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Interaction of bottom-up and top-down processes in the perception of ambiguous figures

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Abstract

Ambiguous figures reverse their appearance during prolonged viewing and can be perceived in two (or more) available interpretations. Both physical stimulus manipulations and cognitive control influence the perception of ambiguous figures, but the underlying mechanisms remain poorly understood. In the current study, the perception of an ambiguous figure was manipulated by adaptation to unambiguous figures and / or placing the ambiguous figure into a context of unambiguous figures. Our results indicate that both adaptation and context can effectively modulate perception of the ambiguous figure. When manipulated together, adaptation and context processes showed additive effects upon the perception of the ambiguous figure implying the independent mechanisms. Thus, top-down and bottom-up processes seem to influence the perception of the ambiguous figures independently and neither seems to be uniquely responsible for the generation of perceptual changes.

Keywords: ambiguous figures, overlapping squares, Necker cube, adaptation, context, visual perception

Interaction of bottom-up and top-down processes in the perception of ambiguous figures

Visual perception is a dynamic brain function modulated by both bottom-up and top-down processes. Although sensory input changes constantly and often may even be ambiguous, humans usually perceive their environment as clear and stable. The visual system uses several strategies to accomplish this: visual cues and features are organised, categorised, and grouped in order to create an accurate representation of the world. However, in the case of ambiguous figures (e.g., Necker cube) the visual system fails to provide us with a definite answer. In that case perception constantly switches between two (or more) alternative perceptual interpretations. Explanations proposed for the bistability of ambiguous figures tend to fall into two categories, emphasizing the operation of either bottom-up or top-down perceptual processes (for a review, see Long & Toppino, 2004). The bottom-up based theories suggest that perceptual reversals are the result of adaptation processes occurring in competing neural channels in early visual areas where reversals occur via cycles of adaptation, recovery, and mutual inhibition (e.g., Orbach, Ehrlich, & Heath, 1963; Toppino & Long, 1987). The cognitive theories suggest that reversals are caused by feedback operations from central mechanisms to lower level sensory activities, for example, by activation of a high-level "exploratory" mechanism that directs selective attention in a way that forces lower-level perceptual systems to periodically "refresh" (e.g., Leopold & Logothetis, 1999). Although most of the authors suggested either a bottom-up or a top-down based explanation, an increasing number of studies indicate that both types of perceptual processes are important in the perception of ambiguous images (Hochberg & Peterson 1987; Kornmeier & Bach, 2012; Leopold & Logothetis 1999; Long, Toppino & Kostenbauder, 1983; Long & Toppino 2004).

The adaptation effect is commonly classified as depending on sensory processes. In the studies testing the adaptation effect participants are presented with an unambiguous stimulus representing one of the possible interpretations of a subsequently presented ambiguous figure. Typically, after prolonged (i.e., from ~ 60 to ~ 150 s) inspection of one of the unambiguous versions, the adaptation effect is obtained, that is participants initially report the alternative interpretation of the presented ambiguous figure (Long & Moran, 2007; Long & Olszweski 1999; Long, Stewart, & Glancey, 2002; Long, Toppino, & Mondin, 1992; Orbach et al., 1963; Toppino & Long, 1987; von Grünau, Wiggin, & Reed, 1984). Such results are usually explained in the framework of neural adaptation: the neural channels underlying the percept that is compatible to the unambiguous version get saturated; therefore, an alternative version of the ambiguous figure becomes dominant through reversal. In line with this view, recent research shows that adaptation is highly localised. In order to obtain the adaptation effect, adapting and testing stimuli have to be presented at the same retinal location and match in size (Long & Moran, 2007). The adaptation effect is known to be transient and it is possible to significantly reduce it by prolonging the delay period between adapting and test stimuli to approximately 10 s (Long & Moran, 2007). If any of these conditions is modified (i.e., the unambiguous adapting stimulus is viewed for a period shorter than ~ 60 s, adapting and test stimuli are presented at different spatial locations, or the delay between the stimuli is ≥ 10 s), then a priming effect is obtained. In that case, the ambiguous figure is initially perceived in the same interpretation as the previously presented unambiguous adapting stimulus (Long & Olszweski, 1999; Long & Moran, 2007; Long et al., 1992).

However, there is increasing evidence for the impact of top-down processes on perceptual effects that cannot be readily ascribed to passive and automatic processes such as adaptation (Girgus et al., 1977; Strüber & Stadler, 1999). An example for such a top-down process is the context effect. Contextual cues may influence perceptual organisation of the presented ambiguous figure by making its first perceived interpretation compatible with the contextual bias (Bruner & Minturn, 1955; Goolkasian, 1987).

Top-down modulation of ambiguous figures was previously examined mostly in the framework of *temporal* context when the presentation of the ambiguous figure was preceded with: (1) segments of the ambiguous test figure (Chastain & Burnham, 1975), (2) images that were categorically related to the ambiguous test figure (Bruner & Minturn, 1955; Bugelski & Alampay, 1961), or (3) a figure biasing the participant to the one or the other possible interpretation (Goolkasian, 1987), in order to find out to what extent the effect of context determines the observer's first interpretation of an ambiguous figure. Compared to the adaptation paradigm when a pre-test stimulus is usually presented for several minutes, the pre-test stimulus duration in the temporal context paradigm is much shorter, namely up to one minute. Regarding *spatial* context manipulations, Wallace (1988) showed that once the Necker cube is presented in a context consisting of geometric figures (i.e., squares, triangles, crosses, or parallelograms) the reported rate of reversals is slower than that obtained in response to a single cube viewing condition.

Previous research revealed that the adaptation effect is highly susceptible to physical and temporal manipulations of stimuli (Long & Moran, 2007; Long & Olszweski 1999; Long et al., 2002; Long & Toppino, 1994; Toppino & Long, 1987; von Grünau et al., 1984), but to our knowledge there are no studies examining the possible interrelations of top-down manipulations and the bottom-up adaptation effect. Hence, it is not clear whether the effects of adaptation and context would be related in an additive manner that is, suggesting independent mechanisms, or would reduce each other depending on the experimental condition.

In the present study, we developed a paradigm, which allowed us to investigate both adaptation and context effects. Participants were adapted to an unambiguous squares stimulus in either 'downwards' or 'upwards' orientation that preceded the ambiguous squares stimulus. Top-down modulation of the perception of the ambiguous squares stimulus was manipulated by presenting the ambiguous squares stimulus in the context of four surrounding identical unambiguous squares stimuli. Adaptation and context effects were tested either separately or within the same trials. In the latter case, the orientation of the context stimuli either matched the previously presented adapting stimulus or not, resulting in overall four conditions: an adaptation condition, a context condition, an adaptation different from context condition, and an adaptation identical to context condition. We expected the typical adaptation effect in the adaptation condition and the context effect in the context condition. Furthermore, we hypothesised that the context effect would be additive to the adaptation effect when both are combined. In particular, in the adaptation different from context condition, in which the orientations of the adapting and context stimuli did not match, the adaptation and context manipulations should both independently affect perception which should be demonstrated by the additivity of both effects (i.e., context should add to the strength of the adaptation effect). Predictions with respect to whether the adaptation or the context effect would exert a stronger influence on perception of ambiguous figures if tested in competition (in the adaptation identical to context condition) are not possible to make on the basis of current knowledge. If the adaptation effect would be stronger, then the perceptual outcome would resemble the adaptation effect, whereas if context would be stronger, then the perceptual outcome would be similar to the context effect.

Methods

Participants

A total of 70 participants took part in the present study. Seven participants were excluded from analyses: five because of an inability to report reversals (in spite of being able to see both interpretations of the ambiguous squares stimulus during the practice period), two for providing erroneous responses (i.e., repeatedly reporting the same percept of the ambiguous stimulus instead of perceptual changes) and one because he did not follow the instructions. Thus, the data of 62 healthy participants (twenty males; mean age = 21.45 years, *SD* = 2.22) were entered into the analyses. Fifty eight participants were right-handed (Oldfield, 1971). Each participant had normal or corrected-to-normal vision and had no prior experience with psychophysical testing. They were completely naïve to the hypotheses and goals of the study and received credit toward partial fulfilment of the requirements of their study programmes. Informed consent was obtained from all participants and the study was formally approved by the Lithuanian Bioethics Committee.

Design and Procedure

An ambiguous, two-dimensional drawing of a Necker cube-like figure composed of five overlapping squares was chosen as the main experimental stimulus. This figure had previously been used in other studies (Long, Toppino, & Mondin, 1992; von Grünau, Wiggin, & Reed, 1984), and it was named ‘the overlapping squares’ by Long et al. (1992). During the experiment the participants were presented in each trial with a 120 s adaptation period followed by a blank screen presented for 1 s. Subsequently, participants were presented with an ambiguous squares stimulus (in the four different conditions described below) for 30 s and had to respond to the perceived changes of the square’s orientation by pressing one of the two keys (upwards or downwards) on the response box. Each trial was followed by an intertrial interval of 120 s. The four conditions were randomly presented and had the following characteristics (see Fig. 1):

1) The adaptation condition (hereafter AC) replicated a standard adaptation paradigm – an unambiguous squares stimulus oriented either 'downwards' or 'upwards' was presented in the adaptation period followed by an ambiguous squares stimulus during the test period (Fig. 1A);
2) The context condition (hereafter CC) examined the effect of a spatial context on the perception of the ambiguous squares stimulus. A fixation point was presented during the adaptation period and participants were instructed to fixate on it in order to equalise this condition to the other experimental conditions. During the test period participants were presented with an ambiguous squares stimulus in the context of surrounding unambiguous squares stimuli in either 'downwards' or 'upwards' orientation (Fig. 1B);
3) In the adaptation different from context (hereafter ADC) condition an unambiguous squares stimulus oriented either 'downwards' or 'upwards' was presented in the adaptation period followed by an ambiguous squares stimulus in the context of surrounding unambiguous squares stimuli in either 'upwards' or 'downwards' orientation, respectively (Fig. 1C); thus in this condition the orientation of the adaptation stimulus was different from the orientation of the context stimuli.
4) In the adaptation identical to context (hereafter AIC) condition an unambiguous squares stimulus oriented either 'downwards' or 'upwards' was presented in the adaptation period followed by an ambiguous squares stimulus in the context of surrounding unambiguous squares stimuli in either 'downwards' or 'upwards'

orientation, respectively (Fig. 1D); thus, in this condition the orientation of the adaptation stimulus was the same as the orientation of the context stimuli.

All stimuli were drawn in black, presented on a white background and viewed binocularly. A single figure subtended a visual angle of 1.72° × 1.64° and the entire display consisting of ambiguous squares in the context of unambiguous squares subtended a visual angle of 6.03° × 5.87°. The fixation point subtended a visual angle of 0.04°. Stimuli were presented on a 21 inch computer screen with a frame rate of 85 Hz at a viewing distance of 70 cm. The position of the fixation point on the unambiguous squares was adjusted to match the centre of the subsequently presented ambiguous squares. During the experiment the participants were asked to keep their eyes focused on the central fixation point.

Each participant took part in a 90 min individual testing session. Before testing commenced, the ambiguous squares stimulus was shown to each participant, and they were instructed to watch it until reversals were perceived.

In the beginning of the session, each participant performed two practice trials (the AC and the CC conditions) in order to get acquainted with the task requirements. After the practice trials, and before the beginning of the experiment, participants were given a 2 min rest so that any potential adaptation or contextual effects from the practice session would have attenuated.

<<<<Figure 1 about here >>>>

During the experiment every participant in each experimental condition viewed the ambiguous squares stimulus twice after each of the ‘downwards’ and the ‘upwards’ unambiguous squares stimulus. Thus, each of the four conditions consisted of four trials, and every participant completed 16 experimental trials in total. The experiment was divided into two blocks, which were separated by a 5 min break. Each block contained two trials (one of each unambiguous orientation) from every experimental condition presented in a random order. Adaptation and test stimuli were presented at the same spatial location in the centre of the screen. The participants were instructed to let the perceptual reversals to occur naturally and were asked not to manipulate their perceptions intentionally. No feedback on performance was given.

Dependent measures used in the analyses were the first response regarding the percept of the orientation of the ambiguous squares stimulus (hereafter Orientation First Percept), the reaction time to the first reversal (hereafter RT First Reversal) and the average durations of ‘upwards’ and ‘downwards’ percepts during the 30-sec test period (hereafter Perceptual Durations). Concerning the analysis of Orientation First Percept, the initial interpretations were coded in terms of whether the ambiguous squares stimulus was perceived in the predicted (score = 1) or unpredicted (score = 0) orientation with respect to the experimental hypotheses. For the AC condition (Fig. 1A), the ambiguous squares stimulus was predicted to be perceived in the opposite orientation (score = 1) to the unambiguous squares stimulus viewed in the adaptation period. This prediction was based on the known effect of adaptation, which shows that participants, after prolonged (i.e., from ~ 60 to ~ 150 s) viewing of one of the unambiguous versions, more frequently report the alternative version of the subsequently presented ambiguous figure (Long et al., 1992; Long & Olszweski, 1999; Long et al., 2002; Long & Moran, 2007; von Grünau et al., 1984).

For the CC condition (Fig. 1B), the reported first orientation of the ambiguous squares stimulus was predicted to match (score = 1) the orientation of the context stimuli it was presented in. This prediction was based on the effect of context, which shows that participants, after viewing the cues in the context of the ambiguous test figure, more frequently report the cue-compatible first orientation of the subsequently presented ambiguous figure (Bruner & Minturn, 1955; Bugelski & Alampay, 1961; Chastain & Burnham, 1975; Goolkasian, 1987).

In the ADC condition (Fig. 1C) the orientation of the unambiguous squares stimulus presented during the adaptation period did not match the orientations of subsequently presented unambiguous context stimuli. Therefore, it was predicted that the ambiguous squares stimulus will be perceived in the opposite orientation (score = 1) to the unambiguous squares stimulus viewed in the adaptation period and in the same orientation as the unambiguous context stimuli.

In the AIC condition (Fig. 1D) the orientation of the unambiguous squares stimulus presented during the adaptation period matched the orientations of subsequently presented unambiguous context stimuli, thereby creating a competition between adaptation and context effects. As discussed in the Introduction, we did not have a specific prediction with respect to dominance of either the adaptation or the context effect (i.e., whether the adaptation or the context effect would exert a stronger influence on the perception of the ambiguous squares stimulus). Therefore, the prediction for the AIC condition was derived after analyses of the AC and the CC data (see Results section), that is, the ambiguous squares stimulus was predicted to be perceived in the same (score = 1) orientation as the unambiguous context stimuli and the unambiguous squares stimulus viewed in the adaptation period (i.e., dominance of context effect).

The unpredicted directions for all the conditions (score = 0) were as follows: the same orientation as that of the unambiguous squares stimulus viewed in the adaptation period for the AC and the ADC conditions and the opposite orientation to that of unambiguous context stimuli for the CC and AIC conditions.

For the Orientation First Percept and RT First Reversal data, the responses provided for ‘downwards’ and ‘upwards’ orientations were averaged together, because we coded the responses with respect to the predictions for the ambiguous squares stimulus to be perceived either in the same, or in the opposite orientation as the unambiguous squares stimulus presented in the AC condition (or as the unambiguous context stimuli in the CC condition). An average Orientation First Percept score was derived individually for each participant in each experimental condition and it could range from 0 to 1 (i.e., 0, 0.25, 0.5, 0.75, or 1).

Kolmogorov-Smirnov tests revealed that RT First Reversal and Perceptual Durations did not meet the condition of normality. The distribution of raw scores of RT First Percept and Perceptual Durations were leptokurtic and positively skewed. Square root transformations were applied to RT First Percept data and lognormal transformations were applied to data of Perceptual Durations (Howell, 2009). Additionally, one sample *t* tests (effect size: Cohen’s d) were conducted on the Orientation First Percept data in order to determine whether the mean values of all the experimental conditions were obtained by chance or whether real adaptation and context effects were obtained. Separate repeated measures ANOVAs with one within-participant factor of Condition (AC, CC, ADC, AIC) were conducted on Orientation First percept and RT First Reversal (Table 1). Repeated measures ANOVA with three within-participant factors of Condition (AC, CC, ADC, AIC), Perceptual response (downwards, upwards) and Adapting (or context) stimulus (downwards, upwards) were conducted on the data of perceptual durations. One-way ANOVAs (Bonferroni-Holm corrected according to Holm, 1979) were used for post-hoc pairwise comparison of conditions in the case of a main effect of Condition. In all cases of significant violations of sphericity, Huynh-Feldt corrections were applied to the analyses of repeated measures.

Results

Orientation First Percept

One sample *t* tests indicated that the mean values of all the experimental conditions were significantly different from random responding (i.e., 0.5): AC $t(61) = 3.56$, $p<.002$, d = .45, CC $t(61) = 8.79$, $p<.001$, d = 1.11, ADC $t(61) = 13.57$, $p<.001$, d = 1.72, and AIC $t(61) = 4.78$, $p<.001$, d = .61 (see Table 1).

<<<< Table 1 about here >>>>

The repeated measures ANOVA revealed a significant effect of Condition $F(3, 183) = 22.03$, $p < .001$, $\eta_p^2 = .27$. Comparing the AC and CC conditions in order to check which of these two conditions had a stronger influence on the first ambiguous squares figure percept, revealed that the manipulation of context ($M = 0.80$; $SD = 0.27$) was stronger than that of adaptation ($M = 0.60$; $SD = 0.21$), $F(1, 61) = 19.27$, $p < .001$, $\eta_p^2 = .24$ (Fig. 2). In addition, more participants had a stronger Orientation First Percept effect in the context condition (39 participants) than in the adaptation condition (13 participants). Based on these findings we predicted that context should be dominant over adaptation with respect to the first percept in the AIC condition. Therefore, the orientation of first percept of the ambiguous squares stimulus in the AIC condition should be equivalent to the previously viewed adapting stimulus and the context stimuli.

<<<< Figure 2 about here >>>>

Further we only compared conditions that had the same predicted orientations of responses; that is we compared the AC with the ADC (opposite first interpretation of ambiguous squares stimulus with respect to adapting stimulus) and the CC with the AIC (the same first interpretation of the ambiguous squares stimulus with respect to the context stimuli).

In addition, we anticipated the additivity of adaptation and context effects in the ADC and AIC conditions and calculated difference values: first percept responses minus random responding (i.e., 0.5): AC (0.6 – 0.5 = 0.1), CC (0.80 – 0.5 = 0.30), ADC (0.91 – 0.5 = 0.41), and AIC (0.70 – 0.5 = 0.20). These difference values were termed dAC, dCC, dADC, and dAIC, respectively. Assuming additivity of adaptation and context effects, it was predicted that the value of dADC should be roughly equal to the sum of dAC and dCC (i.e., 0.1 + 0.30 = 0.40). Regarding the AIC condition, we expected that context will be stronger than adaptation, that is, dAIC should be roughly equal to the subtraction of dAC from dCC (i.e., 0.30 – 0.1 = 0.20) (Fig. 3).

<<<< Figure 3 about here >>>>

The AC and the ADC conditions were compared to find out whether the introduction of the context stimulus of the opposite interpretation with respect to the previously presented adapting stimulus had any effect on the choice of the first percept of the ambiguous squares stimulus. A significant effect of Condition $F(1, 61) = 69.97$, $p < .001$, $\eta_p^2 = .53$, showed that when the orientations of the adapting and the context stimuli did not match, the overall effect was higher than the adaptation effect, and the participants reported more adapting stimulus incompatible first interpretations than in response to the adaptation condition. Moreover, the results suggest the additivity of adaptation and context effects as reflected in the value obtained in the ADC condition (0.41) which was only slightly higher than the predicted value in this condition (0.40).

The CC and the AIC conditions were compared with the aim of finding out whether the introduction of the context stimulus in the same orientation as the previously presented adapting stimulus had any effect on the choice of the first percept of the ambiguous squares stimulus. A significant effect of Condition $F(1, 61) = 9.99$, $p <.003$, $\eta_p^2 = .14$, showed that when the orientations of adapting and context stimuli matched, the overall effect was lower than the context effect. In addition, the difference value obtained in the AIC condition (0.20) was equal to the predicted value of this condition (0.20), once again confirming the additive interaction between the context and adaptation effects.

RT First Reversal

The repeated measures ANOVA revealed a significant effect of Condition $F(3, 183) = 24.33$, $p < .001$, $\eta_p^2 = .29$. Further analyses showed that the RT in response to the first reversal was significantly longer in ADC compared to AC $F(1, 61) = 15.25$, $p < .001$, $\eta_p^2 = .20$, to CC $F(1, 61) = 48.98$, $p < .001$, $\eta_p^2 = .45$, and to AIC $F(1, 61) = 53.39$, $p < .001$, $\eta_p^2 = .47$ (Fig. 4). In addition, the RT in response to AC was significantly longer than that in response to the AIC condition $F(1, 61) = 11.60$, $p < .002$, $\eta_p^2 = .16$.

<<<< Figure 4 about here >>>>

There were no other significant differences between conditions (largest $F = 6.63$).

Perceptual Durations

The repeated measures ANOVA (Condition × Perceptual response × Adapting stimulus) revealed significant effects of Condition $F(3, 183) = 12.28$, $p < .001$, $\eta_p^2 = .17$ and Perceptual response $F(1, 61) = 18.66$, $p < .001$, $\eta_p^2 = .23$. Significant Perceptual response × Adapting stimulus $F(1, 61) = 36.00$, $p < .001$, $\eta_p^2 = .37$ and Condition × Perceptual response × Adapting stimulus $F(3, 183) = 28.10$, $p < .001$, $\eta_p^2 = .32$ interactions were also obtained. Further analyses, conducted on each condition separately, revealed significant Perceptual response × Adapting stimulus interactions only in the AC $F(1, 61) = 40.49$, $p < .001$, $\eta_p^2 = .40$, the CC $F(1, 61) = 17.96$, $p < .001$, $\eta_p^2 = .23$, and the ADC $F(1, 61) = 43.79$, $p < .001$, $\eta_p^2 = .42$ conditions.

Significant effects of the Adapting stimulus were obtained in the AC and the ADC conditions: when participants were adapted to the 'downwards' $F(1, 61) = 11.09$, $p < .002$, $\eta_p^2 = .15$ (the ADC: $F(1, 61) = 17.56$, $p < .001$, $\eta_p^2 = .22$) or the 'upwards' $F(1, 61) = 19.72$, $p < .001$, $\eta_p^2 = .24$ (the ADC: $F(1, 61) = 42.00$, $p < .001$, $\eta_p^2 = .41$) unambiguous squares stimulus, they perceived the ambiguous test stimulus in the opposite interpretation with respect to the adapting stimulus for significantly longer durations. In the context condition, only when participants were viewing the ambiguous test stimulus in the context of 'downwards' unambiguous stimuli $F(1, 61) = 24.79$, $p < .001$, $\eta_p^2 = .29$, they tended to perceive the ambiguous test stimulus in 'downwards' orientation for significantly longer durations.

Discussion

The aim of the current study was to examine the impact of spatial context on the perception of ambiguous squares stimuli after the participants were adapted to an unambiguous stimulus, representing one of the two available orientations of the ambiguous squares stimulus. Previous findings of adaptation (Long & Moran, 2007; Long & Olszweski 1999; Long et al. 2002; Long et al. 1992; Orbach et al. 1963; Toppino & Long, 1987; von Grünau et al. 1984) were replicated in our study and spatial context effects on the perception of an ambiguous figure were obtained (Bruner & Minturn, 1955; Bugelski & Alampay, 1961; Wallace, 1988). The adaptation effect was found in the AC condition and it was weaker than a context effect obtained in the CC condition. This result suggests that global top-down processes responsible for the context effect might have a stronger influence on the perception of ambiguous figures than the localised neural channels causing the adaptation effect (Long & Moran, 2007). The effects of adaptation and context on the perception of ambiguous squares stimulus were further supported by RT First Reversal data. It is known that after a few minutes' adaptation participants tend to perceive less perceptual reversals in comparison to priming or neutral viewing conditions (Long & Moran, 2007; Long & Olszweski, 1999; Long et al., 1992), therefore, we expected longer RTs in the AC and ADC conditions where adaptation effect was estimated to be stronger. In the ADC condition, the sum of adaptation and context effects was obtained, as participants needed significantly more time to perceive a subsequent reversal of ambiguous squares stimulus in comparison to other experimental conditions. In addition, the RT to First Reversal was longer in response to the AC than in the AIC condition, revealing that adapting figure compatible context contributed to the decrease of the overall effect. This result supported the high susceptibility of adaptation to physical and temporal manipulations of stimuli

(Long & Moran, 2007; Long & Olszweski, 1999; Long et al., 1992). The RTs obtained in response to the CC and the AIC conditions had similar durations (see Table 1). This gives further support to the conclusion that the adapting figure incompatible context was stronger than the adaptation effect. To sum up, both adaptation and context effects influenced the initial percept of the ambiguous figure in an additive manner in the ADC and AIC conditions. These findings indicate that both bottom-up factors and top-down factors can influence perception concurrently.

The results add to converging evidence of additivity of top-down and bottom-up processes operating in the human visual system (Kornmeier, Hein and Bach, 2009; Long & Moran, 2007; Long & Toppino, 2004; Toppino, 2003). The perception of the ambiguous squares stimulus was modulated by both the adaptation effect and the subsequently presented context. In particular, the adaptation and context stimuli influence the perception to similar degrees in the conditions ADC and AIC as in the conditions AC and CC. It is also important to note that all the prerequisites necessary to obtain the adaptation effect were used in our study, that is, the adaptation period was sufficiently long, the adapting and test stimuli had the same retinal location, the delay between adapting and test stimuli lasted only one second (Long & Moran, 2007), and within all trials the participants were instructed to keep their eyes focused on the central fixation point (Long & Olszweski, 1999; von Grünau et al., 1984).

It has been speculated that the adaptation process occurs in early visual areas where visual inputs are organised retinotopically (Orbach et al., 1963; Toppino & Long, 1987); therefore, the effects of spatial context on the first reported percept in the CC, AIC and ADC conditions cannot be explained by neural adaptation. The cognitive theory is also insufficient for the explanation of current results as according to this theory the adaptation effect, which was revealed in the AC, ADC and AIC conditions should not have been obtained even if unambiguous (or biasing) figures preceded the ambiguous test figure for a period of 2 (or more) minutes.

Several theories tried to reconcile the on-going debate regarding the function of bottom-up versus top-down processes in ambiguous figure perception (Hochberg & Peterson 1987; Kornmeier & Bach, 2012; Leopold & Logothetis 1999; Long et al., 1983; Long & Toppino 2004). Visual bistability as a result of changes in the attractor states of a neural network has been extensively studied to explain the phenomenon of binocular rivalry (Lehky, 1988; Noest, van Ee, Nijs & van Wezel, 2007; Wilson, 2003). Kornmeier and Bach (2012) proposed an integrative theory according to which representations of objects in the brain are modelled as attractors (i.e., each perceived state that can be occupied by a physical stimulus) and their depth is a measure of the current representation's stability. Usually, when we view an image there is only one attractor to perceive (stable perception), but with ambiguous stimuli there are at least two. The authors assume that during prolonged observation of an ambiguous stimulus (i.e., for several minutes) a transiently stable percept gets destabilised (i.e., it changes from one available percept to the other) in a slow and constant manner. Once the percept gets 'destabilised', a fast restabilisation (disambiguation) occurs resulting in an alternative percept of the ambiguous stimulus. Kornmeier and Bach (2012) hypothesised that adaptation causes a slow reduction in the depth of the attractor (due to the impact of the adapting stimulus) and, as a result, participants tend to perceive the alternative orientation of the subsequently presented ambiguous figure. In addition, the integrative theory is supported by an electroencephalographic study exploring the perception of intermittently presented ambiguous figures (Intaitė, Koivisto & Revonsuo, 2013), which revealed that the event-related potentials induced by the perceptual changes may be interpreted within the framework of destabilization and restabilisation processes.

The results of the current study are in accordance with the integrative theory. The adaptation effect was obtained, which is known to have an effect on the destabilisation process (Kornmeier & Bach, 2012). Due to adaptation, the destabilisation process reached a point of maximal instability and the perceptual system tried to detect a 'more stable' state as fast as possible (Kornmeier & Bach, 2012). Therefore, once a context (which did not match the adapting stimulus) was presented together with an ambiguous squares stimulus in the ADC condition, the overall effect of experimental manipulation was stronger than in the AC or CC conditions, suggesting that the context manipulation combined with the adaptation enhanced the destabilisation in response to the first reported percept: the ambiguous squares stimulus was perceived in the opposite orientation with respect to the unambiguous adapting stimulus even more often than in the AC condition. The adaptation effects were mimicked by data of perceptual durations: the participants continued to perceive the adapting stimulus incompatible orientation of the ambiguous squares stimulus for significantly longer time in both the AC and ADC conditions.

However, when the ambiguous stimulus was presented in the context matching the preceding adapting stimulus (the AIC condition) the context not only overruled the adaptation effect, but as well equalized perceptual durations. This result supports the premise of the different operational time scales in destabilisation and restabilisation (Kornmeier & Bach, 2012): the destabilisation process again reached its point of instability (due to adaptation), but as the orientation of the contextual stimuli matched the orientation of the adapting stimulus, the destabilisation was interrupted by restabilisation and a context-matching first percept of the ambiguous squares stimulus was preferred. It could be speculated that even though the attractor was flattened through adaptation, the context broadened the attractor towards the alternative percept and thus made the context-compatible orientation available for perception.

One of the reviewers pointed out that our adapting stimuli might be slightly ambiguous, limiting the study design. However, as the results of our experiment, and experiments of other researchers using the same stimuli (Long & Olszweski, 1999; Long et al., 1992; von Grünau et al., 1984) were comparable to the results obtained with other ambiguous stimuli (Long & Batterman, 2012; Long & Moran, 2007; Long & Olszweski, 1999; Long et al., 1992) and due to the fact that participants may not be able to understand the possible ambiguity of the stimuli if they are not informed about it (Girgus et al., 1977; Rock, Hall, & Davis, 1994; Rock & Mitchener, 1992), we conclude that it was not a major issue in this experimental study. However, we strongly agree that in future studies additional screening of the participants (and the data obtained) with an aim to avoid this problem is highly recommended.

In summary, an adaptation to unambiguous versions of the ambiguous figure prior to the inspection of the ambiguous squares figure produced localised adaptation (i.e., bottom-up) effects, whereas positioning the ambiguous squares figure in a context produced a context (i.e., top-down) effect. Moreover, when influences of adaptation and context were tested against each other, the additivity of adaptation and context effects was shown with the context effect exerting a stronger influence on perceptual outcome than the adaptation effect. We suggest, in line with Kornmeier and Bach (2012) that a mechanism based on the operation of destabilisation and restabilisation processes might be responsible for perceptual reversals.

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Figure captions

Figure 1. An illustration of an experimental trial in all four conditions: A) The 'Adaptation Condition' (AC), B) The 'Context Condition' (CC), C) The 'Adaptation Different from Context' condition (ADC), and D) The 'Adaptation Identical to Context' condition (AIC).

Figure 2. Number of times that participants first reported the 'predicted' orientation of the ambiguous squares stimulus according to the orientation of the unambiguous squares stimulus ('upwards' or 'downwards') viewed in the preceding adaptation period or that viewed in the subsequent context period (in the CC) (* $p \leq .01$). Error bars represent standard deviations (SD) above and below the mean. The dashed line represents the performance at chance level.

Figure 3. A. The differences from random responding of adaptation (dAC) and context (dCC) summate in the adaptation different from context (dADC) condition. B. The context and adaptation effects have opposite directions in the adaptation identical to context (dAIC) condition.

Figure 4. Average reaction times to the first reversal of the ambiguous squares stimulus in all conditions (* $p \leq .01$). Error bars represent SD above and below the mean.

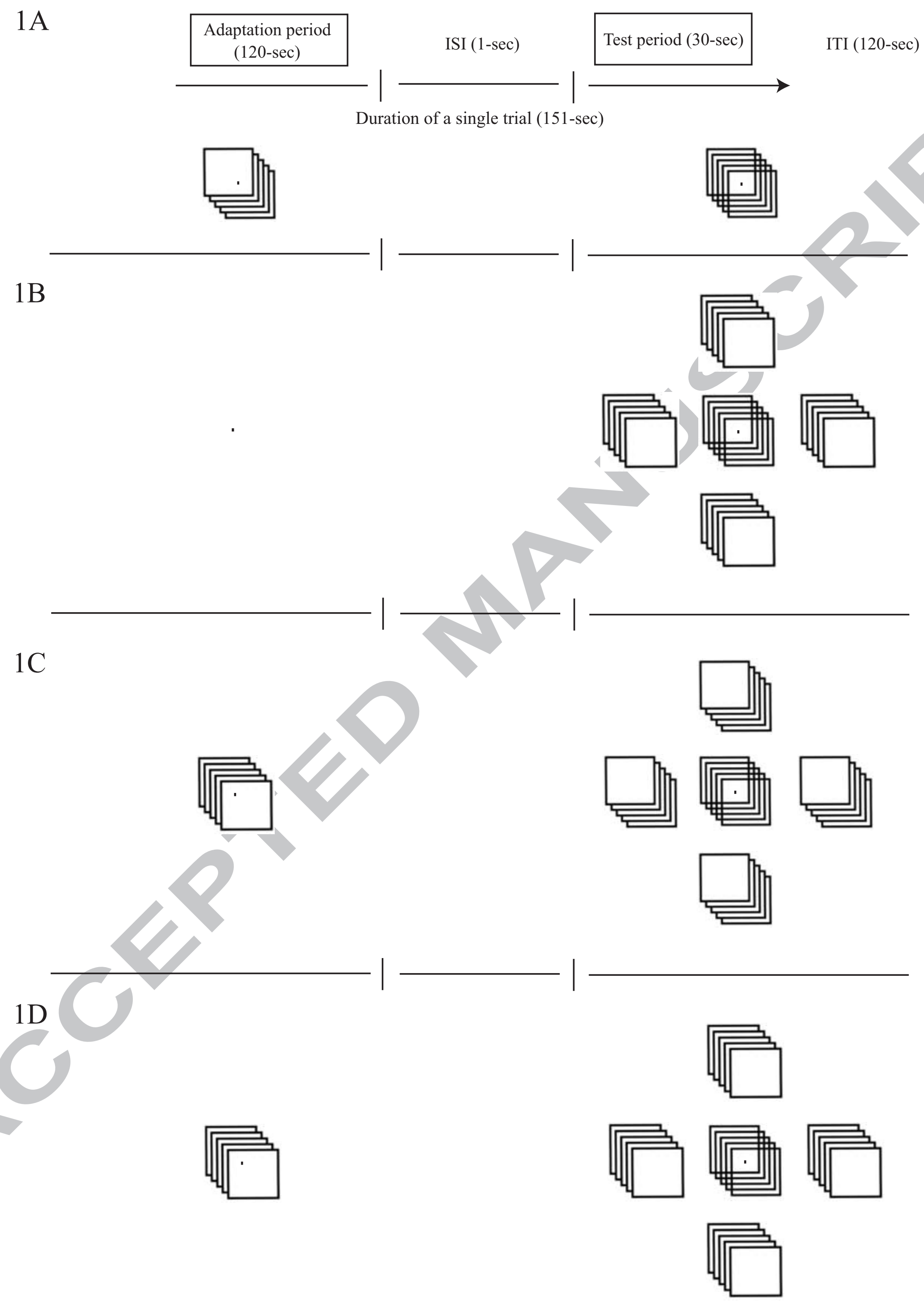
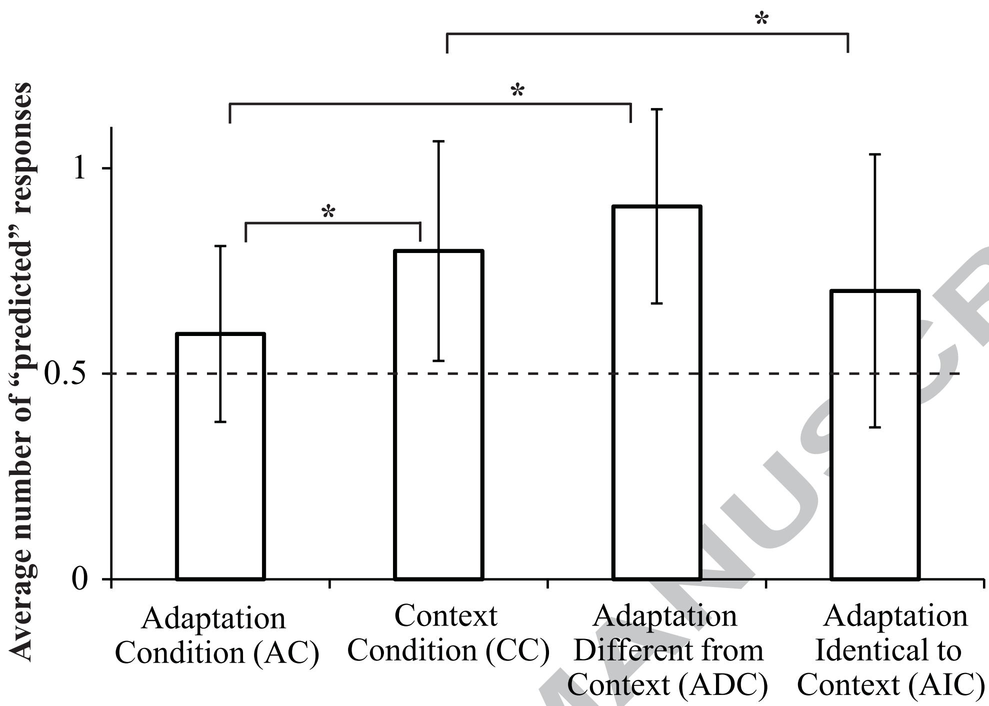

1A
Adaptation period (120-sec)
ISI (1-sec)
Test period (30-sec)
ITI (120-sec)
Duration of a single trial (151-sec)
1B
1C
1D

Fig. 1



Average number of "predicted" responses
1
0.5
0
*
*
*
Adaptation Condition (AC)
Context Condition (CC)
Adaptation Different from Context (ADC)
Adaptation Identical to Context (AIC)

Fig. 2

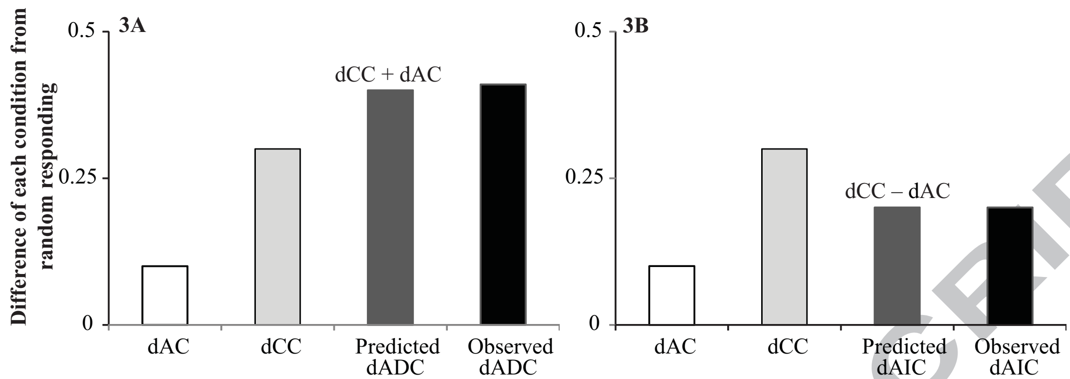

3A
3B
Difference of each condition from random responding
0.5
0.25
0
dCC + dAC
dCC – dAC
dAC
dCC
Predicted dADC
Observed dADC
Predicted dAIC
Observed dAIC

Fig. 3

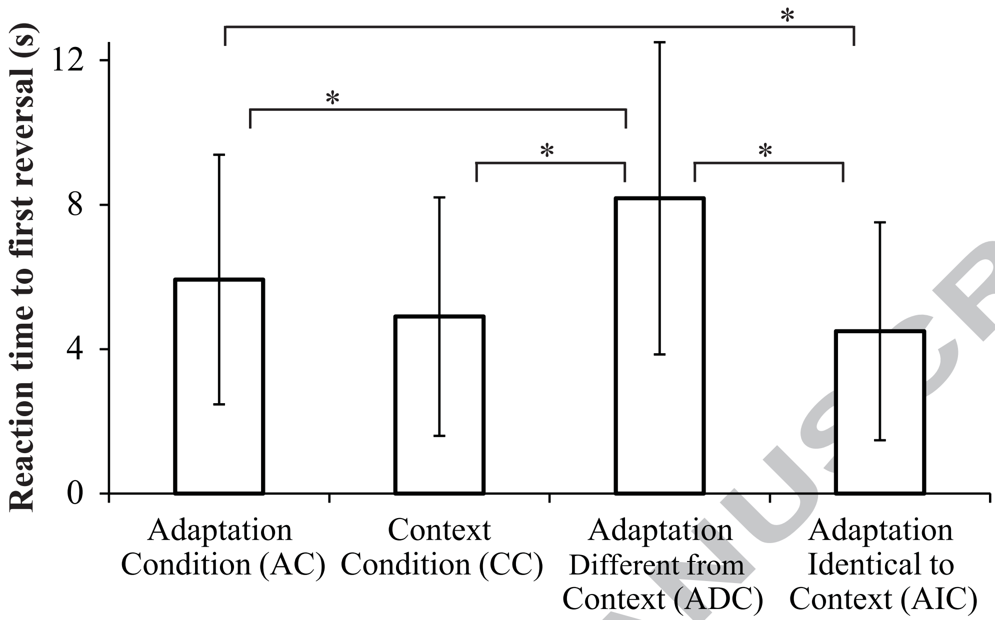

Reaction time to first reversal (s)
12
8
4
0
*
*
*
*
Adaptation Condition (AC)
Context Condition (CC)
Adaptation Different from Context (ADC)
Adaptation Identical to Context (AIC)

Fig. 4

Table 1. Means (SD) of Orientation First Percept and RTs to first reversal in all experimental conditions.

	Adaptation condition (AC)	Context condition (CC)	Adaptation Different from Context (ADC)	Adaptation Identical to Context (AIC)
Orientation First Percept	0.60 (0.21)	0.80 (0.27)	0.91 (0.24)	0.70 (0.33)
RT First reversal	5.93 (3.46)	4.90 (3.30)	8.18 (4.32)	4.49 (3.02)

Highlights

- Adaptation and context modulate the dynamics of perceptual reversals.
- Perceptual top-down and bottom-up processes are operating in an additive manner.
- Destabilisation and restabilisation are essential for perceptual reversals.