Necker cube: Stimulus-related (low-level) and percept-related (high-level) EEG signatures early in occipital cortex

Jürgen Kornmeier
Institute for Frontier Areas of Psychology and Mental Health, Freiburg, Germany, & University Eye Clinic, Freiburg, Germany
Miriam Pfäffle
Karlsruher Institut für Technologie (KIT), Karlsruhe, Germany
Michael Bach
University Eye Clinic, Freiburg, Germany

During observation of an ambiguous Necker cube, our percept changes spontaneously although the external stimulus does not. An EEG paradigm allowing time-resolved EEG measurement during endogenous perceptual reversals recently revealed a chain of ERP correlates beginning with an early occipital positivity at around 130 ms (Reversal Positivity, “RP”). In order to better understand the functional role of this RP, we investigated its relation to the P100, which is spatiotemporally closely, typically occurring 100 ms after onset of a visual stimulus at occipital electrodes. We compared the relation of the ERP amplitudes to varying sizes of ambiguous Necker cubes. The main results are: (1) The P100 amplitude increases monotonically with stimulus size but is independent of the participants’ percept. (2) The RP, in contrast, is percept-related and largely unaffected by stimulus size. (3) A similar pattern to RP was found for reaction times: They depend on the percept but not on stimulus size. We speculate that the P100 reflects processing of elementary visual features, while the RP is related to a processing conflict during 3D interpretation that precedes a reversal. The present results indicate that low-level visual processing (related to stimulus size) and (relative) high-level processing (related to perceptual reversal) occur in close spatial and temporal vicinity.

Keywords: electrophysiology, evoked potentials, ambiguous figures, multistable perception, Necker cube, Reversal Positivity


Introduction

When we observe an ambiguous figure, like the Necker cube (Necker, 1832), our perceptual system is unstable and alternates spontaneously between two or more possible interpretations. Ambiguous stimuli are of great significance in neuroscience because they seem to allow experimental separation of low-level processing of unchanged visual information from repeatedly changing higher level perceptual interpretations (e.g., Blake & Logothetis, 2002).

EEG, with its high temporal resolution, in principle allows the study of the mechanisms underlying perceptual reversals in detail. However, knowledge of the precise time instant of the purely endogenous alternation process is mandatory but difficult to access (the time reference problem). Backward averaging from participants’ manual response revealed a P300-like positivity between 500 ms and 250 ms before key press (Basar-Eroglu, Strüber, Stadler, & Başar, 1996; İ́șoḡlu-Alkaç et al., 2000; Strüber, Basar-Eroglu, Miener, & Stadler, 2001). Reaction times as time reference, however, suffer from intraindividual temporal jitter of roughly ±200 ms (Kornmeier & Bach, 2004a). We thus explored an alternative experimental paradigm. As in previous work from, e.g., O’Donnell, Hendler, and Squires (1988) and Orbach, Ehrlich, and Heath (1963), we presented the stimuli discontinuously with short interstimulus intervals (ISIs). In two separate conditions, subjects either indicated perceptual reversal or perceptual stability (identical percepts) between succeeding stimuli. We thus synchronized perceptual reversals with stimulus onset (Onset Paradigm) with a temporal precision of ±30 ms (Kornmeier & Bach, 2005). Using stimulus onset as time reference for averaging the EEG, we subtracted the stability traces (control conditions) from the reversal traces (test conditions) and discovered a chain of four event-related potentials (ERPs) associated with endogenous perceptual reversals of a Necker-type stimulus (Kornmeier & Bach, 2006). The chain starts at 130 ms with an occipital distributed positivity (Reversal Positivity, RP) and continues with an...
occipital/parietal negativity at around 250 ms, followed by frontopolar and parietal positivities between 300 ms and 500 ms after stimulus onset. The latter two components may reflect the same processes as the above-mentioned P300-like positivity resulting from backward averaging as discussed in detail in Kornmeier and Bach (2006). With exogenously induced reversals of unambiguous stimulus variants, a very similar ERP chain occurred with two deviations: (1) the ERP peaks occurred with shorter latencies and (2) the early occipital RP was missing.

Until today, this Onset Paradigm has been applied in several laboratories (e.g., Intaite, Koivisto, Ruksenas, & Revonsuo, 2010; Pitts, Nerger, & Davis, 2007; Shen et al., 2009) with different types of stimuli inducing perceptual instabilities (e.g., Britz, Pitts, & Michel, 2010; O’Shea, Kornmeier, & Roebel, 2009; Pitts, Martinez, & Hillyard, 2010; Pitts et al., 2007) and our results were mainly replicated. The early occipital RP is restricted to ambiguous stimuli and has been found with Necker-cube-like stimuli (Britz, Landis, & Michel, 2009; Kornmeier & Bach, 2004a, 2005, 2006; Kornmeier, Ehm, Bigalke, & Bach, 2007) and also with Boring’s Old/Young woman stimulus (Kornmeier, Hein, & Bach, 2007). Its specific functional role, however, is unknown so far. Its occurrence during early visual processing together with its occipital distribution puts the RP into close vicinity to the well-known visual P100 component (Luck, Woodman, & Vogel, 2000).

The goal of the present study was to investigate whether the RP is simply a modulation of the visual P100 or whether these two components reflect independent neural processes. We tested this in two ways: (1) It is well known that the P100 component is sensitive to basic visual dimensions, like stimulus size (e.g., Zani & Proverbio, 1995). We thus analyzed the dependence of both the P100 and the RP on the size of a Necker cube. (2) The RP is the first residuum of the difference between a perceptual reversal condition and a stability condition (see above and Methods section). We thus tested whether the two conditions would also have differential effects on the P100.

## Methods

### Participants

Nine female and seven male participants aged 22 to 27 with a median age of 23 years and with normal or corrected visual acuity took part in the experiment. All participants were naive as to the experimental question and gave their informed written consent. They were paid for their participation. The study was performed in accordance with the ethical standards of the Declaration of Helsinki (World Medical Association, 2000) and was approved by the local ethics review board.

### Stimuli

We used Necker cubes of three different sizes: 4.5°, 7.8°, and 13.5°, with bright edges (20 cd/m²) on a dark background (0.01 cd/m²). The stimuli were generated with a Macintosh G4 computer and presented on a Philips GD 402 monochrome monitor with a frame rate of 85 Hz. A small cross in the center of the screen served as fixation target.

### Procedure

In each of three separate experiments, one of three differently sized Necker cubes was presented discontinuously for 800 ms ± a random interval between 12 ms and 96 ms. The Necker cube alternated with a blank screen interstimulus interval (ISI) of 35 ms (three frames). Participants compared in a go/no go task the perceived front–back orientation of the current stimulus with that of the preceding one. In two separate experimental conditions, they indicated either perceived orientation reversal (Figure 1a, reversal condition) or perceived orientation stability (i.e., perceived orientation stays identical across presentations; Figure 1b, stability condition) by pressing a key. After those stimulus intervals where the participants had pressed a key, the subsequent ISI was extended to 1000 ms. Before the start of the experiment, the task was explained and the participants performed a training session (5–10 min) until they individually felt sufficiently familiar with the task.

### EEG recording

EEG was recorded from 6 gold-cup scalp electrodes at Oz, O1, O2, Pz, Fz, and Fpz (American Clinical Neurophysiology Society, 2006) with averaged ears as reference. Vertical and horizontal EOG electrodes controlled for blinks and eye movements. Impedance of each electrode was kept below 10 kΩ. Signals were amplified, filtered (first-order analog band-pass 0.5–70 Hz), digitized with a resolution of 12 bits at a sampling rate of 500 Hz, and streamed to disk. EEG sweeps containing artifacts from eye movements and amplitude excursions exceeding ±100 µV were rejected offline.

### Data analysis

#### Psychophysics

Reaction time was defined as the temporal period from stimulus onset to the participants’ response. The average number of perceptual reversals per minute (reversal rate) was calculated from participants’ response. Participants’ median reaction times and their reversal rates were analyzed by repeated measures ANOVAs with the factors

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CONDITION (reversal vs. stability) and STIMULUS SIZE (3 different sizes) and post-hoc randomization tests (Edgington & Onghena, 2007).

EEG

EEG sweeps were sorted according to 4 different experimental factors, namely, STIMULUS SIZE (3), CONDITION (reversal, stability), RESPONSE (go, no go), and CHANNEL (3). They were selectively averaged into ERPs with respect to stimulus onset as time reference and digitally filtered with a latency-neutral low-pass filter at 25 Hz. Peak amplitudes were measured relative to baseline, which was defined as the average from 60 ms before to 40 ms after stimulus onset.

We selectively focused on two ERP components, the occipital P100 from the raw ERP data and the occipital Reversal Positivity (RP) from the difference traces (reversal condition minus stability condition). For each participant, the P100 peak amplitudes were determined from the maximal excursions in spatial (occipital electrodes) and temporal (±30 ms around the grand mean peak, 114 ms) regions of interest (ROIs). Individual amplitudes of the RP were determined in the same way but from the occipital difference ERP traces (reversal minus stability; 144 ms ± 30 ms). The ROIs were motivated by previous reports (Britz et al., 2009; Kornmeier & Bach, 2005, 2006; Luck, 2005). In cases with no definite maximum in the ROI (e.g., monotonically rising or falling parts of the trace), we calculated the mean amplitude across the ROI.

The peak amplitudes were analyzed separately by repeated measures ANOVAs for each of the two ERP components, with the dependent variable AMPLITUDE and the factors STIMULUS SIZE (3), RESPONSE (go, no go), CHANNEL (O1, Oz, O2), and CONDITION (reversal vs. stability; only for the P100). Particular ANOVA results were further analyzed by post-hoc randomization tests (Edgington & Onghena, 2007). Additionally, we calculated for each participant the Spearman correlation coefficients and linear regressions between the ERP components’ amplitudes and cube sizes and tested for significant deviation of the linear slopes from zero with Wilcoxon Rank Tests for repeated data.

Figure 1. Experimental paradigm. Stimuli were presented discontinuously for 800 ms ± a random interval ε between 12 ms and 96 ms. The Necker cubes alternated with blank-screen interstimulus intervals (ISIs) of 35 ms (three frames). Participants compared in a go/no go task the perceived front–back orientation of the current stimulus with that of the preceding one. In two separate experimental conditions, they indicated either perceived orientation reversal ((a) reversal condition) or perceived orientation stability (i.e., perceived orientation stays identical across presentations; (b) stability condition) by pressing a key. Each key press extended the subsequent ISI to 1000 ms.
All post-hoc tests were corrected for the total number of orthogonal tests with the Bonferroni correction variant introduced by Holm (1979).

## Results

### Psychophysics: Reversal rates

Mean reversal rates are listed in Table 1. No significant difference in reversal rates for the differently sized cubes was found.

### Psychophysics: Reaction times

Median reaction times together with the lower and upper quartiles are depicted in Figure 2. The repeated measures ANOVA indicated significantly longer reaction times with perceptual reversal compared to perceptual stability \((p = 0.003, F(2,30) = 6.23)\).

### EEG: The P100

Figure 3a depicts a schematic head with separate traces for each electrode position. The three differently colored ERP traces on each graph correspond to the three differently sized Necker cubes, averaged across the factors CONDITION and RESPONSE. The traces represent grand means across participants. Error traces were omitted for the sake of distinctiveness of the three ERP traces within one graph. The statistical analysis of the ERP components is based on peak amplitudes from predefined ROIs. These amplitudes may deviate slightly from the grand mean traces. In Figure 3c, we present bar graphs (± SEMs) representing the ROI peak data. The following observations can be made:

1. The P100 ERP component occurs around 114 ms after stimulus onset with maximal amplitudes at occipital electrode positions.
2. The P100 amplitude correlates with cube size \((F(2,30) = 21.54, p < 0.001 \text{ for the factor STIMULUS SIZE})\). Post-hoc randomization tests indicate significantly smaller P100 amplitudes for the small compared to the medium cube \((p \approx 0.005, \text{corrected})\) and compared to the large cube \((p \approx 0.001, \text{corrected})\).

### EEG: The reversal positivity (RP)

Figure 3b depicts the difference traces (reversal traces minus stability traces) on a schematic head. Again, each trace corresponds to one Necker cube size. Figure 3d shows the grand mean peak amplitudes ± SEM from the predefined ROI. The following observations can be made:

1. RP is most prominent at the occipital electrode and significantly smaller amplitudes for the medium cube compared to the large cube \((p \approx 0.03, \text{corrected})\).
2. The ANOVA further indicates significant amplitude modulations for the factor CHANNEL with \(F(2,30) = 17.86, p < 0.001\). Post-hoc randomization tests indicate significant larger P100 amplitudes at the Oz electrode compared to the O1 electrode \((p \approx 0.006, \text{corrected})\) and the O2 electrode \((p < 0.001, \text{corrected})\). No significant amplitude modulation for the factor CONDITION \((F(1,15) = 3, p = 0.08)\) nor interactions were found.

Figure 4 displays the ERP traces from electrode Oz for the two conditions separately and confirms the ANOVA results: a clear pattern of P100 amplitude increase from the small to the large cube reflects the effect of STIMULUS SIZE. No clear picture can be seen, however, for the factor CONDITION. The two P100 traces from the large cube are identical, and although the medium cube and the small cube show slight differences between conditions, these differences point in opposite direction. Around the time region of the RP (140 ms), no clear separation between size-related traces is seen. However, for each cube size, the pairs of ERP traces show smaller amplitudes for the reversal traces compared to the stability traces.

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**Table 1.** Mean reversal rates (number of reversals per minute) ± standard errors (SEM).

<table>
<thead>
<tr>
<th></th>
<th>Small cube</th>
<th>Medium cube</th>
<th>Large cube</th>
</tr>
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<tbody>
<tr>
<td>Mean</td>
<td>8.7 ± 0.5</td>
<td>8.9 ± 0.5</td>
<td>8.5 ± 0.5</td>
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</tbody>
</table>

Figure 2. Reaction times. Median reaction times (white lines) with interquartile range (rectangles) and ±45 percentiles (antennas). SR: small cube, reversal condition; MR: medium cube, reversal condition; LR: large cube, reversal condition; SS: small cube, stability condition; MS: medium cube, stability condition; LS: large cube, stability condition. Reaction times are shorter in the stability condition but do not differ between cube sizes.
positions and occurs at around 140 ms. (2) The RP amplitude does not differ significantly between the occipital electrodes. (3) The RP amplitudes related to the medium-sized cube and to the large cube are roughly equal to and larger than that of the small cube. The ANOVA’s $p$-value for the factor STIMULUS SIZE, however, does not indicate this difference as significant ($p \approx 0.06 > a$, $F(2,30) = 3.81$). No other factor or interaction was indicated as significant.

**EEG: Correlation coefficients and linear regressions**

Visual inspection of Figures 3a and 3c and the ANOVA results indicate a strictly monotonic (non-saturating) relation between P100 amplitude and cube size (over the current range).

For the RP, Figures 3b and 3d together with the ANOVA result do not support a monotonic relation.
between size and RP component. Thus, we additionally calculated individual and average Spearman correlations and linear regressions between each of the two ERP components and cube size. The results are listed in Table 2.

For each ERP component, we tested whether the slope of the linear regression was significantly different from zero. Only the linear slope of the P100 cube size regression differs significantly from zero with $p = 0.002$ (one-tailed Wilcoxon Test for paired data, corrected).

Figure 5 depicts the individual slopes of the P100 cube size linear regressions versus those of the RP cube size linear regression. On the horizontal zero line (zero slope of the RP cube size regression), the individual points scatter in a range of about 0.5 around zero. Ten points are above and 6 points are below zero slope, whereas on the ordinate zero line (zero slope of the P100 cube size regression) the values scatter in a range of only 0.3 around zero, and only two points are below but 13 points are above a zero slope. Further, the Spearman correlation between P100 and cube size is about twice that of the RP and cube size.

### Table 2

<table>
<thead>
<tr>
<th>Component</th>
<th>Average Spearman correlation ± SEM</th>
<th>Average linear regression slope ± SEM</th>
</tr>
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<tbody>
<tr>
<td>P100 amplitude</td>
<td>0.55 ± 0.16</td>
<td>0.1 ± 0.02</td>
</tr>
<tr>
<td>RP amplitude</td>
<td>0.23 ± 0.2</td>
<td>0.05 ± 0.04</td>
</tr>
</tbody>
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### Discussion

In order to better understand the functional role of the reversal-related RP, we investigated its relation to the spatiotemporal close stimulus-related P100 ERP component, typically occurring 100 ms after onset of a visual stimulus at occipital electrodes. We compared the amplitude modulations of the two ERP components as functions of stimulus size. The major results are: (1) Both the P100 and the RP occur early after stimulus onset at the occipital electrode position. (2) The P100 is most prominent at Oz and weaker at the lateral occipital electrode positions (O1 and O2), whereas the RP shows no amplitude difference between occipital electrode positions. (3) The P100 amplitude increases monotonically with the size of the Necker cube but stays largely unaffected by the participants’ percepts. (4) The RP correlates with the participants’ percepts but stays largely unaffected by changes in
stimulus size.\(^1\) (5) Similarly, RTs depend on participants’ percepts but not on cube size.

The EEG has a very high temporal but low spatial resolution. A surface ERP potential typically reflects the sum of parallel and/or combined activity of several different neural generators. Two adjacent ERP components can thus indicate both independent and shared neural generators. Keeping this in mind, the present findings indicate that at least some relevant parts of the neural processes underlying the P100 and the RP are temporally and functionally different (but not necessarily independent). Larger amplitudes of the P100 compared to the RP may just indicate that the processes specific for the P100 involved more neurons than those specific for the RP.

What does the RP reveal about endogenous perceptual reversals?

The RP is the earliest residual ERP component after the subtraction of the stability ERP traces from the reversal ERP traces. It occurs with endogenous reversals of ambiguous figures (Britz et al., 2009; Kornmeier & Bach, 2005, 2006; Kornmeier, Ehm et al., 2007) and is absent with exogenously induced reversals of unambiguous stimulus variants (Kornmeier & Bach, 2006).

One of the major findings in the present study is that the RP is largely unaffected by cube size and only correlates significantly with the participant’s percept. The P100, occurring 30 ms earlier with the same occipital distribution, behaves inversely: it increases monotonically with stimulus size but is unaffected by the participant’s percept.

The occipital distribution and the early peak time (140 ms and 110 ms) compared to reaction times at about 440 ms suggest low-level visual processes as generators for both components. However, how early or late is this in terms of perceptual processing time?

The earliest visually evocable ERP component is the C1. It is maximal about 60 ms after stimulus onset (e.g., Jeffreys & Axford, 1972) and seems to be at least partially generated in the striate cortex (V1, e.g., Di Russo, Martinez, & Hillyard, 2003; Foxe & Simpson, 2002). It is sensitive to basic stimulus features (e.g., spatial frequency, Pitts et al., 2010) but unaffected by high-level factors like attention (Luck et al., 2000; for contrary results, see, e.g., Rauss, Pourtois, Vuilleumier, & Schwartz, 2009).

Like the C1, the P100 is sensitive to basic visual dimensions like spatial frequency (e.g., Pitts et al., 2010) and stimulus size (the present data and, e.g., Zani & Proverbio, 1995). In contrast to the C1, it can be modulated by attentional factors as well (e.g., Di Russo et al., 2003; Luck et al., 2000). Several authors suggest that basic visual feature extraction (e.g., shape) and category building may take place at the processing stage of the P100 (e.g., Fahrenfort, Scholte, & Lamme, 2008; VanRullen & Thorpe, 2001). Results from a scalp current density analysis of EEG data, recorded during visual stimulations, indicate that the time frame of “early visual processing” is much more condensed than previously assumed (Foxe & Simpson, 2002). Visual information seems to need only about 30 ms from striate (at about 50 ms) to prefrontal cortex (at about 80 ms). Both the P100 and the RP may thus occur after one or more loops of recurrent activity between early visual and high-level cortical areas. Thus, high-level mechanisms may define and control features or spatial regions of interest in early visual areas via recurrent activity within the first 100 ms after stimulus onset. Such mechanisms may be reflected in the P100 component, but when identical for reversal and stability percepts, they will be eliminated in the difference traces.

In the case of the cube stimulus, one may speculate that the identification of line orientations and the binding together of individual lines (in the sense of early visual binding, e.g., Ehm, Bach, & Kornmeier, 2010) to tetragon objects are the first visual processing steps. Subsequently, acute and obtuse angles have to be interpreted as orthogonal, and depth values have to be allocated to the different square plains in order to perceive a 3D cube. Here, activation and/or inhibition of potential representations stored in memory may be relevant.

Exactly at this processing stage, cube ambiguity comes into play and a decision has to be made between two almost equally likely interpretations/representations potentially stored in memory. The assumption that visual ambiguity only affects processing after the P100 stage is confirmed by the observation that the P100 latency is identical for both ambiguous Necker stimuli and their unambiguous variants (Figure 2c in Kornmeier & Bach, 2006, and Figure 4 from the present study), whereas all subsequent ERP components related to the change in perceived cube orientation are delayed if the cube is ambiguous, compared to unambiguous cubes (Figure 3 in Kornmeier & Bach, 2006). Kornmeier and Bach (2006) propose an upper limit for the disambiguation process at 250 ms after stimulus onset and a disambiguation time of about 40 ms, which could be translated into approximately one (additional) loop of recurrent activity according to Foxe and Simpson (2002). In this sense, the RP could be interpreted as some neural signal reflecting the “detection” of the ambiguity or of the conflict arising with it and thus could mark the start of the decision or disambiguation process.

Is discontinuous stimulation a good model for the continuous case?

The above interpretations are supported by both current and previous psychophysical and physiological findings, but one problem remains: It seems to fit only to perceptual choice events, where a decision has to be made after the new onset of the discontinuously presented ambiguous
stimulus (Noest, van Ee, Nijs, & van Wezel, 2007). What about the continuous case?

If the ambiguous stimulus is continuously presented, some higher level updating instance may periodically reevaluate and reinterpret the visual input in order to notice even slight environmental changes. Thus, periodic choice or decision events may also take place during continuous observation of an ambiguous figure. Such a concept is inherent in the Necker–Zeno Model for Bistable Perception (Atmanspacher, Bach, Filk, Kornmeier, & Römer, 2008; Atmanspacher, Filk, & Römer, 2004) and also in earlier explanatory approaches (Vickers, 1972). According to this assumption, in an EEG experiment with continuous presentation of an ambiguous figure and concurrently a sufficient temporal precision of the reversal instance, the low-level ERPs, like the P100, should thus be absent, but the RP should persist.

How can our results be related to findings from binocular rivalry experiments?

Another class of stimuli, namely, binocular rivalry stimuli, can also induce perceptual instability: When the observers’ two eyes view different stimuli, e.g., orthogonal gratings, competition between the two possible percepts takes place, very similar to the perceptual competition between the interpretations of the current Necker lattice. Interestingly, several binocular rivalry studies did find percept-related P100 modulations.

In a very clever EEG paradigm with binocular rivalry stimuli, Roeber et al. first present rivalrous stimuli (each eye sees a different grating), then exchanged one eye’s stimulus to so-called fusion stimuli (the two eyes now see the identical stimuli) and used the change from rivalry to fusion as time reference for calculating ERPs. They found higher P100 amplitudes when grating orientation changes were consciously perceived and lower ones when the orientation changes were not consciously perceived (Roeber & Schroger, 2004; Roeber et al., 2008). Pitts et al. (2010) used binocular rivalry grating stimuli, differing in orientation, color, and spatial frequency, and presented them in an onset paradigm similar to the present one. They found a difference in P100 amplitude when their participants perceived low vs. high spatial frequency gratings.

How can these P100 results be reconciled with our negative findings concerning the relation between P100 amplitude and percept? One principal difference between the two phenomena is the following: With ambiguous figures, rivalry takes place between different perceptual interpretations of one unchanged stimulus. Thus, during a perceptual alternation, the interpretation of the identical visual information changes, whereas the unchanged P100 indicates that the low-level stimulus processing is the same. With binocular rivalry stimuli, the rivalry takes place between two different visual stimuli. Thus, each perceptual outcome is related to one of the two different physical stimuli and different input-specific low-level processing. If one stimulus is consciously perceived, the other may be processed up to a certain unconscious processing level. In the case of a perceptual alternation, unconscious visual information gets conscious and consciously perceived visual information gets unconscious. Thus, a perceptual alternation may be coupled with de- and reactivation of lower level processing contents/steps from separate stimuli (e.g., Blake, 2001). This may explain the modulation of early visual ERP components like the P100 with gratings or the N100 with colors (e.g., Roeber & Veser, 2009). In the above-mentioned studies, the early visual ERP amplitudes are increased when a certain stimulus gets conscious in contrast to when it stays unconscious (e.g., Roeber & Schroger, 2004; Roeber et al., 2008). Similar findings have been reported by Valle-Inclan, Hackley, de Labra, and Alvarez (1999). This fits well with reports of neural processing being enhanced when the stimulus is consciously perceived compared to neural processing, when the stimulus stays unconscious (e.g., Kouider & Dehaene, 2007). In summary, it seems quite plausible that there is a P100 modulation when rivalry changes, but none when multistable figures undergo perceptual reversal.

Why at all is there an early ERP difference between reversal and stability conditions?

All our visual information is, to some degree, incomplete and inherently ambiguous. Its interpretation by the perceptual system is influenced (among other things) by previous experiences (on different time scales), as several priming and adaptation studies have demonstrated (e.g., Long, Toppino, & Mondin, 1992; Woerner, Bach, & Kornmeier, 2009). In the case of ambiguous figures, such an inherent bias may prevent the interpretation conflict described above. Examples are the stability cases of the current experiment where such a bias could be induced by the preceding percept. Then, disambiguation of the visual information is not necessary and participants’ reaction times should be reduced by about 40 ms (the missing disambiguation time) compared to the reversal cases. Indeed, we found that reaction times in the stability conditions were, on average, 45 ms shorter than in the reversal conditions (Figure 2).

In the reversal case, the bias effect has diminished due to adaptation effects or volitional control (Kornmeier, Hein, & Bach, 2009). Then, decision and disambiguation processes have to take place.

Conclusions

The stimulus-related P100 ERP component seems to reflect early visual processing relevant for both possible
perceptual outcomes. Its occurrence and intensity is related to low-level features of the visual information (e.g., stimulus size in the present data or spatial frequency in Pitts et al., 2010). The RP component, on the other hand, may reflect the detection of the visual input’s ambiguity or some early perceptual decision conflict arising from it. So far, we do not know what “detection of ambiguity” or “decision conflict” by the visual system would mean in concrete neural processing terms. Thus, it is still unclear what the RP reflects in detail. The current result of the insensitivity of reversal rates and RP toward stimulus size hints toward a more abstract process beyond the level of stimulus details. This assumption is additionally supported by the result that the occipital Reversal Positivity is not restricted to the geometric category of ambiguous figures (Necker cubes and lattices) but occurs with identical spatiotemporal distribution with Boring’s Old/Young Woman (Boring, 1930; Kornmeier & Bach, 2004b). Future experiments with stepwise reduction of stimulus ambiguity may reveal some more details about the functional role of the RP.

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Commercial relationships: none.
Corresponding author: Jürgen Kornmeier.
Email: kornmeier@igpp.de.
Address: Wilhelmstraß e 3a, Freiburg 79098, Germany.

Footnote

1Clearly, RP and stimulus size cannot be completely independent of each other. A minimal cube size is necessary for the participants to identify its spatial orientation and thus to experience an endogenous perceptual reversal and to produce an RP. One could assume a saturating curve, which is indicated in Figure 3d, albeit statistically not substantiated.

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