Dissociation of reversal- and motor-related delta- and alpha-band responses during visual multistable perception

Birgit Mathesa, Ulrich Pompea, Peter Wallac, Canan Basar-Eroglua

Abstract

Multistable visual perception refers to phenomena, in which one invariant stimulus pattern is perceived in at least two different, mutually exclusive ways. In this EEG study we differentiate between perceptual- and motor-related processes during perceptual reversals. Delta- and alpha-band activity was analyzed while participants answered to a perceptual reversal either immediately or with a delay of approximately 1500 ms, thereby separating reversal-related and motor-related activity. On the single sweep level a reversal-related positive delta response and reversal-related desynchronisation of alpha activity could be detected irrespective of the motor response. Both conditions elicited the strongest reversal-related modulations at posterior locations. Contrary, motor-related responses were found predominantly at central locations. These findings were supported by a control experiment, using a slightly modified stimulus that allowed unambiguous perceptual changes to be triggered exogenously. In conclusion, this study demonstrates that the brain response to perceptual reversals differs from motor-related processes elicited by the button press indicating the perceptual reversal. The results of this study, therefore, indicate that perceptual- and motor-related processes are achieved in multiple selectively distributed and parallel working oscillatory networks of the brain.

This study was undertaken to better differentiate perceptual from motor processes in the oscillatory EEG activity during continuous viewing of ambiguous visual patterns, such as the Stroboscopic Alternate Motion (SAM, see Fig. 1A) or the Necker Cube.

When subjects indicate a perceptual reversal by pressing a button a reversal-related slow positive wave, which is prominent in the delta band (0–4 Hz), can be detected [3]. This delta component, by its functional and topographical similarity to the P300, was interpreted as reflecting the conscious recognition of the perceptual change and the closure of the reversal process [3, 6, 14, 20]. However, these bottom-up processes might predominantly occur in low alpha-sub-bands (6–8 Hz), while upper alpha-sub-bands might also be involved [12, 13, 16, 21]. Importantly, Basar-Eroglu et al. have shown that the endur-
reversal. The aim of this study was, therefore, to better differentiate between the oscillatory delta and alpha activities related to the perceptual reversal and the motor response. Specifically, we utilized two task conditions during which participants either indicated a perceptual change immediately after its occurrence (standard) or approximately after 1500 ms, thereby separating the reversal-related from the motor-related response (dissociated). The two tasks were performed with the SAM, a multistable stimulus that during constant viewing induces internally generated changes in the perceived direction of motion (ambiguous) and a slightly modified control stimulus that allowed directional changes to be applied exogenously (unambiguous; see Fig. 1A).

Fourteen right-handed volunteers (8 females) between 20 and 30 years (22.8, SD: 2.7) gave written consent on their participation, from neurological or psychiatric diseases. At the subjects viewing distance of 150 cm, the horizontal and vertical distance between the dots comprising the visual stimuli was 2.4 cm (visual angle: 0.92°) and 3.8 cm (1.45°), respectively. The dots were displayed in white on a black background. A continuously presented central white dot served as fixation. The stimuli were displayed for 165 ms and separated by an inter-stimulus interval of 85 ms during which only the central fixation dot was presented. Thus, as long as no external change of the stimulus pattern was constrained that the ambiguous/dissociated condition never occurred first. A short learning session ensured understanding of the instructions. EEG was recorded with Ag-AgCl electrodes from standard locations (F3, F4, C3, Cz, C4, P3, Pz, P4, O1, O2) of the international 10–20 system, with linked earlobes serving as reference. The signal was amplified by means of a Nihon Kohden system (EEG-4421 G) with band limits between 0.1 and 70 Hz (24 dB/octave) and an additional notch filter at 50 Hz. The data was digitized at a 500 Hz sampling rate and analyzed off-line. Recording time for each condition was 7.5 min. Epochs from –3000 ms before to 998 ms after the button press were extracted from the continuous data. EOG was recorded from electrodes placed above and to the right of the right eye and epochs contaminated by eye or other artifacts were manually rejected off-line. In addition, epochs containing multiple button presses were excluded, leading on average to 42 analyzed epochs per participant and condition. To allow comparability with earlier studies of our group, the data was digitally filtered within the delta (0–4 Hz) and alpha (8–12 Hz) frequency range using Fast Fourier Transformation.

To compensate for the inter- and intraindividual variability of the reversal-related delta response [3,7,14,20] the occurrence of the positive delta maxima was determined for each stimulus type, condition and participant (1) across the electrode sites P3, Pz and P4 and (2) across all epochs within the time windows ranging from 2250 to 1000 ms before the button press as well as 750 ms before to 350 ms after the button press. For both time windows the median time of occurrence of the positive delta maxima is referred to as t1 and t2, respectively. The selected time windows comprise the perceptual unstable state during which the perceptual reversals occur of either the standard or dissociated task condition (Fig. 1B illustrates data processing and Fig. 2 variability of the delta response). Subsequently, the delta and alpha activity was investigated time-locked to t1 and t2. For delta, mean values of the maximum positive deflection within –375 ms before to 375 ms after t1 and t2 were computed over single epochs for each stimulus type, condition, participant and electrode site (see Fig. 1B). As the reversal-related alpha decrease starts before the reversal-related delta response reaches its maximum, root mean square (RMS) values of the alpha

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**Fig. 1.** (A) Stimuli: Ambiguous motion perception was induced by alternating the two stimuli Amb1 and Amb2. The unambiguous vertical motion was generated by an alternating presentation of the two stimuli Vert1 and Vert2. Alternation of Horz1 and Horz2 produced unambiguous horizontal motion (adapted from [20]). (B) Schematic illustration of data analysis: Within the time windows –2250 to –1000 ms and –750 to 350 ms (grey lines) t1 and t2 reflect the individually selected time points of the main positive delta responses which were used for the analysis of delta (350 ms before until 350 ms after the t1 or t2, black lines) and alpha (500 ms before t1 or t2) activity. When participants indicate perceptual reversals immediately, the perceptual unstable state occurs around t2 (standard). During the dissociated task condition the participants respond to perceptual reversals approximately after 1500 ms, i.e. the perceptual unstable state around t1 is separated from motor-related responses occurring during the perceptual stable state around t2.
oscillatory alpha activity (the sum of evoked and induced activity)
t1 and t2. Computation of RMS values allowed to analyze the total
activity were computed for the time window of 500 ms preceding
t1 and t2. Computation of RMS values allowed to analyze the total
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Averaged delta response of three representative observers elicited during
Fig. 2. Averaged delta response of three representative observers elicited during

Ambiguous task condition

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<thead>
<tr>
<th>Subject</th>
<th>F4</th>
<th>C4</th>
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Unambiguous task condition

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The response pattern of the maximum positive delta deflection for unambiguous pattern reversals is similar but more pronounced
when compared to ambiguous pattern reversals (see Fig. 3B). Again,
the delta response has a posterior maximum (ROI: F(3,36) = 18.6,
p < .001; frontal < central, parietal, occipital; p < .05 for all post hoc comparisons) and is larger around the button press (t2) than
during the preceding time window (t1; time window: F(1,12) = 8.7, p < .05). However, compared to the dissociated condition is the delta response for the standard condition again smaller around
t1 and larger around t2 as reflected in a significant time window × condition interaction (F(1,12) = 26.4, p < .001; p < .01 for post hoc comparisons). Around t1 all ROIs display larger delta responses for the dissociated condition. Contrary, the enhancement of the
t2-delta response for the standard condition is predominantly accounted for by parietal and occipital ROIs with a parieto-occipital
maximum, while the smaller response for the dissociated condition has a central maximum (time window × condition × ROI interaction: F(3,36) = 6.9, p < .01; t2-delta response for standard > dissociated at parietal and occipital ROIs: p < .05 for all post hoc comparisons; see
Figs. 2 and 3A).

The mean reversal rates for the ambiguous task conditions do not differ significantly (ambiguous/standard: 79 (SD: 41); ambiguous/dissociated: 71 (SD: 35)) and are comparable to the 71 externally
induced alternations between horizontal and vertical apparent
motion perception during both unambiguous task conditions.

The maximum of the positive delta response (0–4 Hz) for
ambiguous pattern reversals has a posterior maximum (ROI:
F(3,36) = 11.4, p < .01; frontal < central, parietal, occipital; p < .05 for all post hoc comparisons, see Fig. 3A) and is generally enhanced for the standard condition (condition: F(1,12) = 5.4, p < .05). Fur-
thermore, the delta response is generally larger around the button press (t2) than during the preceding time window where no motor
response occurs (t1; time window: F(1,12) = 12.8, p < .01). How-
ever, closer inspection of the data revealed that the enhancement for the standard condition is only observable around t2, while
around t1 the delta response is larger for the dissociated condition as reflected in a significant time window × condition interaction
(F(1,12) = 13.8, p < .01; t2-delta response of standard > dissociated: p < .01 for post hoc comparison, see Fig. 3A). Furthermore, the enhancement of the delta response for the standard condition occurs predominately at posterior electrode sites (condition × ROI interaction: F(3,36) = 4.6, p < .05; standard > dissociated at occipital and parietal ROIs: for post hoc comparisons p < .05 and p = .056, respectively). Therefore, it was the posterior response of the
t2-delta activity accounting predominately for the difference between the standard and dissociated task condition as the larger response for the standard condition has a parieto-occipital maximum,
while the smaller response for the dissociated condition has a central maximum (time window × condition × ROI interaction: F(3,36) = 6.9, p < .01; t2-delta response for standard > dissociated at parietal and occipital ROIs: p < .05 for all post hoc comparisons; see
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The response pattern of the maximum positive delta deflection for unambiguous pattern reversals is similar but more pronounced
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t2-delta response for the standard condition is predominantly accounted for by parietal and occipital ROIs with a parieto-occipital
maximum for the standard and a central maximum for the dissociated condition (condition × ROI interaction: F(3,36) = 15.2, p < .001; time window × condition × ROI interaction: F(3,36) = 27.2, p < .001, p < .01 for all post hoc comparisons, see Figs. 2 and 3B).

The oscillatory alpha activity (8–12 Hz) during ambiguous pat-
ttern reversals has a fronto-central minimum (ROI: F(3,36) = 15.9, p < .01; frontal < central, parietal, occipital and central < parietal: p < .01 for all post hoc comparisons) and is generally diminished for the dissociated condition (condition: F(1,12) = 8.3, p < .05). Impor-
tantly, the task related alpha desynchronisation for the dissociated condition is predominantly accounted for by parieto-occipital ROIs preceding t1 and by the central ROI preceding t2 (time window × condition × ROI interaction: F(3,36) = 6.3, p < .05, p < .05 for all post hoc comparisons, see Fig. 3C).

Alpha and delta band responses of the two stimulus types (ambiguous and unambiguous) were analyzed separately in a 3-way
analysis of variance using 2 conditions (standard and dissoci-
ated), 2 time windows (according to t1 and t2, see above) and
4 regions of interest (ROI: frontal (F3/F4), central (C3/Cz/C4), parietal (P3/Pz/P4) and occipital (O1/O2)). For two participants
data files either for the ambiguous/dissociated or the unambigu-
Fig. 3. Mean delta and alpha responses elicited during the ambiguous (A and C) and unambiguous (B and D) task condition for the time window t1 (black: standard, white: dissociated) and t2 (horizontal stripes: standard, oblique stripes: dissociated). Importantly, larger delta amplitudes and smaller alpha RMS values reflect the pattern reversal occurring during the time window t1 for the dissociated task condition when no motor-related processes overlap with the perceptual reversal (see ellipses and text for further information).

These results demonstrate that reversal-related changes in the delta- and alpha-band can be detected, disregarding if participants indicate their reversals immediately or with a time lag of approximately 1500 ms. For both task conditions (standard and dissociated) and stimuli (ambiguous and unambiguous) a positive delta response was detected approximately 1500 ms before the button press. For the dissociated task conditions an additional positive delta response was detected approximately 1500 ms before the button press. Importantly, the topography of the delta responses displayed a posterior maximum, except when only motor-related processes occurred (time window around t2 for dissociated, see Fig. 2). It can, therefore, be assumed that reversal-related processes elicit a positive delta response with a posterior maximum, which predominately governs the shape of the oscillatory response disregarding if motor-related processes overlap with the perceptual reversal (around t2 for standard) or not (around t1 for dissociated). The posterior topography of the reversal-related delta response, therefore, mirrors the P300 [17] and underlines the functional relation between the two components [3,14].

Dissociating the perceptual switch from the motor response presumably increases attentional demands and, accordingly, the requirements of top-down resources during the task. Only during the dissociated task condition it is of importance to attend to the specific stimulus configurations of the flashing dots in order to achieve proper timing between reversals of the perceived direction of apparent motion and the motor response. As expected, increased requirements of top-down resources are reflected in the delta band activity. The amplitude of the reversal-related delta response is smaller during the dissociated than the standard task conditions, as the amplitude of the P300 decreases with increasing attentional resource allocation given that the number of occurrences of the perceptual reversal is similar between task conditions [17]. The decrease of the P300 with increasing task difficulty has also been described for single trial ERP analysis [8]. Furthermore, reduction of the reversal-related delta response occurs when participants voluntarily increase their reversal rate by shifting their focus of attention towards other aspects of the task after perceiving a perceptual switch [14], a process that might be also necessary for the timing of the motor response during the dissociated task condition. Thus, in analogy to the P300, the reversal-related delta response seems to reflect top-down processes accounting for multistable perception [3,13,14,21]. The similar pattern in amplitude modulation found for the reversal-related positive delta response of ambiguous and unambiguous reversals indicates that for both stimuli similar processes, such as the conscious recognition of a perceptual change and the closure of the reversal process, are reflected by the delta response [3,6,14,20].

Similar to the positive delta response the topography of alpha desynchronisation induced by ambiguous perceptual reversals is different to when only motor-related processes occur: for the dissociated task condition alpha desynchronisation preceding the perceptual reversal was maximal at parieto-occipital locations while alpha desynchronisation induced during the preparation of the motor response was maximal at central locations, as described
earlier for the preparation of voluntary finger movements [15]. This indicates that during the dissociated task condition reversal- and motor-related processes differ during timing and topography. Furthermore, alpha-band activity differs between ambiguous and unambiguous pattern reversals. While ambiguous pattern reversals are preceded by a slow desynchronisation of alpha, for unambiguous pattern reversals the alpha decrease is steep and occurs for a shorter period of time [20]. In this study, alpha activity during the standard condition of the unambiguous stimulus was minimal around the button press at occipital sites. This result tentatively implies that desynchronisation of alpha is better time-locked to the motor response when induced by externally applied changes of the stimulus configuration than by internally generated changes of the current percept. However, this has to be tested explicitly in future studies by taking alpha-sub-bands into account because these differ in topography and their functional contribution to sensory-cognitive demands [7,9,10].

In conclusion, the reversal-related positive delta response, reflecting top-down processes during the closure of the reversal process, and the reversal-related alpha decrease, reflecting both top-down and bottom-up processes during the destabilization of the percept, differ from the brain activity induced by the subject’s motor response to indicate a perceptual reversal. Although both perceptual- and motor-related processes lead to changes in the delta- and alpha-band they can be differentiated by timing and topography. In accordance with the theoretical framework laid out by Basar [1], the results of this study indicate that perceptual- and motor-related processes are achieved by multiple selectively distributed and selectively coherent, parallel working, oscillatory networks of the brain.

Acknowledgements

Ulrich Pomper was supported by Erasmus, a European student exchange program. We thank Joscha Schmied (B.Sc. of Physics) for help with data analysis and Dr. C. Schmiedt-Fehr for discussions.

References