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Multistable perception: When bottom-up and top-down coincide

Jürgen Kornmeier [a,b,*], Christine Maira Hein [c], Michael Bach [a]

[a] Univ.-Augenklinik, Killianstraße 5, 79106 Freiburg, Germany
[b] Institut für Grenzgebiete der Psychologie, Wilhelmstraße 3a, Germany
[c] Carl-von-Ossietzky-Universität Oldenburg, Germany

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ABSTRACT

During prolonged observation of an ambiguous figure sudden perceptual reversals occur, while the stimulus itself stays unchanged. There is a vivid debate about whether bottom-up or top-down mechanisms underlie this phenomenon. In the present study, we investigated the interrelation of two experimental factors: volitional control and discontinuous stimulus presentation. Both factors strongly modulate the rate of perceptual reversals and each is attributed either as top-down or bottom-up. We found that participants can apply specific strategies to volitionally increase and/or decrease the stability duration of each of the possible percepts according to the experimental instructions. When attempts of volitional control are combined with discontinuous stimulus presentation the effects are fully additive. Our results indicate that perceptual reversals can originate from different neural mechanisms on different time scales.

1. Introduction

Our brain receives only a restricted amount of information about the visual world not least because the 3D world is projected onto 2D retinae. Each percept is thus the result of a constructive process, starting already at the earliest steps of visual analysis, as several optical illusions demonstrate impressively (Bach, 1997). Sometimes our perceptual system fails to produce a stable unambiguous percept, especially if the visual information is equally compatible with different perceptual interpretations as in the case of ambiguous figures. A prominent example is the Necker cube (Fig. 1A, Necker, 1832) whose perceived front-back orientation reverses spontaneously while the figure itself stays unchanged.

Almost two centuries of research on the phenomena of perceptual instability culminated in two explanatory approaches: The "bottom-up" approach assumes "passive", automatic and locally adaptable mechanisms during early visual processing as underlying perceptual reversals (e.g., Köhler, 1940; Toppino & Long, 1987). In apparent contradiction, the "top-down" approach assumes that "active", volitional processes near perceptual awareness cause reversals (e.g. Horlitz & O'Leary, 1993; Leopold & Logothetis, 1999; Rock, Hall, & Davis, 1994). Both approaches are based on numerous experimental evidence (for a review see Long & Toppino, 2004) and although several authors suggest that both bottom-up factors and top-down factors play an important role for perceptual reversals (Blake & Logothetis, 2002; Kornmeier & Bach, 2005, 2006; Long & Toppino, 2004; Roeber et al., 2008; Strüber & Herrmann, 2002), a theory integrating all empirical findings is still missing to date.

The present study focuses on two experimental factors that strongly modulate the dynamics of perceptual reversal, each being regarded as supportive for one of the two competing explanational approaches.

1.1. Volitional control

Reversal rates are modulated when participants exert volitional control, i.e., when they either volitionally increase or decrease the number of reversals (Strüber & Stadler, 1999; Toppino, 2003; van Ee, van Dam, & Brouwer, 2005). These results were interpreted as supporting the top-down approach.

1.2. Discontinuous stimulus presentation

Considerable modulation of the reversal rate was also reported in studies with "discontinuous stimulus presentation". This presentation mode was introduced by Orbach et al. with the Necker cube as early as 1963 (Orbach, Ehrlich, & Heath, 1963) and has recently regained scientific attention (Grossmann & Dobbins, 2006; Kornmeier, Ehm, Bigalke, & Bach, 2007; Kornmeier, Heinrich, & Bach, 2002; Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003; Sterzer & Rees, 2008). Discontinuous stimulus presentation has two opposing effects on perceptual stability of ambiguous figures: Short ISIs (up to 400 ms) can

* Corresponding author. Address: Univ.-Augenklinik, Killianstraße 5, 79106 Freiburg, Germany. Fax: +49 761 270 4108.
E-mail address: juergen.kornmeier@uni-freiburg.de (J. Kornmeier).

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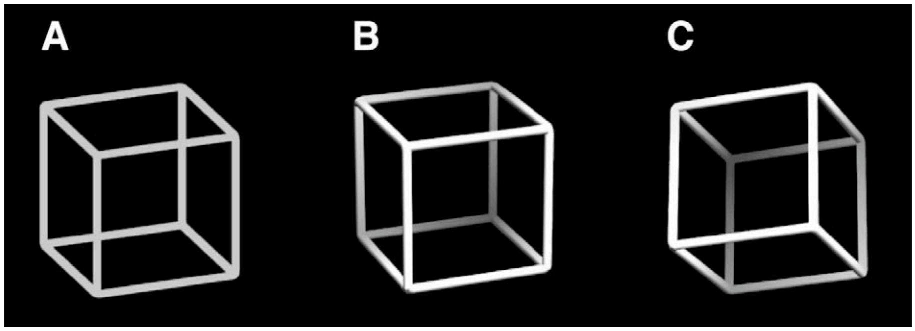


Fig. 1. (A) Ambiguous Necker cube; (B) unambiguous cube-variant with the front cube-side oriented towards bottom-right ("FB"); (C) unambiguous cube-variant with the front cube-side oriented towards top-left ("FT").

increase reversal rates up to twice the rate than during continuous presentation (Kornmeier et al., 2007; Kornmeier et al., 2002; Orbach et al., 1963) and concurrently decrease stability durations. Presentation times seem to play thereby a minor role (Orbach, Zucker, & Olson, 1966; Orbach et al., 1963). With longer ISIs (>400 ms) reversal rates decrease dramatically, down to zero reversals (Leopold et al., 2002; Maier et al., 2003; Sterzer & Rees, 2008). However, this is only the case if presentation times are shorter than the individual average stability duration. Thus, for presentation times below a certain threshold, reversal rates can be described as an inverted-U-shaped function of ISI (see Fig. 1, page 553, in Kornmeier et al., 2007). Orbach et al. (1963) explained their findings as the result of the interplay between bottom-up adaptation and recovery of neural populations representing the competing perceptual interpretations and thus as evidence for a bottom-up driven influence. In other studies the role of memory was emphasized (Leopold & Logothetis, 1999; Maier et al., 2003), however, it is still unclear how exactly and which kind of memory may be involved. Kornmeier et al. (2007) interpreted the existence of an ascending and a descending part of the function as evidence for two different neural processes underlying perceptual dynamics. Further, they assume that the processes underlying the ascending part of the function are similar to those underlying perceptual reversals during continuous presentation of the ambiguous stimulus, because there is a smooth monotonous transition of reversal rate from an ISI of 400 ms to an ISI of 0 ms (continuous presentation).

In the present study, we investigated the interrelation of volitional control and a discontinuous presentation mode regarding the dynamics of reversal rates and stability durations. In the first of two experiments, ambiguous Necker cubes were presented continuously with five different instructions concerning volitional control of the perceived cube orientation. In the second experiment, we combined volitional control instructions with the variation of presentation times and ISIs during discontinuous stimulus presentation. We restricted this experiment to ISIs covering the ascending part of the above-mentioned function, because we assume that the reversal processes are more related to those during continuous stimulus presentation from Experiment 1.[1] The results indicate full additivity of the two experimental factors.

[1] The selection of presentation times was motivated by a subsequent EEG study, where we also combined discontinuous stimulus presentation with volitional control. We focused on presentation times short enough to prevent re-reversals during one presentation and concurrently long enough to record all ERP components recently reported in Kornmeier and Bach (2006).

2. Experiment 1

2.1. Methods

2.1.1. Participants

Ten participants with a mean age of 26.5 years took part in the experiment. They were all naive as to the specific experimental question (i.e., the interrelation between volitional control and stimulation mode regarding perceptual instability) and gave their informed written consent. All of them had normal or corrected-to-normal visual acuity. The study was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2000) and was approved by the local ethics review board.

2.1.2. Stimuli

The ambiguous stimulus was a Necker cube with light grey edges on a black background (Fig. 1A), presented with a frame rate of 70 Hz at a viewing angle of $7.5^{\circ} \times 7.5^{\circ}$. Luminance of the cube was 20 cd/m^2; background luminance was 0.01 cd/m^2. A cross in the centre of the cube served as fixation target.

2.1.3. Procedure

The participants were instructed to look at the Necker cube for 3 min, to fixate the fixation cross in the center and to perform the following tasks (where the "i" denotes an instruction and "p" denotes an indicated percept):

Hold Unspecific ("iHU"): Hold whichever interpretation is currently dominant (pFT or pFB, see below) as long as possible and try to prevent reversals. Press the appropriate button whenever you perceive a reversal.

Hold Bottom ("iHB"): Hold that perceptual interpretation of the cube with the front side oriented downwards to the right (**p**ercept **F**ront **B**ottom "pFT", Fig. 1B) as long as possible and reverse back to it as quickly as possible in the case of an unwanted reversal towards the opposite interpretation. Press the appropriate button whenever you perceive a reversal.

Hold Top ("iHT"): Hold that perceptual interpretation of the cube with the front side oriented upwards to the left (**p**ercept **F**ront **T**op "pFT", Fig. 1C) as long as possible and reverse back to it as quickly as possible in the case of an unwanted reversal towards the opposite interpretation. Press the appropriate button whenever you perceive a reversal.

Passive ("iP"): Keep a passive attitude towards the stimulus and press the appropriate button whenever you perceive a reversal of the stimulus.

Reverse ("iRE"): Reverse your percept as often as possible between the two interpretations and press the appropriate button whenever you perceive a reversal.

Participants indicated perceived orientation reversals of the Necker cube from pFB to pFT and from pFT to pFB with different hands, pressing different keys. All participants started with the passive instruction to avoid a potential inability of keeping a passive attitude towards the stimulus after having passed an experimental block with volitional control. The consecutive conditions were separated by breaks of 30 s with a blank screen and the order was randomized across participants. This experiment lasted for about 17 min.

At the beginning, all participants were informed about the reversibility of the Necker cube and the two possible perceptual alternatives (Fig. 1B and C) were demonstrated. After the participants were able to identify both cube versions, they performed a short training run of 3 to 5 min to become familiar with the experimental situation. In the training, we presented unambiguous versions of the Necker cube, which the computer program exchanged randomly. Participants indicated perceived orientation reversals with the appropriate key. The program indicated errors by short beeps.

2.1.4. Data analysis

Reversal rates were calculated as the mean number of key presses per minute. Stability durations were computed as the mean duration between pressing one key and pressing the alternate one. Although it is generally assumed that reversal rates are inversely proportional to stability durations, this holds only under restricted conditions, as will be demonstrated. If participants occasionally pressed the same key two times consecutively (e.g., if they indicated two times consecutively a reversal from cube front side left top to right bottom they had missed or neglected to indicate one reversal from cube front side right bottom to left top), these trials were excluded from the analysis of the stability durations. Reversal rates and the two stability durations were the three dependent variables in a one-factorial repeated measures MANOVA with corrections of potential violations of the sphericity-assumption according to Geisser and Greenhouse (1958) and with the factor Condition (iHU, iHB, iHT, iP, iRE). The results of post-hoc permutation-tests (Edgington, 1995) were corrected for the number of orthogonal tests according to Holm (1979).

2.2. Results

2.2.1. Reversal rates

The mean reversal rates ± SEM across 10 participants of the five experimental blocks are depicted as white circles in Fig. 2A.

The MANOVA indicated significant effects of the experimental conditions on reversal rates ($F(4,36) = 11.152$, $P < .05$, $\eta_p^2 = .563$). The results from post-hoc permutation tests are depicted in Table 1. The following can be observed (the values in parentheses are *P*-values before multiple-testing-correction):

(1) Reversal rates increase from the unspecific hold-condition over the specific hold-conditions, the passive-condition to the reverse-condition and they were arranged in all figures and tables in that order.
(2) The unspecific hold-condition almost halves the mean reversal rate (7 reversals/min) compared to the passive condition (12.5 reversals/min; iHU < iP, $P < .01$, [.003]), whereas the reverse-condition almost doubles it (21.6 reversals/min; iRE > iP, $P < .05$ [.02]).
(3) Reversal rates are higher in the specific hold-condition than in the unspecific hold-conditions (iHB > iHU, $P < .01$ [.002]; iHU > iHT, $P < .05$ [.02]; Table 1).
(4) Reversal rates are lower in the specific hold-conditions than in the passive condition (iHB < iP, $P < .05$ [.015]; iHT < iP, $P < .05$ [.018]) and lower than in the reverse condition (iHB < iRE, $P < .01$ [.001]; iHT < iRE, $P < .01$ [.001]).

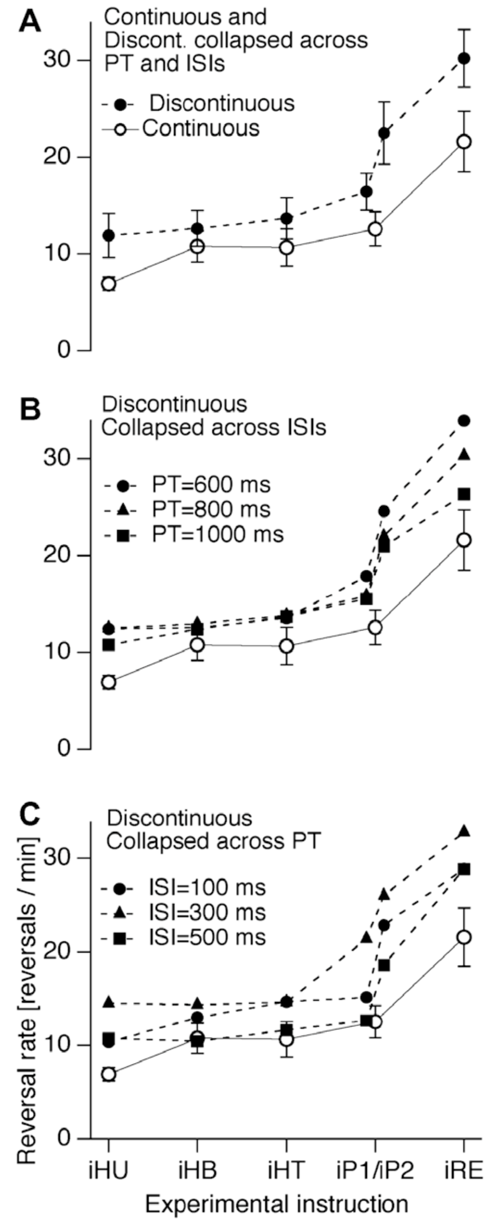


Fig. 2. Mean reversal rates across conditions. (A–C) White circles: Mean reversal rates (± standard errors of the mean, "SEM") across participants from continuous stimulus presentation (Experiment 1) for the different conditions concerning volitional control. (A) Black circles: Mean reversal rates across participants, presentation times and ISIs ± SEMs. (B) Black symbols: Mean reversal rates across participants and ISIs for the three different presentation times. (C) Black symbols: Mean reversal rates across participants and presentation times for the three different ISIs. The connecting lines along the nominal abscissa between the data points are for illustrative purposes only. (PT, presentation time; Continuous, continuous stimulus presentation; Discontinuous, discontinuous stimulus presentation; ISI, inter-stimulus interval). Note that Experiment 1 contains only one passive condition (only one white circle at iP1/iP2) whereas Experiment 2 contained two passive conditions (Two adjacent black symbols at iP1/iP2).

Inspection of the individual reversal rates (Fig. 3) shows the following:

(1) In both the hold-condition and the passive condition, the individual mean reversal rates are equally distributed around the grand mean. In the case of the reverse condition the distribution is non-symmetric where low reversal rates are more frequent than high rates.

Table 1
Experiment 1, reversal rates

	iHB	iHT	iP	iRE
iHU	**	*	**	**
iHB		ns	*	**
iHT			*	**
iP				*

*P < .05; **P < .01.
Post-hoc permutation tests across experimental blocks, corrected for the number of orthogonal tests according to Holm (1979); iHU, hold unspecific; iHT, hold top; iHB, hold bottom; iP, passive attitude; iRE, reverse.

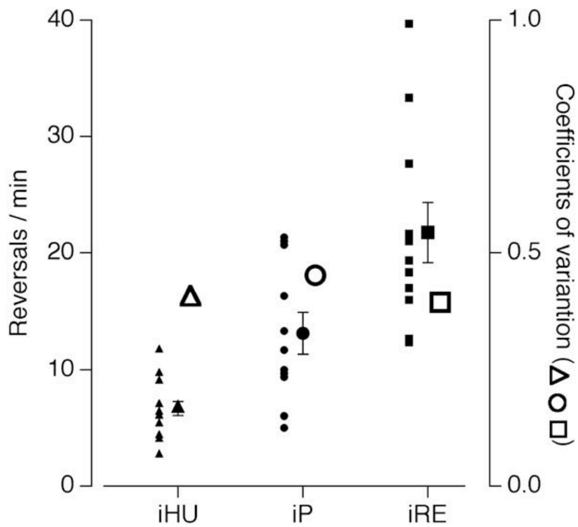


Fig. 3. Left: Mean reversal rates of the individual participants together with grand means ± SEMs across participants. Circles, passive condition (iP); triangles, hold-condition (iHU); squares, reverse-condition (iRE). Open symbols: coefficient of variation ("CV": standard deviation divided by mean) for the three experimental conditions

(2) Variability between participants is proportional to the reversal rate, since coefficients of variation ("CV") are very similar: CV(HU) = 0.4; CV(P1) = 0.45; CV(RE) = 0.39.
(3) No participant was able to completely stop the reversal process volitionally.

2.2.2. Stability duration

The mean stability durations ± SEM of the two possible 3D orientations of the Necker cube are depicted in Fig. 4A (black symbols: cube perceived with its front side oriented to the bottom right = pFB; white symbols: perceived front side oriented to the top left = pFT).

The repeated measures MANOVA indicated for both dependent variables pFB and pFT significant effects for the factor condition (pFB: $F(4,36) = 8.54$, $P < .001$, $\eta_p^2 = .49$; pFT: $F(4,36) = 8.59$, $P<.001$, $\eta_p^2 = .49$). Results from the post-hoc permutation-tests are listed in Table 2.

The following can be observed (see also Table 2):

Target percepts [percepts which correspond to the instruction: pFB(iHB) and pFT(iHT)]

(1) There is no significant difference between the stability durations of the target percept in the specific hold-condition and the stability duration of the same percepts in the unspecific hold-conditions.
(2) The stability durations of the target percepts in the specific hold-conditions are either longer than the stability durations

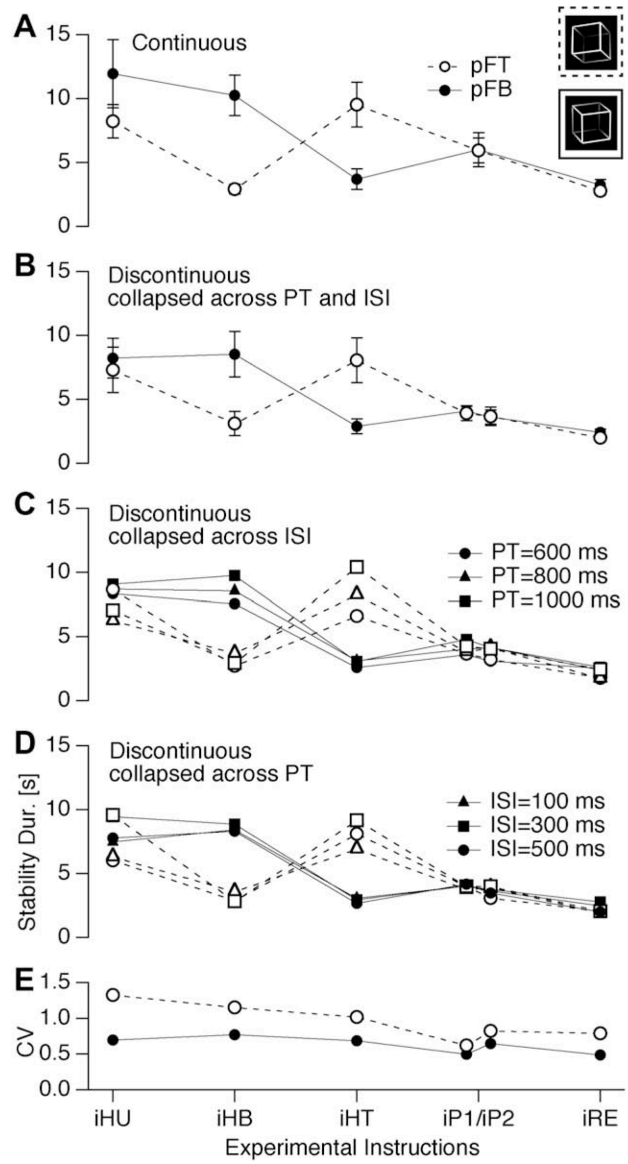


Fig. 4. Stability durations. (A–E) White circles represent mean stability durations of the **p**erceived cube-**F**ront-side at left **T**op (pFT); black circles represent stability durations of the **p**erceived cube-**F**ront-side at right **B**ottom (pFB). (A) Mean stability durations (±SEMs) across participants for the different volitional-control instructions with continuous stimulus presentation (Experiment 1). (B) Mean stability durations ± SEMs across participants, presentation times and ISIs with discontinuous stimulus presentation (Experiment 2). (C) Mean stability durations across participants and ISIs for the three different presentation times (Experiment 2). (D) Mean stability durations across participants and presentation times for the three different ISIs (Experiment 2). (E) Coefficients of variance from the data in (B). The connecting lines along the nominal abscissa between the data points are for illustrative purposes only. Note that Experiment 1 contains only one passive condition (Only one white circle at iP1/iP2) whereas Experiment 2 contains two passive conditions (Two adjacent black symbols at iP1/iP2). (PT, presentation time; Continuous, continuous stimulus presentation; Discontinuous, discontinuous stimulus presentation; ISI, inter-stimulus interval)

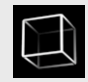
of the same percepts in the passive condition (pFB(iHB) > pFB(iP): $P < .05$ [.001]) or they do not differ significantly (pFT(iHT) vs pFT(iP): ns [.06]). Further, the stability durations of the target percepts in the specific hold-conditions are longer than the same percepts in the reverse condition (pFB(iHB) > pFB(iRE): $P < .05$ [.003]; pFT(iHT) > pFT(iRE): $P < .01$ [.005]).

Table 2
Experiment 1, stability durations

		iHB	iHT	iP	iRE
iHU	pFB	ns	**	**	**
	pFT	**	ns	ns	**
iHB	pFB		**	*	**
	pFT		**	**	ns
iHT	pFB			ns	ns
	pFT			ns	**
iP1	pFB				*
	pFT				**

*$P < .05$; **$P < .01$.
Post-hoc permutation tests across experimental blocks, corrected for the number of orthogonal tests according to Holm (1979); iHU, hold unspecific; iHT, hold top; iHB, hold bottom; iP, passive attitude; iRE, reverse.

Table 3
Predicted and applied control strategies

Instruction	Hold-strategy ...				Predicted effect on reversal rate	Observed effect on reversal rate
	Front bottom 		Front top 			
Hold front bottom	(1)	↑↑	(1)	∅	↓↓	↓
	(2)	∅	(2)	↓↓	↑↑	
	(3)	↑↑	(3)	↓↓	∅	
Hold front top	(1)	∅	(1)	↑↑	↓↓	↓
	(2)	↓↓	(2)	∅	↑↑	
	(3)	↓↓	(3)	↑↑	∅	
Hold unspecific	(4)	↑↑	(4)	↑↑	↓↓	↓↓

Schematic overview of possible strategies to hold a percept of the Necker cube according to the instructions together with predicted and observed effects on reversal rates compared to results from the passive condition as reference. For the predictions it is assumed that increasing and decreasing the stability duration of one percept is equally effective. ↑↑, strong increase of reversal rates; ↓↓, strong decrease of reversal rates; ↓, small decrease of reversal rates; ∅, unchanged reversal rates.

Non-target percepts [percepts which do not correspond to the instruction: pFB(iHT) and pFT(iHB)]

(1) The stability durations of the non-target percepts in the specific hold-conditions are shorter than the stability durations of the same percepts in the unspecific hold-conditions (pFB(iHT) < pFB(iHU): $P < .01$ [.001]; pFT(iHB) < pFT(iHU): $P < .01$ [.001])
(2) The stability durations of the non-target percepts in the specific hold-conditions are either shorter than the stability durations of the same percepts in the passive condition (pFT(iHB) < pFT(iP): $P < .01$ [.007]) or they do not differ significantly (pFB(iHT) vs pFB(iP): ns [.1]).
(3) The stability durations of the non-target percepts in the specific hold-conditions do not differ from the stability durations of the same percepts in the reverse condition.

Target percepts versus non-target percepts

(1) The stability durations of the target percepts in the specific hold-conditions are longer than the stability durations of the non-target percepts (pFB(iHB) > pFB(iHT): $P < .01$ [.0005]; pFT(iHT) > pFT(iHB): $P < .01$ [.0005]).

2.3. Discussion

When participants tried to "hold" their percept of an ambiguous Necker cube as long as possible, reversal rates decreased and stability durations increased compared to passive observation of the cube without any volitional bias. The instruction to reverse the percept as often as possible caused opposite effects. The results are in agreement with results from several other studies of volitional control about the percept of ambiguous figures (e.g. Ammons & Ulrich, 1959; Hochberg & Peterson, 1987; Liebert & Burk, 1985; Pelton & Solley, 1968; Peterson & Hochberg, 1983; Strüber & Stadler, 1999; Toppino, 2003; van Ee et al., 2005).

2.3.1. Do stability duration and reversal rate reflect different neural processes?

Since the mean stability duration is per definition the reciprocal of the reversal rate, one might suggest that both variables reflect the same neural process. However, this assumption is inconsistent with the following findings: Comparing the passive condition with the reverse-condition, both reversal rates (e.g., Strüber & Stadler, 1999) and stability durations (e.g., Toppino, 2003; van Ee et al., 2005) differ significantly between conditions. However, between the passive condition and the hold-condition only stability durations differ significantly while no significant effects were seen for reversal rates (Liebert & Burk, 1985; Toppino, 2003). Thus reversal rates can be determined by stability durations, but this operation is not reciprocal. Toppino's (2003) findings indicate independent neural processes underlying perceptual stability and perceptual reversals of ambiguous figures.

The apparent contradiction with reciprocity can easily be resolved by the following considerations:

As can be seen in our data and as van Ee et al. (2005) already remarked, the specific hold-instructions could be carried out by applying specific "strategies" (see Table 3 for a schematic overview): (1) increasing the stability duration of the target percept, which decreases the reversal rate compared to the passive condition; (2) decreasing the stability duration of the non-target percept, which increases the reversal rate; or (3) doing both, which may leave the reversal rate more or less unchanged. The unspecific hold-instruction, on the other hand, could be carried out by (4) increasing stability durations of both percepts, thereby decreasing reversal rates.

The analyses of the particular stability durations (of each of the possible percepts) reveal observers' specific strategies to stabilize or destabilize perceptual variants. By calculating the mean stability durations (across percepts), however, this information gets lost, which may be the reason for the apparent contradiction regarding reciprocity.

Fig. 4A, and the results from van Ee et al. (2005) indicate that in the specific hold-conditions participants increased the stability duration of the target percept and decreased the duration of the non-target percept compared to the passive condition. This keeps the corresponding mean reversal rates similar to those in the passive condition (item 3 and Fig. 2A). Increasing the stability duration seems thereby to be slightly more effective than decreasing it. Thus reversal rates are affected in the specific hold conditions but to a lesser degree than in the unspecific hold condition. There, our data and those from van Ee et al. (2005) indicate that stability durations are increased for both perceptual variants causing a decrease in reversal rate compared to the passive condition. This decrease is much stronger than in the case of the specific hold-conditions, which was expected from consideration (4) above.

The present study is—to our knowledge—the first to compare all three hold-conditions (one unspecific and two specific), the reverse condition and the passive condition with each other, and to access both reversal rates and stability durations. According to Table 3 our data suggest the following:

(1) Participants can apply specific strategies to increase or decrease the stability duration of each of the possible percepts of an ambiguous figure.
(2) Analysing separately the mean stability durations of each of the two possible percepts can reveal the applied strategies.
(3) The mean stability duration across both percepts and its reciprocal, the mean reversal rate, can obscure this information. This may explain the asymmetric results in the studies from Toppino (2003) and Liebert & Burk, (1985).

2.3.2. Individual differences regarding reversal rates

Several studies reported systematic differences between a group of "fast reversers", i.e., participants with high reversal rates and "slow reversers," i.e., participants with slow reversal rates (Borsellino et al., 1982; Strüber, Basar-Eroglu, Hoff, & Stadler, 2000; Strüber & Stadler, 1999). While in the passive condition from the present data the mean reversal rate of the fastest reverser differs by more than factor 3 from that of the slowest reverser (Fig. 3), individual mean reversal rates seem to be equally distributed among the grand mean. Further, the data from the hold-condition and those from the reverse condition do not indicate a specific pattern that separates fast observers from slow observers (defined from the passive condition). Thus, the present data do not support the assumption of two distinct subpopulations of perceptual reversers.

2.3.3. Results in the context of bottom-up and top-down approaches

Our participants were able to strongly influence volitionally the dynamics of perceptual reversals. In particular, they applied differing mental strategies to accomplish each given experimental instruction.

However, no participant was able to fully prevent perceptual reversals during the 3 min observation interval not even with volitional effort, as can be seen in Fig. 3. Thus, during processing of an ambiguous figure, there seem to be processes at work that cannot be suppressed volitionally and that lead to perceptual reversals, which is in accordance with considerations from Toppino (2003) and recent findings from Pastukhov and Braun (2007). Exceptions may be Buddhist monks, who are highly experienced with meditation. They seem to be able to significantly prolong the durations of stable percepts when they observe binocular rivalling stimuli during and after meditation (Carter et al., 2005). Binocular rivalry is a form of multistable perception, whereby ambiguity is induced by projecting different unambiguous stimuli in each of the observer's two eyes, rather than projecting the same ambiguous figures in both eyes like in the present study.

An increasing number of authors suppose that both volitional processes and low-level processes contribute to perceptual reversals (Blake & Logothetis, 2002; Kornmeier & Bach, 2005, 2006; Long & Toppino, 2004; Strüber & Herrmann, 2002). In the first experiment, we found the strongest effect, labelled as top-down, on the reversal dynamics of ambiguous figures, namely volitional control. In the second experiment, to be described subsequently, we investigated the interrelation of this effect with the strongest known effect that was interpreted as support for the bottom-up approach, namely discontinuous stimulus presentation. Do the two effects interact, which would indicate a single process that may be affected by different types of manipulation? Or are they additive? If the latter is true, is this evidence for independent neural mechanisms perhaps operating at different steps along the perceptual processing chain (Kornmeier & Bach, 2006)?

3. Experiment 2

3.1. Methods

3.1.1. Participants

The same 10 participants from Experiment 1 and one new participant took part in the second experiment. Details can be found in Experiment 1.

3.1.2. Stimuli

The same type of Necker cube as in the previous experiment was used as stimulus.

3.1.3. Procedure

The second experiment followed the first experiment after a break of between 5 and 10 min, depending on each participant. The ambiguous Necker cube was presented intermittently for trial duration of 2 min. In each trial, values for presentation time and inter-stimulus-interval ("ISI"; with blank screen) were randomly chosen out of nine possible combinations of three presentation times (600, 800, 1000 ms) and three ISIs (100, 300, 500 ms). Successive trials were separated by short breaks of 30 s with a blank screen, where participants were allowed to close their eyes and relax. The successive experimental conditions were separated by 2.5 min breaks with a blank screen. At the end of each break (3 s before stimulus onset) a short beep signalled the beginning of the next trial.

The experiment consisted of the same five conditions as in Experiment 1, defined by instruction: Hold Unspecific (iHU); Hold Bottom (iHB); Hold Top (iHT); Passive (iP); Reverse (iRE). Participants indicated perceived orientation reversals of the Necker cube from pFB (perceived cube-front-side bottom-right) to pFT (perceived cube-front-side top-left) and from pFT to pFB with different hands by pressing different keys.

During pilot experiments participants had reported that the experimental task was very demanding, especially, if the experiment exceeded one hour. We thus decided to reduce the duration of an experimental run from three (Experiment 1) to two minutes (Experiment 2) and to divide the experiment into two sessions at different days, separated by 6 weeks at most. Each session of the second experiment took about 70 min. The first session contained the following conditions: iHU; iP1; iRE. The passive condition was repeated in the second session to estimate potential long term learning effects. The second session thus contained the following conditions: iP2; iHB; iHT. At the beginning of the second session, participants were asked if they could still see both versions of the stimulus; and were allowed to practise the instructions if necessary. In each session the order of conditions was randomized across participants. Participants were instructed to fixate the fixation cross during observation of the Necker cube.

3.1.4. Data analysis

Reversal rates were calculated as the mean number of key presses per minute. Stability durations were computed as the mean duration between pressing one key and pressing the other one, thus including the ISIs between stimuli that were perceived in the same orientation. Reversal rates and stability durations for the two percepts were the three dependent variables in a one-factorial repeated measures MANOVA with corrections for potential violations of the sphericity-assumption according to Geisser and Greenhouse (1958) with the factors Condition (iHU, iHB, iHT, iP1, iP2, iRE), Presentation Time (600, 800, 1000 ms) and ISI (100, 300, 500 ms). Post-hoc permutation-tests (Edgington, 1995) were corrected for the number of orthogonal tests according to Holm (1979).

3.2. Results

3.2.1. Reversal rates

The mean reversal rate across participants, presentation times and ISIs for each condition are depicted in Fig. 2B (black symbols). As in Experiment 1, a strong effect of condition can be observed ($F(5,50) = 13.16$, $P < .0001$; $\eta_p^2 = .57$).

The results from the post-hoc permutation-tests are listed in Table 4 and can be summarized as follows:

(1) Reversal rates increase from the hold-conditions over the passive-condition to the reverse-condition and they were arranged in all figures and tables in that order.
(2) The unspecific hold-condition almost halves the mean reversal rate (11 reversals/min) compared to the passive condition (19 reversals/min on average; iHU < iP1, $P < .01$, [.0005]; iHU < iP2, $P < .05$, [.001]), whereas the reverse-condition strongly increase it (30 reversals/min; iP1 < iRE, $P < .01$ [.0005]; iP2 < iRE, $P < .05$ [.04]).
(3) Reversal rates of the unspecific hold-condition do not differ from those of the hold-bottom condition but they are significantly lower than those of the hold-top condition (iHU < iHT, $P < 0.05$ [.03]).
(4) None of the two specific hold-conditions (iHB, iHT) differs significantly from the passive condition in the first session (iP1), however, both show significantly lower reversal rates than the passive condition in the second session (iHB < iP2, $P < .05$ [.005]; iHT < iP2, $P < .05$ [.008]).
(5) Reversal rates are significantly higher in the second compared to the first session ($P < .05$ [.03]).

Fig. 2B depicts the mean reversal rate across participants and ISIs for each condition (abscissa) and each presentation time (black circles, triangles and squares). Fig. 2C depicts the mean reversal rate across participants and presentation times for each condition (abscissa) and each ISI (black symbols). In both graphs (Figs. 2B and C) the white symbols represent the reversal rate data from Experiment 1 for comparison. There are significant effects for the factors Presentation Time ($F(2,20) = 12.28$, $P < .01$; $\eta_p^2 = .55$) and ISI ($F(2,20) = 8.28$, $P < .01$; $\eta_p^2 = .45$) but no significant interaction.

3.2.2. Stability durations

Fig. 4B depicts the mean stability durations across participants, presentation times and ISIs for the two alternative 3D-percepts (perceived front side top = pFT and perceived front side bottom = pFB) of the Necker cube. Both variables pFB and pFT show significant effects for the factor Condition (pFB: $F(5,50) = 7.79$, $P < .01$; $\eta_p^2 = .44$; pFT: $F(5,50) = 5.14$, $P < .05$; $\eta_p^2 = .34$).

The results from post-hoc permutation tests are listed in Table 5 and can be summarized as follows:

Target percepts [percepts which correspond to the instruction: pFB(iHB) and pFT(iHT)]:

(1) There is no significant difference between the stability durations of the target percepts in the specific hold-condition and the stability duration of the same percepts in the unspecific hold-conditions.
(2) The stability durations of the target percepts in the specific hold-conditions are longer than the stability durations of the same percepts in the passive conditions (pFB(iHB) > pFB(iP1): $P < .05$ [.001]; pFB(iHB) > pFB(iP2): $P < .05$ [.001]; pFT(iHT) > pFT(iP1): $P < .05$ [.005]; pFT(iHT) > pFT(iP2): $P < .05$ [.01]) and the reverse condition (pFB(iHB) > pFB(iRE): $P < .05$ [.002]; pFT(iHT) > pFT(iRE): $P < .05$ [.002]).

Non-target percepts: [percepts which do not correspond to the instruction: pFB(iHT) and pFT(iHB)]:

(1) The stability durations of the non-target percepts in the specific hold-conditions are shorter than the stability durations of the same percepts in the unspecific hold-conditions (pFB(iHT) < pFB(iHU): $P < .05$ [.001]; pFT(iHB) < pFT(iHU): $P < .05$ [.01]).
(2) The stability durations of the non-target percepts in the specific hold-conditions do not differ significantly from the stability durations of the same percepts in the passive condition.
(3) The stability durations of the non-target percepts in the specific hold-conditions do not differ from the stability durations of the same percepts in the reverse condition.

Target percepts versus non-target percepts:

(1) The stability durations of the target percepts in the specific hold-conditions are longer than the stability durations of the non-target percepts (pFB(iHB) > pFB(iHT): $P < .05$ [.005]; pFT(iHT) > pFT(iHB): $P < .05$ [.02]).

There is no significant difference between the two passive conditions concerning stability duration (Fig. 4).

The mean stability durations across participants and ISIs for each condition and presentation time are depicted in Fig. 4C, those across participants and presentation times for each condition and ISI are depicted in Fig. 4D. There are significant effects for the factors Presentation Time ($F(2,20) = 4.93$, $P < .05$; $\eta_p^2 = .33$) and ISI ($F(2,20) = 6.22$, $P < .01$; $\eta_p^2 = .38$) regarding the mean duration of the front-bottom-perception of the Necker cube (pFB) as dependent variable. However, no significant effects for the factors Presentation Time and ISI could be found for the mean duration of the front-top-perception (pFT) as dependent variable.

Table 4
Experiment 2, reversal rates

	iHB	iHT	iP1	iP2	iRE
iHU	ns	*	**	*	**
iHB		ns	ns	*	**
iHT			ns	*	**
iP1				*	**
iP2					*

*$P < .05$; **$P < .01$.
Post-hoc permutation tests across experimental blocks, corrected for the number of orthogonal tests according to Holm (1979); iHU, hold unspecific; iHT, hold top; iHB, hold bottom; iP1, passive attitude; iRE, reverse.

Table 5
Experiment 2, stability durations

		iHB	iHT	iP1	iP2	iRE
iHU	pFB	ns	*	*	*	**
	pFT	*	ns	*	*	**
iHB	pFB		*	*	*	*
	pFT		*	ns	ns	ns
iHT	pFB			ns	ns	ns
	pFT			*	*	*
iP1	pFB				ns	*
	pFT				ns	*
iP2	pFB					*
	pFT					*

*$P < .05$; **$P < .01$.
Post-hoc permutation tests across experimental blocks, corrected for the number of orthogonal tests according to Holm (1979); iHU, hold unspecific; iHT, hold top; iHB, hold bottom; iP1, passive attitude; iRE, reverse.

3.3. Discussion

Discontinuous presentation of an ambiguous Necker cube can modulate the dynamics of perceptual reversals, e.g., reversal rates can be increased to twice the rate during continuous stimulus presentation (26 reversals/min versus 13 reversals/min in the passive conditions) mainly as a function of ISI. The present results replicate these earlier findings (Kornmeier et al., 2007; Orbach et al., 1963, 1966).

Effects of volitional control can also almost double reversal rates (22 reversals/min in the reverse condition), as seen in Experiment 1. Volitional control combined with discontinuous stimulus presentation lead to full additivity of effects (maximum: 34 reversals/min in the reverse-condition). This additivity is seen in Fig. 2 where the white circles representing the mean reversal rates from the continuous presentation mode (Experiment 1) and the corresponding black symbols from the discontinuous presentation mode (Experiment 2) are nearly parallel. Similarly, the shapes of the traces connecting the mean stability durations from the continuous presentation mode (Experiment 1, Fig. 4A) are also nearly parallel to the shapes of the corresponding traces from the discontinuous presentation mode (Experiment 2, Fig. 4B–D).

3.4. How can asymmetries in results between the two cube orientations be explained?

Two different asymmetries in results regarding the two cube orientations can be observed:

(1) Post-hoc tests indicate a significant difference between reversal rates from the unspecific hold condition (iHU) and the hold-top condition (iHT) but no significant difference between iHU and iHB (Table 4).
(2) The MANOVA indicates marked effects of presentation time and ISI on the stability duration of the cube-front-side bottom (pFB), but no such effects for the cube-front-side top (pFT).

We explain these asymmetric results by higher inter-individual variability concerning the ability to control the perception of the cube-front-side top compared to the cube-front-side bottom perception as the causal factor: It is well known that the cube-front-side bottom is the preferred initial percept of most observers (Keeler, New, & Parshall, 1929; Price, 1967, 1969), which may be due to the fact that we more often look down on objects than look up on them. Perhaps it was less easy for some participants to exert volitional control over the non-preferred cube-orientation than over the preferred orientation. This may have introduced higher inter-individual variability in stability durations of the front-top view (non-preferred) and especially in the hold-top condition. Higher inter-individual variability in front-top stability duration would result in a lower signal-to-noise ratio and a higher variation coefficient compared to the stability duration of the front-bottom view. This difference in variation coefficients can be seen in Fig. 4E.

4. General discussion

The present results indicate additivity between the influence of discontinuous stimulus presentation and volitional control on the dynamics of perceptual reversals and stability of ambiguous figures. While it is well known that volitional control is differentially effective with different types of ambiguous figures (Strüber & Stadler, 1999), increase (up to duplication) of reversal rates depending on ISI is only known for the Necker cube. We thus restricted our experiments in the present study to this stimulus. Although we expect that the same pattern of results should be obtained with other types of stimuli, this has to be shown in future experiments.

Before, we discuss the implications of the present results for the bottom-up versus top-down discussion, potential confounders should be addressed.

4.1. The potential role of eye-movements

There has been a long discussion about the role of eye-movements as a causal factor for perceptual reversals (e.g., Ellis & Stark, 1978; Zimmer, 1913). The effects we found may thus perhaps be at least partially caused by eye-movements. It is known by now that eye movements and targeted fixation can induce perceptual reversals (e.g., Toppino, 2003), but they are not necessary (Gale & Findlay, 1983). Recently, van Dam and van Ee (2006) found a strong positive correlation between saccades and perceptual reversals in binocular rivalry. However, they found only a week positive correlation between saccades and perceptual reversals of the Necker cube, even without fixation instruction. Toppino (2003) reported that effects of instructed eye movements on reversal rates and stability durations are additive to effects of volitional control.

In the present study, participants were instructed to fixate a small cross in the centre of the screen. In recent EEG experiments with discontinuous presentation of the Necker stimuli and the same fixation instruction, we controlled eye-movements and found that participants had high precision in fixation (e.g., Kornmeier et al., 2007). We thus conclude that our results can be explained by participants' volitional control and the stimulation protocol rather than by artifacts of eye-movements.

4.2. Learning effects during prolonged perception of ambiguous figures

Van Ee et al. (2005) found a slight increase of reversal rate across experimental repetitions separated by days. Furthermore, Long, Toppino, and Kostenbauder (1983) reported similar results with a rotating Necker cube, which they interpreted as evidence for long term learning effects. Since they also found evidence for local adaptation processes they concluded that both bottom-up effects (i.e., adaptation) and top-down effects (i.e., learning) can operate in parallel.

In the present study learning could have been involved at two levels:

(1) Learning may have taken place from the first to the second experiment since we took the same set of participants for both experiments.
(2) Learning may have taken place from the first to the second session in Experiment 2, which was separated by at least one day. Participants performed the passive condition at each of the two sessions (P1 and P2). A clear increase in reversal rate in the second session compared to the first session can be observed (Fig. 2A).

To exclude possible confounds of learning we replicated the whole experiment with seven additional participants (four female, three male, median age: 23) with the following modifications:

- We reversed the order of experiments compared to the first two experiments, starting with discontinuous stimulus presentation, followed by the continuous conditions. Potential differences in results between the first and the second experiment related to learning should now have the opposite sign or should in other ways affect the results compared to the first two experiments.
- All participants performed the two experiments in one session within about 2.5 h with a small break of 5–20 min after approximately 60 min.

- Both the first and the second experiment started with the passive condition. The order of the subsequent conditions within each experiment was randomized between participants.

The results from this additional experiment are shown in Fig. 5, they replicate the findings from Experiments 1 and 2.

4.3. Implications for the bottom-up versus top-down discussion

We found that effects of exogenous manipulations of the presentation mode and effects of endogenous efforts of volitional control on the perception of a Necker cube are additive. Toppino (2003) compared the effects of volitional control on the perceived orientation of the Necker cube with those of fixation location. Similarly to our results he found additivity of effects and concluded that both local data-driven involuntary neural process (adaptation, bottom-up) and independently centrally mediated priming mechanisms (top-down) influence the perception of the Necker cube. Suzuki and Peterson (2000) found an interaction between volitional control and stimulus features of a dynamic ambiguous figure. They postulated the existence of a high-level representation of the motion percept, which could be manipulated by intention.

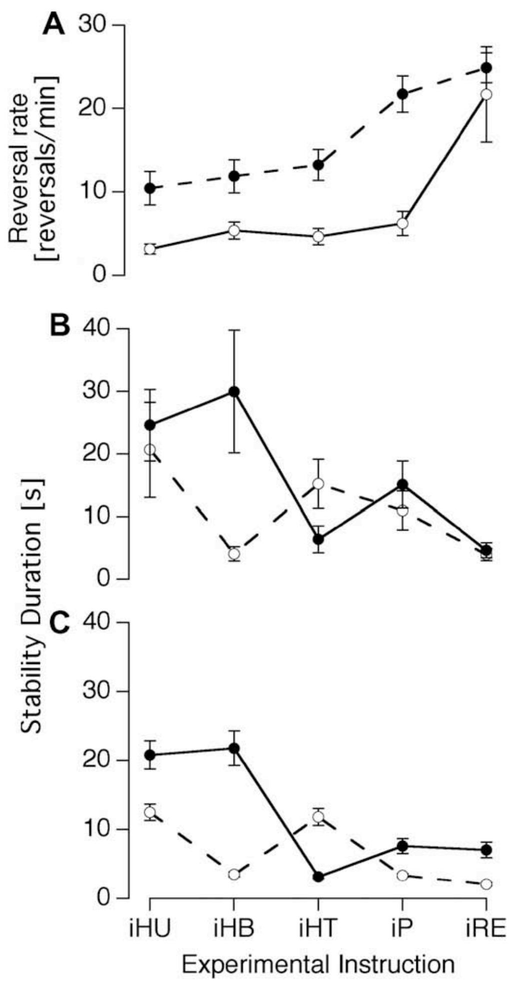


Fig. 5. (A) Mean reversal rates across conditions. White circles: Mean reversal rates ± SEM, across participants from continuous stimulus presentation for the different volitional-control instructions. Black circles: Mean reversal rates across participants, presentation times ("PTs") and Inter stimulus-intervals ("ISIs") ± SEMs. The pattern of results is very similar to Fig. 2. (B) Stability durations from continuous stimulus presentation. White circles represent mean stability durations of the perceived cube-front-side at left top (pFT) ± SEMs; black circles represent mean stability durations of the perceived cube-front-side at right bottom (pFB) ± SEMs across participants for the different volitional-control-instructions. The pattern of results is very similar to Fig. 4A. (C) Stability durations from discontinuous stimulus presentation. White circles represent mean stability durations of pFT across participants, PTs and ISI ± SEMs; black circles represent mean stability durations of pFB across participants, PTs and ISIs ± SEMs for the different volitional-control-instructions. The pattern of results is very similar to Fig. 4B. i, instruction; HU, hold unspecific; HB, hold bottom; HT, hold top; P, passive; R, reverse.

It is unclear for two reasons whether the influence of discontinuous stimulus presentation on the reversal dynamics is better attributed as bottom-up or top-down. First, the neural processes responsible for this modulation of the reversal dynamics are unknown. Second, there are several definitions of "bottom-up" and "top-down" (Engel, Fries, & Singer, 2001) and most often it is unclear what exactly is meant if these terms are used. It may be thus more helpful to classify potential neural processes as 'early' or 'late' with respect to stimulus onset or by the degree of controllability by conscious volition. The interpretations from the studies cited above are in accordance with the assumption that reversals can be induced at several processing steps from the retinal images to a conscious stable percept (e.g., Blake & Logothetis, 2002; Kornmeier & Bach, 2005). However, additivity of effects does not necessarily imply different processing units. Regarding the present experiment, the following evidence at least suggests that the exogenous manipulations of stimulus presentation seem to operate transiently and highly automatic in contrast to endogenous volitional control:

(1) *Complete volitional suppression is impossible:* The present data indicate that an increase of reversal rates caused by discontinuous stimulus presentation cannot be suppressed by the volitional effort to hold one percept as long as possible (Figs. 2 and 5).
(2) *Effects of ISI duration are restricted to the ensuing stimulus:* In most studies with discontinuous stimulus presentation, ISIs were varied between experimental blocks but kept constant within each block (Kornmeier et al., 2002; Leopold et al., 2002; Maier et al., 2003; Orbach et al., 1963, 1966), like in the present study. Kornmeier et al. (2007) recently showed that the effects of discontinuous stimulus presentation on reversal rate could also be obtained if successive ISIs were randomized within experimental blocks. Their results indicate that the ISI-related increase of reversal rates mainly depends on the ISI immediately preceding the reversal.
(3) *Effects of light flashes are restricted to the stimulus that was flashed:* Kanai, Moradi, Shimojo, and Verstraten (2005) presented ambiguous figures continuously but applied transient light flashes on top of the figures. Comparable to the transient removal of the stimulus in the discontinuous presentation mode, this "flash-cue-method" induced immediate perceptual reversals and thus increased reversal rates. In accordance with Orbach et al.'s bottom-up interpretations (Orbach et al., 1963), Kanai et al. (2005) demonstrated that a certain degree of adaptation is necessary for the flashing-effect to occur. They further showed that the effects of these light flashes are restricted to the spatial vicinity of the ambiguous stimulus.

Several authors suggested a description of perceptual instability in terms of non-linear dynamical systems, where the different perceptual alternatives are regarded as energy minima, fixed states or attractors in multistable neural networks (Kanai et al., 2005; Kawamoto & Anderson, 1985; Kornmeier, Bach, & Atmanspacher, 2004). Reversal rates would then depend on the difference between the energies of attractors and noise levels, as well as on the height of the energy separating the attractors. Based on this view, one could speculate that exogenous manipulations of the stimulus presentation mode could transiently change the energy level of the current attractor or the energy separating two competing attractors. Adaptation on the other hand could then be modelled as a slow but temporally finite decrease of attractor depth, while learning effects or volitional control could cause a general stabilizing or destabilizing modification of the "perceptual landscape", which may last for longer periods, e.g., the duration of a whole experiment.

5. Conclusions

The neural process underlying the perception of an ambiguous figure can be modulated by several endogenous and exogenous factors independently and at several steps, leading to instabilities, which are preconditions for perceptual reversals to occur. Whether the influential factors will then be labelled as bottom-up or top-down depends on which of several existing definitions of these terms are used (e.g., Engel et al., 2001; Varela, Lachaux, Rodriguez, & Martinerie, 2001). In the present study, the perceptual process was affected by endogenous volitional control and by exogenously varying the presentation mode of the stimulus. These factors seem to stabilize or destabilize the perceptual system independently. While effects of the presentation mode act in an immediate temporal and spatial vicinity to the stimulus that will be perceived as reversed, further experiments may elucidate in which way endogenous factors like volitional control exert their influence.

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