much slower and the clarity of the perceptual interpretation is much higher (based on post-experimental comments by the participants). In addition, the competition between perceptual organizations in FV and KAT probably involves quite different factors. In the case of FV, as modeled in the DISC model, it is the ownership of the two central borders that is the target of the competition (Fig. 2A). In addition, two semantically different objects, faces and vase, are in competition in FV. Furthermore, the competition is between the region in the center and the two sides. In KAT, on the other hand, an illusory lightness perception and an illusory contour perception are evoked (Fig. 2B), in addition to the reversal of BOWN of the six polygons. Hence, although FV and KAT both evoke bi-stability in depth-order perception, the behavioral properties of these perceptual interpretations appear to differ significantly and also their perceptual switches could involve quite different mechanisms.

Second, we also included another classic image to create bi-stability, the Necker cube (NC, Fig. 1D, Necker, 1832). Here, the depth order of the two squares keeps changing between frontal and rear depth planes, which causes an alternation in the perceived orientation of the cube. Therefore, it is possible that depth-order computation is part of the dynamics of bi-stability in NC, which involves a perceptual switch of 3D structure.

In sum, the above presentation of these three cases of bi-stable perception related to figure–ground, depth order, and 3D structure suggests that there are multiple factors at stake, and it is not clear whether and how intermittent presentation affects these. We therefore investigated the effect of intermittent presentation of FV, KAT, and NC, and report various degrees of stabilization in KAT, NC, and FV. Furthermore, perceptual switches frequently occurred during the short presentation time in the intermittent presentation condition in FV and NC. Higher level factors such as attention and expectation can cause specific changes at the lower level. As illustrated by the present findings, the investigation of the temporal dynamics and its link to the higher level signals in bi-stable perception can lead to further insight in the context-sensitive mechanisms of the figure–ground organization. We will discuss possible factors such as top-down feedback, semantics, and biased responses, that may have affected the different degrees of stabilization.

2. Methods

2.1. Participants

The participants ($n = 54$) consisted of university students, all naive to the purpose of the experiment. All participants had normal or corrected-to-normal vision. All participants signed an informed consent form. The experimental procedure was approved by the Ethical Committee of the University of Leuven.

2.2. Apparatus

The stimuli were shown on a computer screen (resolution 1920×1440). The stimulus figure was presented at the center of the screen. The color of the screen outside of the figure was set to mid-gray. A headrest was used to secure the position of the head and to keep it straight. The viewing distance was 57 cm. The computer consisted of an Intel CPU running a Microsoft Windows operating system. The code for all experimental paradigms were written in Matlab (Mathworks) with Psychtoolbox extension (Brainard, 1997; Pelli, 1997). All experiments were done in a dark room.

2.3. Stimuli

Rubin's face or vase (FV, Fig. 1A), Kanizsa's anomalous transparency (KAT, Fig. 1B), and the Necker cube (NC, Fig. 1D) were used as stimuli to evoke bi-stable perception. The dimensions of the three images are as indicated in the figures. KAT was rotated 90 deg from the original image (Kanizsa, 1979) so that the transparent rectangle is oriented vertically, and the width was reduced. This was done to help participants to understand the task better because of the similarity of the perceptual switches in FV and KAT (central vertical region being front or behind).

In this paper, the two competing perceptual interpretations of each image are called "faces" and "vase" in FV; "transparency" if the central vertical rectangle is perceived to be in front (Fig. 1C top) and "holes" if the same rectangle is perceived to be behind the larger rectangle (Fig. 1C bottom) in KAT; and "left-down" and "right-up" in NC, indicating the orientation of the perceived 3D cube. "Holes" in KAT, "faces" in FV, and "right-up" in NC are called percept 1, and "transparency" in KAT, "vase" in FV, and "left-down" in NC are called percept 2 in this paper.

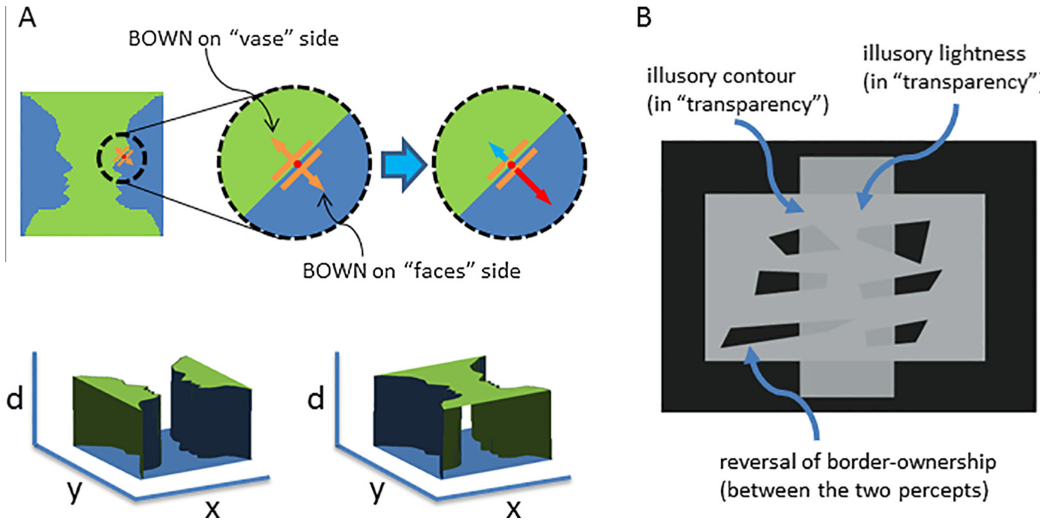

Fig. 2. The role of border ownership in the perceptual organization associated with the FV and the KAT visual stimuli. (A) It is assumed that there are two competing border ownership (BOWN) signals at each location along the borders. The dominance of the BOWN signals determines the figural side and the ground side (Kogo, Galli, & Wagemans, 2011). Perceptual dominance alternates roughly every few seconds during prolonged observation. (B) Multiple factors are involved in the bi-stable perceptual interpretation generated by the KAT stimulus. In the "transparency" percept (Fig. 1C) the vertical rectangle is perceived as transparent accompanied by illusory contours. The six polygons are perceived as objects in the "transparency" interpretation or as holes in the "holes" interpretation.

2.4. Experimental paradigm

Before the experiment started, the three images were presented one by one to the participants who then described what they saw. None of them had seen the KAT image before and most of them did not indicate a spontaneous perceptual switch. However, quickly after we explained the two possible perceptual interpretations of the image (Fig. 1C), spontaneous switches between the two perceptual interpretations started to occur. Some participants had seen the FV and NC images before and were aware of the two possible perceptual interpretations. Other participants had not seen either of the images before. They were instructed to keep a passive attitude and not to exert voluntary control to change the perceptual interpretation intentionally during experiment. Their task was to press a "down" button whenever they perceived "vase" in FV, "transparency" (the central vertical rectangle closer to the participant) in KAT, and "left-down" in NC, and press an "up" button for the competing perceptual interpretations ("faces", "holes", and "right-up", resp.). Before the main experiment started, they practiced the task during the continuous and the intermittent presentations of the three images, just as in the main experiment, but with only 1 min of presentation time for each figure.

Each of the three images (FV, NC, KAT) was presented for 5 min per session, either continuously or intermittently, producing six sessions (3×2) in total. In the continuous session, the image was presented continuously for 5 min. In the intermittent session, the image was presented for a fixed time (ON period) and disappeared, with only a blank (mid-gray) screen for a fixed time (OFF period), and this cycle was repeated for 5 min. The parameters of the intermittent condition were different in each session. The ON period was either 1 or 2 s. The OFF period was either 2, 3, 4, 6, 8, or 10 s (Table 1, # indicates the number of participants). Participants reported the perceptual interpretation at the onset of the presentation and whenever the perceptual interpretation changed during presentation, by pressing the "up" or "down" keys. The "onset" here includes the very beginning of the presentation as well as the onset of each cycle in the intermittent condition. The moment the answers were reported was registered for data analysis. Because of the expected delay of the response by the participants, the responses given after the end of each ON period were recorded as well. The sequence of trials was randomized and participants took a 30-s break between the sessions. The whole experiment, including the instructions and the practice trials, took about 1 h per participant.

2.5. Data analysis

Average percept durations were determined for individual participants for the two percepts separately as well as for both percepts combined. The perceptual bias in the responses of individuals was determined based on the data of the continuous presentation condition (Carter & Cavanagh, 2007). A paired *t*-test was applied to the average percept durations for the two individual percepts, and if a percept had a significantly longer average duration than the other, a "sustained bias" for the longer percept was inferred. We also report the response at the very first onset of the continuous presentation, which is called an "onset bias" if one percept occurs more frequently than the other. To show the individual differences in the sustained bias, the "dominance ratio" was measured as the total dominance duration for one specific perceptual interpretation expressed as a percentage of the total presentation time. In addition, because serial correlation of the responses is indicative of a memory effect (van Ee, 2009), we applied this analysis to assess the cumulative memory effect in the series of perceptual switches in the continuous presentation condition. For this purpose, the autocorrelation of sequences of percept durations for individual percepts (percept 1 and percept 2) was analyzed separately. For this analysis, the perceptual durations that occurred within the first 30 s of presentation and the last percept duration during the presentation time was omitted (van Ee, 2009).

For the intermittent presentation, the percept durations were calculated as follows. The moments of all individual responses were registered, all OFF periods before them were removed, and the intervals between the responses in the concatenated data were determined. Survival probability (SP) was determined by calculating the probability that the last perceptual interpretation from one cycle of intermittent presentation was reproduced as the first response in the subsequent cycle.

The "stabilization effect" was determined based on the averaged SPs of both percepts as follows. Average SPs for the individual percepts were calculated separately (SP1 and SP2). SP1 indicates

Table 1
Parameters used for intermittent presentations. # Indicates the number of participants.

KAT			FV			NC		
ON period(s)	OFF period(s)	#	ON period(s)	OFF period(s)	#	ON period(s)	OFF period(s)	#
1	3	7	1	2	3	1	2	3
1	6	17	1	3	11	1	3	11
1	8	9	1	4	1	1	4	1
2	4	9	1	6	10	1	6	10
2	6	9	1	8	1	1	8	1
2	8	10	1	10	9	1	10	9
2	10	6	2	4	6	2	4	6
			2	6	16	2	6	16
			2	8	16	2	8	16
			2	10	6	2	10	6
Total		67			79			79

the probability that the first percept in a cycle is percept 1 and the last percept in the previous cycle was also percept 1, and vice versa for SP2. If the underlying processes governing bi-stable perception are purely random, the average of the two SP values calculated by Eq. (1) below should be 0.5.

$$(SP1 + SP2)/2 = 0.5 \quad \text{if a random process is assumed} \qquad (1)$$

If the value is higher than 0.5, it indicates stabilization. The advantage of this formulation is that the categorization based on Eq. (1) holds even if SP1 and SP2 reflect onset bias. For example, if the onset bias of one participant is 0.7 for percept 1 and 0.3 for percept 2, and if a random process is assumed and, hence, the percept in the previous cycle does not influence the percept at the onset of each cycle, SP1 and SP2 should be 0.7 and 0.3, respectively. This leads to the average of the two values (Eq. (1)) being 0.5. For statistical analysis to determine whether the left term of Eq. (1) equals the right term, we changed Eq. (1) into,

$$SP1 = 1 - SP2 \qquad (2)$$

If the left term is larger than the right term, it indicates stabilization and if it smaller, it indicates that the effect was opposite, which we call de-stabilization. Statistical analysis with two-proportion z-test was applied to compare the left term and the right term in Eq. (2). The participants were categorized into three groups: subjects with stabilization, subjects with de-stabilization, and subjects with no effect.

The "percept duration ratio" is calculated as a ratio of the average percept durations during the intermittent presentation relative to the average percept durations during continuous presentation. For the pooled data, the SP and "percept duration ratio" were analyzed using the one-sample Wilcoxon signed-rank test with 0.5 and 1.0 as test values, respectively. Tests were performed with an overall alpha level of 0.05.

3. Results

3.1. General properties of responses

Because this is a first study on stabilization for different bi-stable figure–ground stimuli, we first describe the general properties of the bi-stable responses in all three cases. Interestingly, the responses to KAT were quite different quantitatively compared to the other two images, as described here for the continuous presentations and in the next section for the intermittent presentations. Data for the continuous presentations are summarized in Tables 2 and 3. Overall, the average percept durations varied considerably between individual participants as well as between stimuli (Fig. 3A and B), corresponding to previous reports with other classes of bi-stable perception (e.g., van Ee, 2005), but KAT showed the longest average percept duration compared to the other two images. The average durations (in the pooled data) of the two competing perceptual interpretations showed no significant differences in KAT and FV, but, in NC, the "left-down" perceptual interpretation had a significantly longer average percept duration.

Next, we measured the bias of the responses (sustained and onset) in all individuals for each figure (Table 3). 66%, 57%, and 46% of the participants for KAT, FV, and NC, respectively, showed no significant biases (Table 3, sustained bias). However, the other participants showed strong sustained biases to one of the two percepts: 29% of the participants showed a significant bias to "holes" in KAT, 31% to "faces" in FV, and 44% to "left-down" in NC. The dominance ratio for each image is plotted in Fig. 3C to show the individual differences of the sustained bias. At the onset of the presentation, a larger number of participants showed "transparency" responses in KAT, "vase" responses in FV, and "left-down" responses in NC (Table 3, onset bias). In other words, a larger number of participants started with a "transparency" response in KAT

Table 3
The ratio of participants showing sustained biases and onset biases measured in the continuous presentation condition. For the sustained bias, individual percept durations corresponding to the two perceptual interpretations were averaged (and it was statistically tested if they were significantly different). For the onset bias, the first responses in the continuous presentation condition from all participants were corrected and the percentages were calculated for each percept.

	Sustained bias (%)			Onset bias (%)	
	Percept 1	Percept 2	No-bias	Percept 1	Percept 2
KAT	29.0	4.8	66.1	37.1	62.9
FV	31.0	12.1	56.9	31.6	68.4
NC	10.5	43.9	45.6	22.8	77.2

Table 2
Average percept durations and frequencies for individual percepts as well as for both percepts (pooled data for all participants). Percept 1 corresponds to "holes" in KAT, "faces" in FV, and "right-up" in NC, and percept 2 corresponds to "transparency" in KAT, "vase" in FV, and "left-down" in NC (same for Table 3).

	Average percept duration (s)			Average frequency (per second)		
	Percept 1	Percept 2	Both	Percept 1	Percept 2	Both
KAT	7.72 ± 8.57	6.91 ± 11.56	7.47 ± 7.75	0.19 ± 0.10	0.24 ± 0.13	0.21 ± 0.22
FV	5.93 ± 6.97	5.04 ± 5.23	5.46 ± 4.75	0.27 ± 0.19	0.32 ± 0.22	0.28 ± 0.19
NC	3.90 ± 2.71	4.98 ± 3.41	4.45 ± 2.86	0.32 ± 0.15	0.27 ± 0.14	0.29 ± 0.14

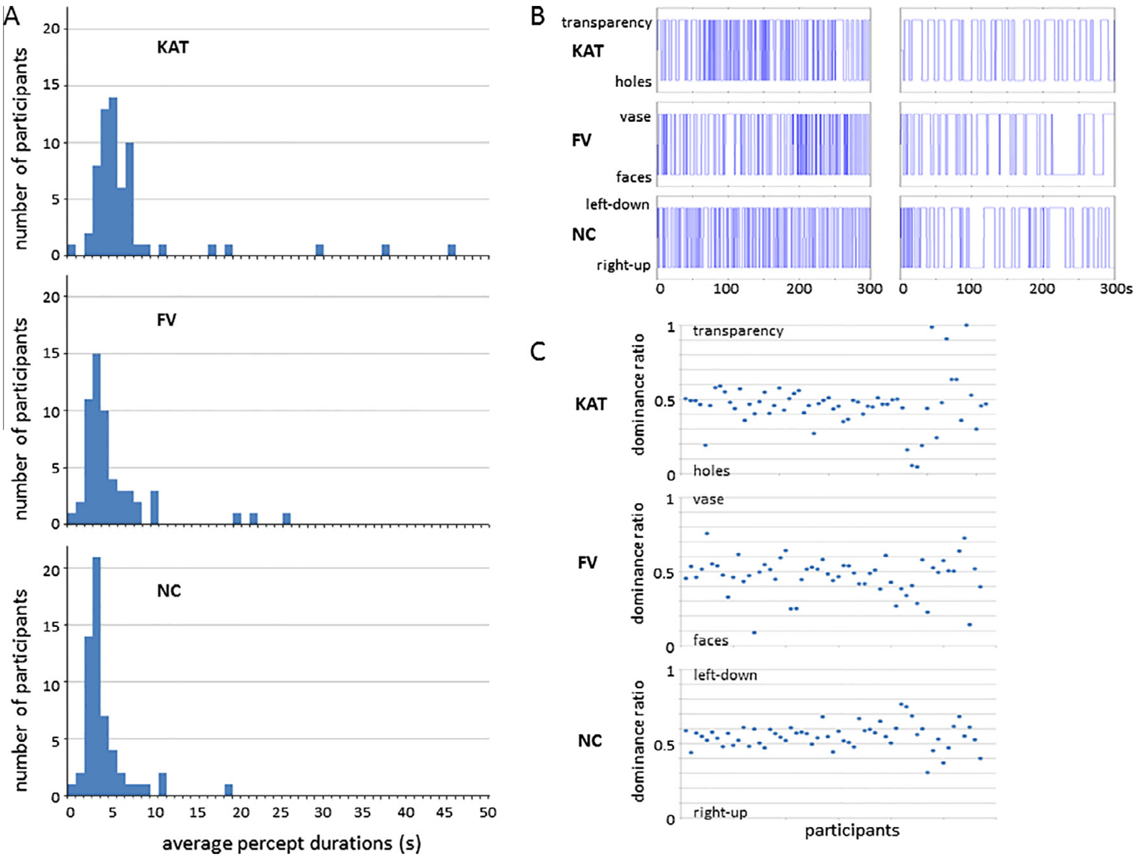

Fig. 3. (A) Distributions of average percept durations of all participants during continuous (prolonged) viewing for KAT (top), FV (middle) and NC (bottom). The KAT stimulus produced the longest percept durations as compared to the percept durations of the other two images. These data show that the average percept durations varied considerably across individual participants. The average percept durations are summarized in Table 2. (B) Examples of the temporal aspects of alternating responses associated with the three images. Left: responses with relatively short percept durations. Right: responses with relatively long percept durations. (C) Perceptual dominance ratio of individual participants calculated as the total dominance duration for one of the two perceptual interpretations ("transparency" for KAT, "vase" for FV, "left-down" for NC) expressed as a percentage of the total presentation time. The majority of the data points are distributed near the 50% line (no sustained bias) while some of them showed strong bias to one of the two percepts (see Table 3 for summary).

and a "vase" response in FV, which corresponds to the perception of the central region being in front, while the sustained bias shifted to the opposite ("holes" and "faces"). On the other hand, responses to NC showed both an onset bias and a sustained bias to the "left-down" perception in the pooled data.

Serial correlations of two percepts were computed for individual participants and averaged across the participants. Although for the first lag serial correlations were observed in FV and NC in the averaged data (Fig. 4A), histograms of the first lag serial correlation values from all participants (Fig. 4B) indicate large variations among individuals.

3.2. Effects of intermittent presentation

Next, we report the response properties for the intermittent presentation condition, which also showed large individual differences. When SPs in the pooled data were averaged, all three bi-stable images showed SPs that were significantly higher than 0.5 (Table 4, left column). Fig. 5 shows selected examples of responses to the three images indicating clear stabilization effects. (See further analysis of SPs later, taking account of onset biases and perceptual switches during ON period.)

However, the degree of the stabilization effect varied between individual participants. Fig. 6A shows SPs of all individual participants (color-coded for different parameter sets). In KAT, the distribution of SPs was strongly skewed toward 1.0, while this effect was less prominent in FV and NC. The data are pooled and SPs are plotted over OFF periods in Fig. 6B. Correlations between SPs and OFF periods are not evident in the pooled data (correlation coefficients, "cor", are indicated in the plots).

SPs of the individual percepts were also analyzed separately: SPs for percept 1 and SPs for percept 2 (Fig. 7A). If the stabilization effects are similar for both percepts, the two data points for the individual participants in Fig. 7A should be close to each other. Conversely, if they are further away, it indicates that the stabilization effects are considerably dependent on the percept. The results showed strong individual differences: Different participants showed either a large or small SP for both percept 1 and percept 2, a large SP for percept 1 and a small SP for percept 2, or a small SP for percept 1 and a large SP for percept 2. The former case indicates participants who showed consistently strong or weak SPs, while the latter two cases indicate that the survival of a perceptual interpretation depends on the percept. The difference of SPs for percept 1 and percept 2 are calculated and the results are plotted as histograms in Fig. 7B to show the wide range of response properties in SPs.

By analyzing the individual data, a key property of the responses becomes evident that may be linked to the various degree of stabilization. In the examples in the left column of Fig. 8 (Fig. 8Aa, Ba, and Ca), the stabilization effect is evident. This is in clear contrast to the examples in the middle column with no stabilization effect. Importantly, these examples in the middle column show the responses where perceptual switches were reported within the ON periods in many cycles of the intermittent presenta-

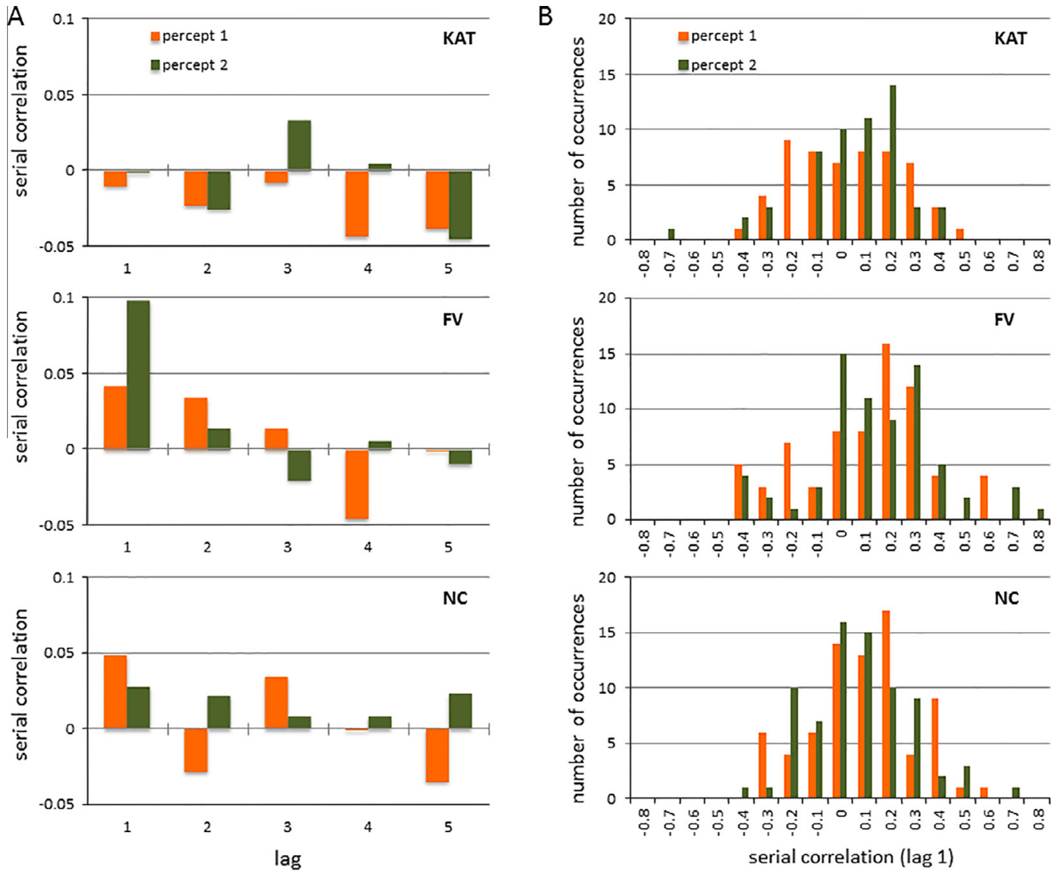

Fig. 4. Histograms of first lag serial correlation analyses (autocorrelation of sequence of percept durations in continuous presentation condition, see Section 2) for KAT (top), FV (middle), and NC (bottom). It shows a wide range of individual differences.

Table 4
Left column: Survival probabilities (SPs) averaged for all participants. An asterisk indicates that the values are significantly higher than 0.5. Right column: Average SPs calculated based on Eq. (1), (SP1 + SP2)/2, after removing pairs of cycles that showed perceptual switches during ON period in the first cycle (see Section 2). A single asterisk indicates that the values are significantly higher than chance level after discounting the onset biases of individuals (Eq. (2)). Double asterisks indicate that the values are significantly different between the figures indicated by the arrows.

	SP	(SP1+SP2)/2 (no SW)
KAT	0.81±0.17*	0.61±0.16* ↕ **
FV	0.59±0.18*	0.51±0.17 ↕ **
NC	0.66±0.23*	0.62±0.23*

tion condition. A portion of the data from Fig. 8Ab is shown enlarged on the right with the perceptual switches indicated by black asterisks. In this example, the participant reported a switch from "transparency" to "holes" and quickly went back to "transparency" within a cycle. Such perceptual switches within the ON periods were frequently found in FV (Fig. 8Bb) and in NC (Fig. 8Cb). The given ON periods (1 or 2 s) during intermittent presentations were much shorter than the average percept duration (7.47 s for KAT, 5.46 s for FV, and 4.45 s for NC, Table 1), so such switches are rather unexpected. This unexpected perceptual switching within the short presentation of the intermittent presentation condition occurs more frequently when the stabilization effect is weaker, as shown next.

It is possible that the intermittent presentation paradigm itself modified the response behavior of individuals, to give rise to the perceptual switches in the short presentations. In Fig. 9, the individual SPs are plotted against the number of perceptual switches that occurred within each cycle of intermittent presentations (i.e., the number of the extra key presses after the first response at the onset of each cycle). There is a clear correlation between the SP and the switch numbers in FV and NC, with increased switching corresponding to decreased SPs. Clearly, data points in KAT are more clustered toward switch numbers of 0 and SPs of 1.0 compared with FV and NC. It should also be noted that Fig. 9 shows some data points with low SPs without high switch numbers. The arrows in Fig. 9 indicates the data points that are shown as examples in Fig. 8. The examples in Fig. 8Bc and Cc show low SPs with small switch numbers, indicating that these participants alternated the percept often at the onset of each cycle.

The occurrence of the perceptual switches during ON periods may influence the SPs as follows. If there are perceptual switches within a cycle, the duration that the percept is held is shorter than the full length of the ON period. The varying durations of the first percept may influence the survival of the percept in the next cycle. In addition, the multiple percepts within a cycle may cause cumulative history effects. Accordingly, we also re-analyzed SPs by removing the cycle pairs where the perceptual switch occurred in the ON period of the first cycle. The goal of this analysis was to test whether the individual SPs are different from chance level in the condition that the percept in the first cycle was reported for the full length of the ON period without a perceptual switch. We then categorized the data into three groups: stabilization, de-stabilization, and no effect (see Section 2). Fig. 10 shows the histograms of SPs (mean of SP1 and SP2, as defined in Eq. (1), (SP1 + SP2)/2) color coded based on the three categories (red = stabilization, green = de-stabilization, and blue = no effect). 33% and

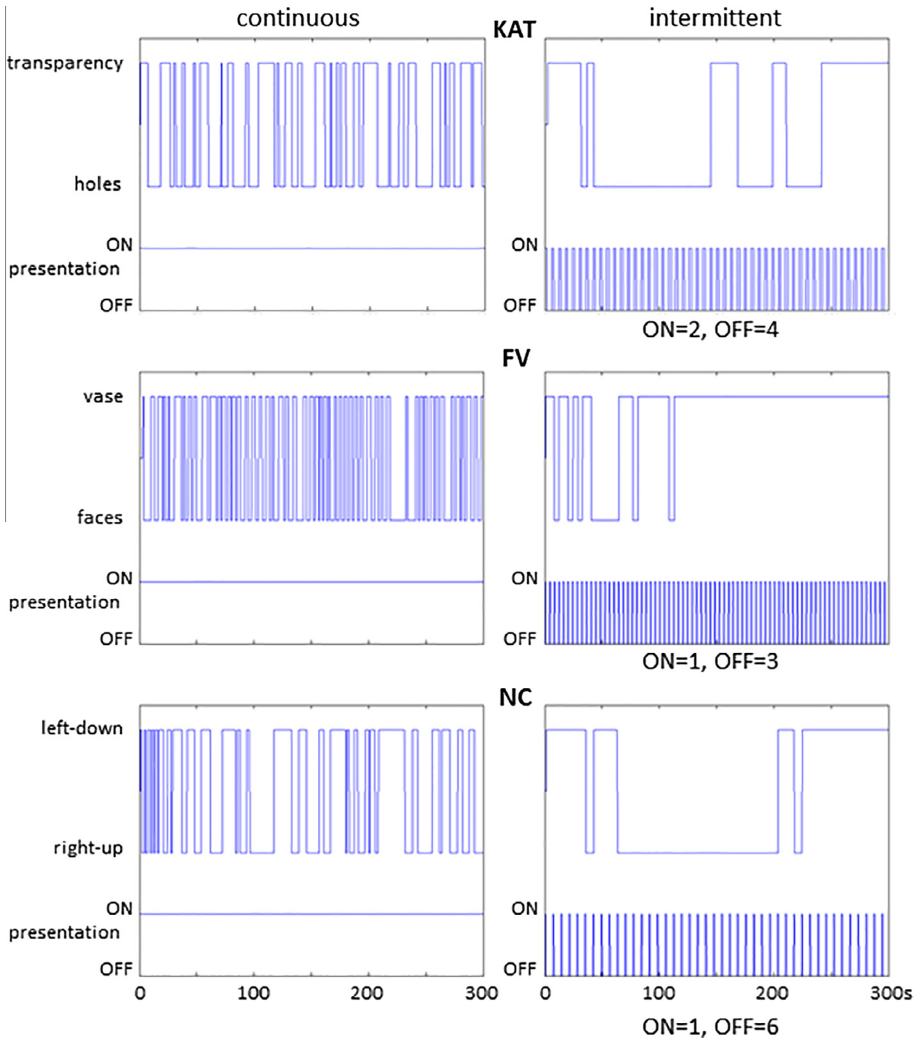

Fig. 5. Examples of responses that showed strong stabilization effects for the three stimuli: KAT (top), FV (middle) and NC (bottom). The left column shows the data for continuous presentation, the right column for intermittent presentation. In each panel, the top plot indicates the responses of the participant, while the bottom plot indicates the physical presentation of the image. Hence, the continuous lines at the bottom of each panel on the left indicate the continuous presentation of the image, while the repetitive pulses on the right indicate the intermittent presentation with the high signals indicating ON periods and the low signals indicating the OFF periods. The temporal parameters of the intermittent presentations (ON period and OFF period) are specified below the plot. The long periods of consistent responses in these examples show a trend that a response in one cycle is repeated frequently in the next cycle.

39% of the participants showed stabilization effect in KAT and NC, respectively while only 14% participants showed the effect in FV. When the SP values were compared between the three figures, KAT and NC were significantly higher than FV, while KAT and NC were not significantly different (Table 4, right column). Furthermore, the average of (SP1 + SP2)/2 values were significantly higher than 0.5 in KAT and NC but not in FV. Therefore, without a perceptual switch during the ON period of the first cycle, the stabilization effect was still weaker in FV than in the other figures.

4. Discussion

Exploring the dynamic properties of perceptual stabilization in figure–ground bi-stability is relevant for the study of how context is taken into account in perceptual organization. As far as we know, the present report is the first to provide data on the dynamic properties of perceptual stabilization in figure–ground bi-stability. We found that survival probabilities pooled across all participants were significantly higher than chance level for all three images. This effect was especially pronounced in Kanizsa's anomalous transparency (KAT) illusory image, which was also accompanied with prolonged average percept durations in the intermittent presentation condition. Interestingly, the stabilization effect was weaker in the "face-or-vase" (FV) illusory image. The weaker stabilization effect correlated negatively with the occurrence of perceptual switches within the ON periods (1 or 2 s). The reasons of these findings are unknown but quite relevant because FV has often been used as the prototypical case of bi-stable figure–ground perception. Computational modeling for figure–ground perceptual bi-stability shows that it is possible, in principle, to produce perceptual stabilization in FV by implementing adaptation and recovery factors (Kogo, Galli, & Wagemans, 2011). For a range of parameters, the stabilization effect was nearly diminished (Fig. 7 of Kogo, Galli, & Wagemans, 2011), although the model did not show the decreased average percept durations (in the range of the parameters that were tested). Interestingly, it has been suggested that the memory effect may be dichotomous, causing a "positive history effect" and a "negative history effect" with SPs that are higher or lower than chance level, respectively, depending on the temporal parameters of the stimulus presentation (in

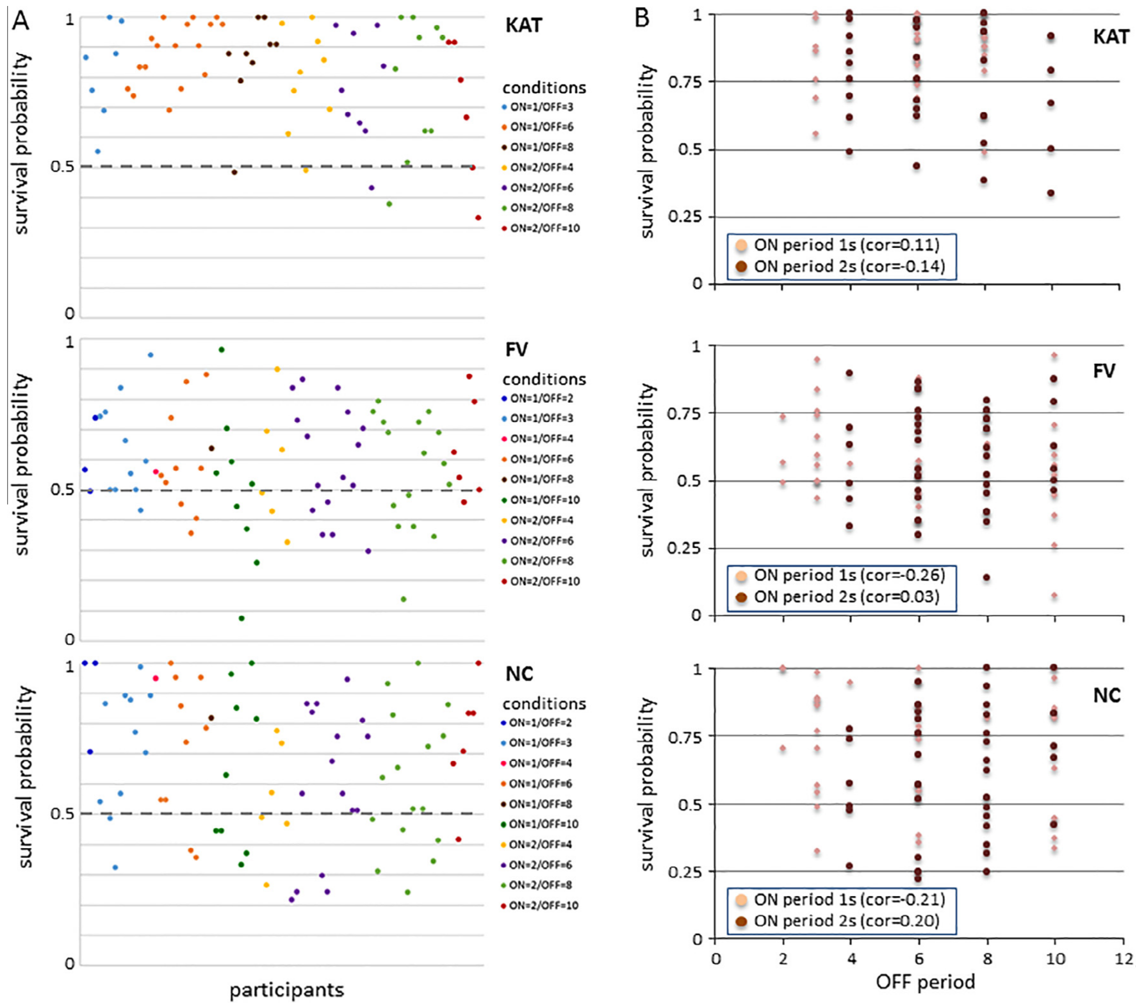

Fig. 6. (A) Survival probabilities of individual participants for intermittent presentation of the three used bi-stable stimuli KAT (top), FV (middle) and NC (bottom), color coded and sorted for different temporal parameters. They are sorted, from left to right, by ON-periods (either 1 s or 2 s) and then by OFF periods. Survival probabilities (SP) are determined by calculating the probability that the perceptual interpretation at the offset of the stimulus reappears upon subsequent presentation of the same stimulus, quantifying the perceptual stability across the OFF period. While KAT produces a distribution of SPs that is clearly skewed toward 1.0 (complete stabilization without perceptual switch), and NC produces a skewed distribution to a lesser extent, the skewedness of the distribution of FV is small. (B) SPs plotted over OFF period (from all participants). Light brown: data with ON period of 1 s. Dark brown: data with ON period of 2 s. The correlation coefficients are shown in the inset ("cor"). There are no evident correlation between SPs and OFF periods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

structure-from-motion illusion, Pastukhov & Braun, 2013). A population of neurons representing one percept may enhance its own activity and inhibit the activity of the other population of neurons representing the other percept, which shifts the bias of the responses to one direction, At the same time, however, adaptation of response properties would progress. Hence, the history effect involved multiple factors. Furthermore, differential development of history effects in activities of excitatory and inhibitory neurons (and synapses) may contribute to the complex overall history effects. In fact, neurons competing for border-ownership at each location of borderlines are assumed to have a mutually inhibiting circuit (Craft et al., 2007; Zhou, Friedman, & von der Heydt, 2000). Continuous presentation involves ongoing mutual excitation, mutual inhibition, and their adaptation, while the adaptation partially recovers during the blank period as well as during the dominance of the other percept. It is possible that the reversal of border-ownership is more dynamic and complex than expected by a simple adaptation and recovery mechanism which, in turn, may cause the history effect to become rather complex in the bi-stable behavior. Moreover, the memory traces observed in bi-stable perceptual interpretations in general involve further complex factors. At the onset of each presentation, individuals may show biased responses. During continuous or intermittent presentation, the additional adaptive or cumulative factors could also influence the bi-stable responses (Pastukhov & Braun, 2011; van Ee, 2009). Furthermore, it has been shown that onset bias and sustained bias are different (Carter & Cavanagh, 2007; Stanley et al., 2011). The apparent stabilization reflects both the intrinsic response bias of the individuals at onset and the changes of the temporal dynamics in the neurons involved. Therefore, it is quite important to investigate the contributions of these factors thoroughly in future experiments to understand the complex interactions of the intrinsic response bias and the properties of temporal dynamics that exhibit cumulative history effects. It would, in turn, help to understand the neural mechanisms underlying figure–ground organization. In this light, it is important that the three images produced different distributions of responses, which may reflect the different perceptual organizations when these images are presented. Below, we discuss the possible reasons for such differential responses.

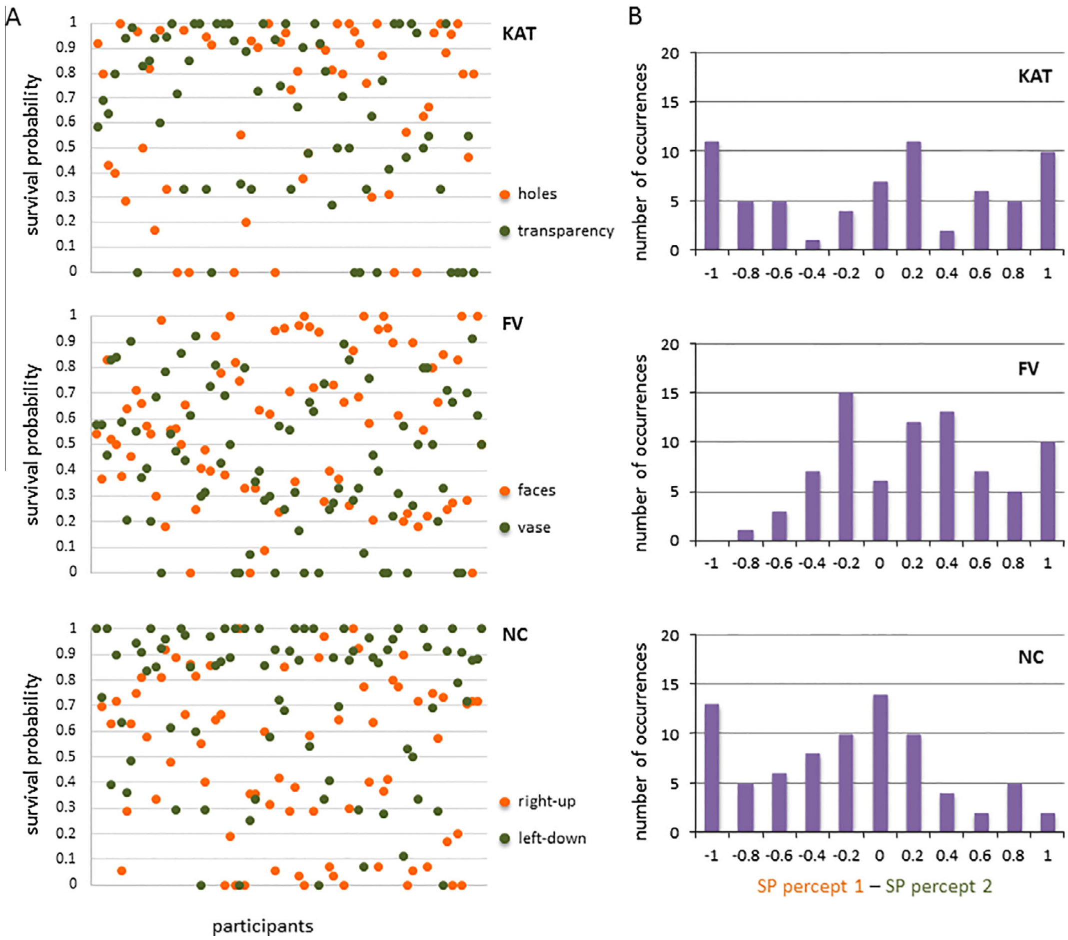

Fig. 7. Survival probabilities averaged separately for percept 1 and percept 2. (A) Survival probabilities of individual participants. It shows strong individual differences: a large or small SP for both percept 1 and percept 2, a large SP for percept 1 and a small SP for percept 2, or a small SP for percept 1 and a large SP for percept 2. (B) Histograms of difference of survival probabilities for percept 1 and percept 2 (SP of percept 1 minus SP of percept 2). It reveals the wide range of the individual differences in the distribution of this difference between participants.

First, qualitative, phenomenological differences occur between the perceptual interpretation for KAT and for FV, namely, the certainty of perceptual interpretations and the percept durations. At any point in time, the perceptual interpretation of the KAT image is quite clear and distinct (Fig. 1C). In the perceptual interpretation of FV, however, there is much more uncertainty: In fact, many participants reported that it was much more difficult to judge which interpretation was dominant during the presentation of FV than during the presentation of KAT. Moreover, the average percept duration in KAT is significantly longer than FV. One of the possible reasons for this difference is that multiple properties in the perceptual organization change when the perceptual interpretation of KAT changes (Fig. 2B), as opposed to a mere reversal of figure–ground in FV. In the "transparency" perceptual interpretation of KAT, the vertical transparent rectangle is perceived (Fig. 1C, top). This means that the area where the large horizontal rectangle and the transparent rectangle overlap becomes darker than the light gray in the horizontal rectangle: an effect of illusory lightness perception. Furthermore, the perceptual interpretation of the transparent rectangle involves the illusory contours. In addition, the black polygons may be perceived as individual objects in the "transparency" percept but as holes in the "holes" percept. This corresponds to reversals of BOWN at the boundaries of the polygons. Therefore, these properties have to change coherently to switch from one perceptual interpretation to the other. The coherent changes of multiple properties in the perceptual organization may be the reason why the dominant percept is more stable (and clearer) and also why the dominant duration is longer (i.e., slower switching because multiple attributes related to the switching process are involved).

Bi-stable stimuli usually produce stabilized perceptual interpretations during intermittent presentation (just as for our KAT stimulus). Stimuli that have been employed are the NC, structure from motion, monocular rivalry and binocular rivalry, quartet dots, and motion-induced blindness (Brascamp et al., 2010; Chen & He, 2004; Kang & Shevell, 2011; Kornmeier & Bach, 2004; Leopold et al., 2002; Orbach, Ehrlich, & Heath, 1963; Pearson & Clifford, 2004; Ross & Ma-Wyatt, 2004). For these images participants are usually confident about their response. Could the uncertainty of the perceptual interpretation in FV be the cause of the decreased stabilization effect? It is known that there are various degrees of top-down effects in bi-stable perception: for binocular rivalry participants are less able to exert voluntary control to influence the perceptual interpretation, while perceptual rivalry with images such as the Necker cube and the Schröder staircase is more strongly affected by voluntary control (Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). Therefore, one may speculate that the uncertainty in the perceptual interpretations of FV makes perceptual interpretation susceptible to top-down influences, and that this leads to the dependency of the response properties on the context of how the image is presented, such as continuous versus intermittent presentation. To address the issue of the uncertainly,

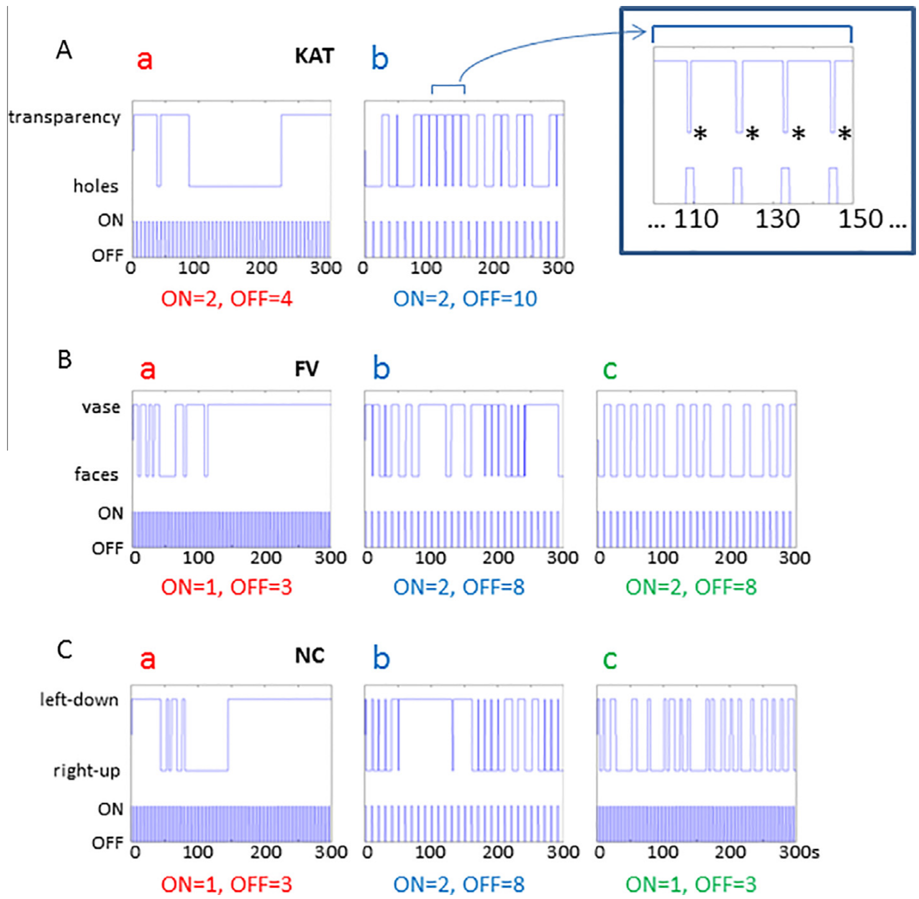

Fig. 8. Examples of responses KAT (A), FV (B) and NC (C). (a) Responses with stabilization effect, (b) no effect, (c) de-stabilization effect (no data for KAT). Top right for KAT: A magnified portion of the response in (b). The perceptual switches during the ON periods are indicated by asterisks. It demonstrates how the "holes" interpretation was perceived briefly, quickly switching back to "transparency". Similar brief perceptions are present for the other two images (Bb and Cb). In (Bc and Cc), perception often alternated upon every stimulus presentation cycle, hence the survival probabilities are low. In these data there are few perceptual switches within each ON period.

it would be quite interesting, in a future study, to ask participants to press a third key when the perception is a mixture or when they cannot decide between the two percepts. (Note, however, that this may be a difficult task for short percept durations and hence this probably requires highly trained participants.)

The relatively short average dominant percept durations in FV may also contribute to the dependency of the responses on the context of presentation. Note that KAT, which showed the strongest stabilization effect, had the longest average dominant percept duration, while FV showed the shortest one. Naber and colleagues indicated that short perceptual dominance durations may have been missed using a conventional key press task (Naber, Frässle, & Einhäuser, 2011). By finding a correlation between perceptual switches and pupil dilation or optokinetic nystagmus, they showed that short events are present in these reflexes without being reported by participants. The number of missed-out events would be larger with images that create shorter percept durations such as FV. Particularly for the stabilization effect, unrecorded perceptual switches may play a significant role. In the conventional intermittent presentation paradigm, the image is presented briefly and disappears *before* the perceptual switch occurs. For this purpose, the ON period is set short enough to avoid the switch during the ON periods based on the average dominant duration estimated from the continuous presentation. This is how the ON periods we used (1 s or 2 s) were determined. However, if an unreported perceptual switch occurs during the ON periods, the "holding effect" of a percept is not measured properly. Furthermore, it may even be possible that the participants reported the fast events more often with the intermittent presentations because, in the intermittent presentation, they were obliged to report the first perceptual interpretation at the onset of every cycle. Indeed, the fact that there were many cases when perceptual switches occurred during the ON periods may suggest that participants tended to report the fast perceptual switches more easily in the intermittent presentation paradigm.

Lastly, the two perceptual interpretations in FV (two faces and a vase) are semantically quite different ("reversal of meaning", see Long & Toppino, 2004 for review). In KAT, the differences of the two perceptual interpretations involve the reversed depth order of two rectangles, and in NC, the two perceptual interpretations involve a cube, only with a different orientation. The two very different and specific semantics of face and vase in FV may be another reason why it creates quite different temporal dynamics in bi-stable perception. However, it is unknown how the semantic difference between two rivaling percepts causes different temporal dynamics in bi-stable perception. In this regard, note that the bi-stability for FV is directly linked to reversals of BOWN. As described in Section 1, BOWN-sensitive neurons are found in V1, V2 and V4 (Zhou, Friedman, & von der Heydt, 2000). They reported that the onset latency of the BOWN signal was short and concluded that BOWN is computed by a feedback circuit (Craft et al., 2007; Sugihara, Qiu, & von der Heydt, 2011). Furthermore, they suggested that selective attention is involved through this feedback circuit (Qiu, Sugihara, & von der Heydt, 2007). Whether these BOWN-sensitive neurons are involved in bi-stable perception of FV is not known, but MEG recordings with a "frequency tagging"

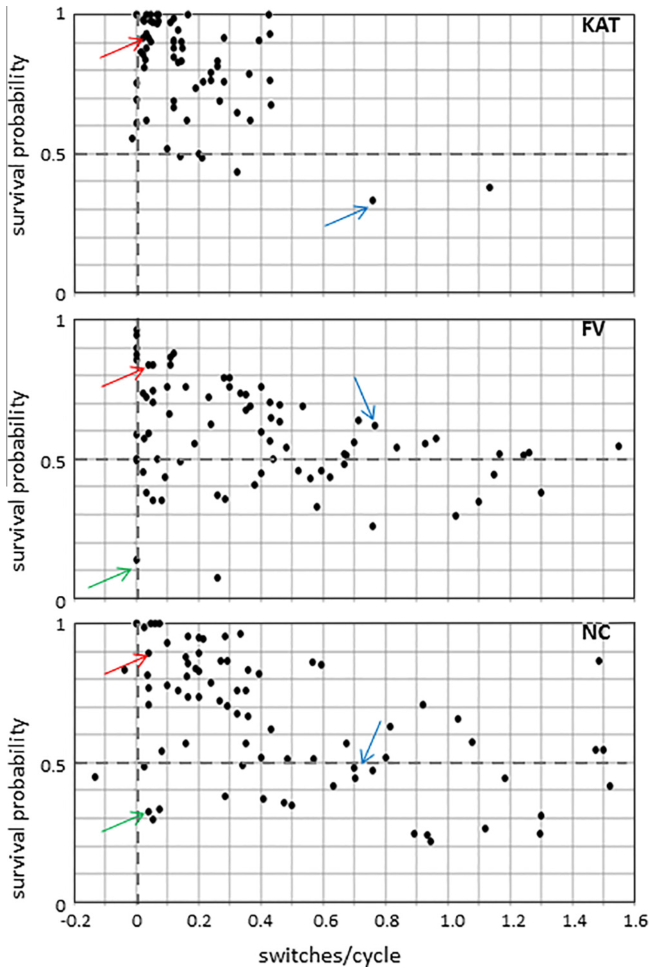

Fig. 9. Survival probabilities (SP) of individual participants as a function of the average number of perceptual switches per cycle during intermittent presentation. Negative values of the switch numbers indicate that some participants failed to respond in some cycles. Arrows indicate the data points corresponding to the data shown in Fig. 8: the red arrows indicate the data points corresponding to the examples shown in Fig. 8Aa, Ba, Ca, the blue arrows to the ones in Fig. 8Ab, Bb, Cb, and the green arrows to the ones in Fig. 8Bc and Cc, respectively. In KAT, many data points are clustered to the left-top corner, indicating that the perceptual switches during ON-periods did not happen often in KAT. In FV and NC, there were many perceptual switches during ON-periods. There is a clear trend of monotonic decay, indicating that the frequencies of the switch correspond with the decrease of survival probability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

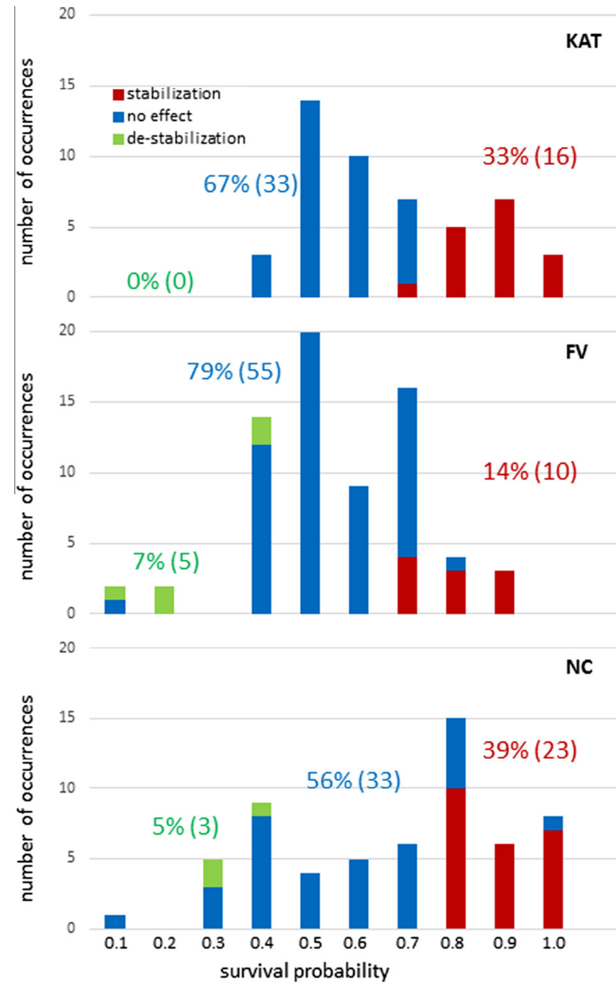

Fig. 10. Ratio and number of occurrences of survival probabilities (SP) of individual participants categorized into three groups. Red: stabilization, blue: no effect, green: de-stabilization. The values above the bars indicate the ratio and numbers (in parenthesis) of data points belonging to the three groups. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

method revealed that the lower level visual cortex shows alternating neural activities corresponding to the perceptual switch reported by the participant while viewing FV image (Parkkonen et al., 2008). This suggests the possibility that BOWN-sensitive neurons may indeed be involved. If this is the case, the mechanisms underlying the perception of FV may exhibit dynamic interactions between the BOWN computation mechanism and higher level computations through a feedback circuit, as suggested by von der Heydt and his colleagues.

In sum, we have investigated the stabilization effect in bi-stable figure–ground perception using the KAT image and the FV image. While the KAT image exhibited the pronounced stabilization effect found in previous work on other cases of bi-stable perception, stabilization was weaker in the FV image. Although the relatively weak stabilization effect in FV is rather surprising, we believe this is an important finding. This result goes against the common assumption that strong stabilization generally occurs in bi-stable perception. Higher-level factors such as semantics, familiarity, attention, and expectation, may all contribute to the complex processes underlying the temporal dynamics of bi-stable perception.

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