

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

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### 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.

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This study was undertaken to better differentiate perceptual from motor processes in the oscillatory EEG activity during continuous viewing of ambiguous visual pattern, 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]. Furthermore, multistable perception elicits enduring frontal enhancement of gamma activity, possibly related to monitoring demands during multistable perception [2,18,19]. The functional involvement of both, the reversal-related delta and gamma response, in cognitive or top-down modulated aspects of multistable perception was underlined by its modulation through the observers' intention to maintain or switch the currently perceived perceptual alternative of a reversible figure [14]. Contrary, slowly decreasing

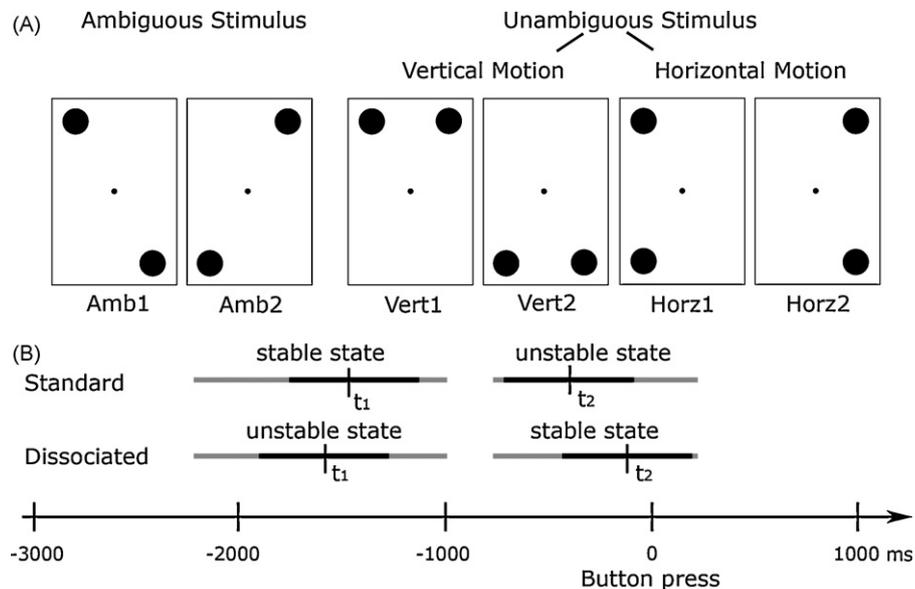
alpha activity preceding the perceptual reversal might mirror satiation of the neural network representing the currently perceived perceptual alternative and the trigger of a perceptual reversal when reaching a certain minimum of alpha activity, i.e. bottom-up processes accounting for multistable perception as originally proposed by Köhler [5,11,20]. 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 in the more cognitive demands of perceptual multistability [7]. Taken together, the results of our research group imply that multistable perception elicits superimposed and selectively distributed oscillatory networks of various frequency ranges which are proposed to contribute to the functional integration of sensory and cognitive processes (for review e.g. [1]). Our results, therefore, point towards an integrative model of top-down and bottom-up processes accounting for an observer's subjective perceptual switch, which is in accordance with psychophysical and ERP data [12,13,16,21].

Importantly, Basar-Eroglu et al. have shown that the enduring increase of frontal gamma activity is not related to any motor behavior because it already occurs during passive viewing of a multistable percept [2]. Contrary, the delta- and alpha-response was observed time-locked to a button press indicating the perceptual

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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)  $t_1$  and  $t_2$  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  $t_1$  or  $t_2$ , black lines) and alpha (500 ms before  $t_1$  or  $t_2$ ) activity. When participants indicate perceptual reversals immediately, the perceptual unstable state occurs around  $t_2$  (*standard*). During the *dissociated* task condition the participants respond to perceptual reversals approximately after 1500 ms, i.e. the perceptual unstable state around  $t_1$  is separated from motor-related responses occurring during the perceptual stable state around  $t_2$ .

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).

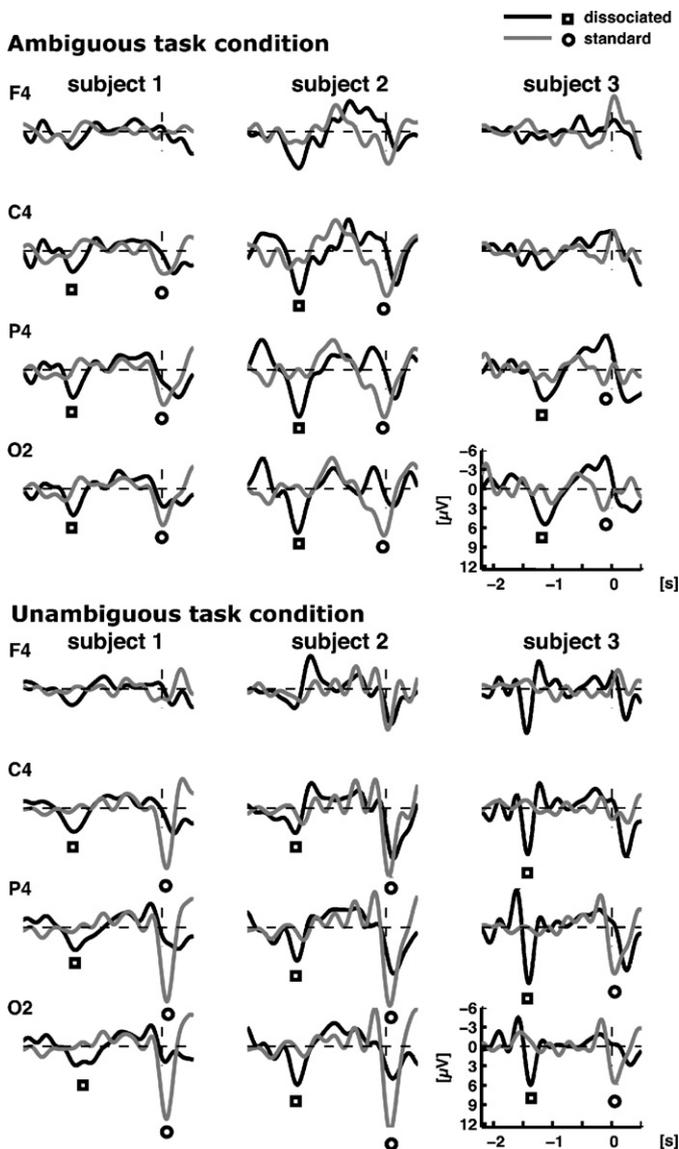
Fourteen right-handed volunteers (8 females) between 20 and 30 years (22.8, SD: 2.7) gave written consent on their participation, had normal or corrected-to-normal vision and reported to be free from neurological or psychiatric diseases. At the subjects viewing distance of 150 cm, the horizontal and vertical distance between possible occurrences of the dots comprising the visual stimuli was 2.4 cm (visual angle:  $0.92^\circ$ ) and 3.8 cm ( $1.45^\circ$ ), 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 applied each stimulus configuration was repeated after 500 ms (see Fig. 1A and [2,3] for further information).

For both, the *ambiguous* and *unambiguous* stimulus two instructional conditions were measured: (1) for the *standard* condition subjects were instructed to press a button immediately after the occurrence of a perceptual reversal. (2) For the *dissociated* condition subjects were asked to delay their motor response until the stimulus configuration during which the perceptual change was perceived re-occurred for the third time, i.e. the continuous flashing of the dots allowed the correct timing for the dissociation of the perceptual reversal and the motor response by 1500 ms.

The four experimental runs were pseudorandomised with the constraint 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  $t_1$  and  $t_2$ , respectively. The selected time windows comprise the perceptual instable 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  $t_1$  and  $t_2$ . For delta, mean values of the maximum positive deflection within  $-375$  ms before to 375 ms after  $t_1$  and  $t_2$  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



**Fig. 2.** Averaged delta response of three representative observers elicited during ambiguous (top) and unambiguous (bottom) pattern reversals. Zero marks the button press. Importantly, the timing of the reversal-related delta responses varies considerably between observers. For the standard task condition the reversal-related delta response occurs between  $-500$  and  $0$  ms with a parieto-occipital maximum (indicated by a circle). During the dissociated task condition the reversal-related delta response is observed around  $-1500$  ms (indicated by a square). Similar to the standard task condition the maximum of the reversal-related delta response is at parieto-occipital sites. Additionally, during the dissociated task condition a motor-related delta response occurs around the button press. The maxima of the motor-related response might be larger than or similar to the reversal-related responses at central electrode sites, however the response decreases posterior, thereby indicating a different topography when compared to the perceptual-related delta response (see text for further information and discussion).

activity were computed for the time window of  $500$  ms preceding  $t_1$  and  $t_2$ . Computation of RMS values allowed to analyze the total oscillatory alpha activity (the sum of evoked and induced activity [4]).

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 *dissociated*), 2 time windows (according to  $t_1$  and  $t_2$ , 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-*

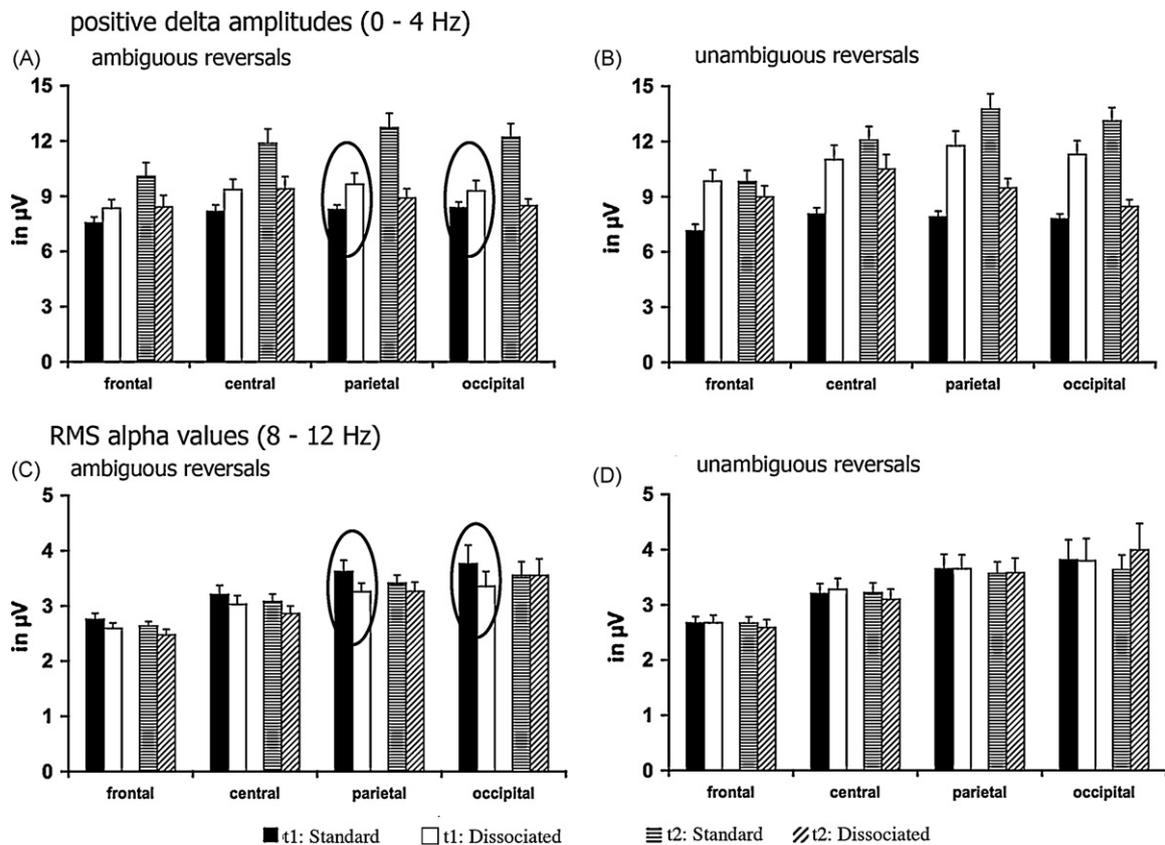
*ous/dissociated* run were corrupted. Therefore, 13 participants were included in the analysis of each stimulus type. Greenhouse-Geisser corrected probabilities are reported where needed. For post hoc comparisons by  $t$ -tests  $p$ -values are corrected using the Bonferroni procedure.

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:  $F(1,12) = 5.4$ ,  $p < .05$ ). Furthermore, the delta response is generally larger around the button press ( $t_2$ ) than during the preceding time window where no motor response occurs ( $t_1$ ; time window:  $F(1,12) = 12.8$ ,  $p < .01$ ). However, closer inspection of the data revealed that the enhancement for the *standard* condition is only observable around  $t_2$ , while around  $t_1$  the delta response is larger for the *dissociated* condition as reflected in a significant time window  $\times$  condition interaction ( $F(1,12) = 13.8$ ,  $p < .01$ ;  $t_2$ -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  $\times$  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  $t_2$ -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  $\times$  condition  $\times$  ROI interaction:  $F(3,36) = 6.9$ ,  $p < .01$ ;  $t_2$ -delta response for *standard* > *dissociated* at parietal and occipital ROIs:  $p < .05$  for all post hoc comparisons; see Figs. 2 and 3A).

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 ( $t_2$ ) than during the preceding time window ( $t_1$ ; 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  $t_1$  and larger around  $t_2$  as reflected in a significant time window  $\times$  condition interaction ( $F(1,12) = 26.4$ ,  $p < .001$ ;  $p < .01$  for post hoc comparisons). Around  $t_1$  all ROIs display larger delta responses for the *dissociated* condition. Contrary, the enhancement of the  $t_2$ -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  $\times$  ROI interaction:  $F(3,36) = 15.2$ ,  $p < .001$ ; time window  $\times$  condition  $\times$  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* pattern 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:  $F(1,12) = 8.3$ ,  $p < .05$ ). Importantly, the task related alpha desynchronisation for the *dissociated* condition is predominantly accounted for by parieto-occipital ROIs preceding  $t_1$  and by the central ROI preceding  $t_2$  (time window  $\times$  condition  $\times$  ROI interaction:  $F(3,36) = 6.3$ ,  $p < .05$ ,  $p < .05$  for all post hoc comparisons, see Fig. 3C).



**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).

Similar, during *unambiguous* pattern reversals, the alpha-response also has a fronto-central minimum (ROI:  $F(3,36) = 14.3$ ,  $p < .01$ ; frontal < central, parietal, occipital and central < parietal:  $p < .01$  for all post hoc comparisons). However, task conditions differ only preceding t2 at the occipital ROI, with only the *standard* condition showing alpha desynchronisation, i.e. smaller RMS-values than for the *dissociated* condition. This is indicated by a time window  $\times$  condition  $\times$  ROI interaction ( $F(3,36) = 8.2$ ,  $p < .01$ , see Fig. 3D).

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 occurred around 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 in 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.

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### References

- [1] E. Basar, Oscillations in "brain-body-mind"—a holistic view including the autonomous system, *Brain Res.* 1235 (2008) 2–11.
- [2] C. Basar-Eroglu, D. Strüber, P. Kruse, E. Basar, M. Stadler, Frontal gamma-band enhancement during multistable visual perception, *Int. J. Psychophysiol.* 24 (1996) 113–125.
- [3] C. Basar-Eroglu, D. Strüber, M. Stadler, P. Kruse, E. Basar, Multistable visual perception induces a slow positive EEG wave, *Int. J. Neurosci.* 73 (1993) 139–151.
- [4] C.S. Herrmann, D. Senkowski, S. Rottger, Phase-locking and amplitude modulations of EEG alpha: two measures reflect different cognitive processes in a working memory task, *Exp. Psychol.* 51 (2004) 311–318.
- [5] U. Isoglu-Alkac, C. Basar-Eroglu, A. Ademoglu, T. Demiralp, M. Miener, M. Stadler, Alpha activity decreases during the perception of Necker cube reversals: an application of wavelet transform, *Biol. Cybern.* 82 (2000) 313–320.
- [6] U. Isoglu-Alkac, C. Basar-Eroglu, A. Ademoglu, T. Demiralp, M. Miener, M. Stadler, Analysis of the electroencephalographic activity during the Necker cube reversals by means of the wavelet transform, *Biol. Cybern.* 79 (1998) 437–442.
- [7] U. Isoglu-Alkac, D. Strüber, Necker cube reversals during long-term EEG recordings: sub-bands of alpha activity, *Int. J. Psychophysiol.* 59 (2006) 179–189.
- [8] K.H. Kim, J.H. Kim, J. Yoon, K.Y. Jung, Influence of task difficulty on the features of event-related potential during visual oddball task, *Neurosci. Lett.* 445 (2008) 179–183.
- [9] W. Klimesch, EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis, *Brain Res. Brain Res. Rev.* 29 (1999) 169–195.
- [10] W. Klimesch, R. Freunberger, P. Sauseng, W. Gruber, A short review of slow phase synchronization and memory: evidence for control processes in different memory systems? *Brain Res.* 1235 (2008) 31–44.
- [11] W. Köhler, *Dynamics in Psychology*, Liveright, New York, 1940.
- [12] J. Kornmeier, M. Bach, Early neural activity in Necker-cube reversal: evidence for low-level processing of a gestalt phenomenon, *Psychophysiology* 41 (2004) 1–8.
- [13] G.M. Long, T.C. Toppino, Enduring interest in perceptual ambiguity: alternating views of reversible figures, *Psychol. Bull.* 130 (2004) 748–768.
- [14] B. Mathes, D. Strüber, M.A. Stadler, C. Basar-Eroglu, Voluntary control of Necker cube reversals modulates the EEG delta- and gamma-band response, *Neurosci. Lett.* 402 (2006) 145–149.
- [15] G. Pfurtscheller, C. Neuper, G. Krausz, Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement, *Clin. Neurophysiol.* 111 (2000) 1873–1879.
- [16] M.A. Pitts, W.J. Gavin, J.L. Nerger, Early top-down influences on bistable perception revealed by event-related potentials, *Brain Cogn.* 67 (2008) 11–24.
- [17] J. Polich, Updating P300: an integrative theory of P3a and P3b, *Clin. Neurophysiol.* 118 (2007) 2128–2148.
- [18] D. Strüber, C. Basar-Eroglu, E. Hoff, M. Stadler, Reversal-rate dependent differences in the EEG gamma-band during multistable visual perception, *Int. J. Psychophysiol.* 38 (2000) 243–252.
- [19] D. Strüber, C. Basar-Eroglu, M. Miener, M. Stadler, EEG gamma-band response during the perception of Necker-cube reversals, *Vis. Cogn.* 8 (2001) 609–621.
- [20] D. Strüber, C.S. Herrmann, MEG alpha activity decrease reflects destabilization of multistable percepts, *Brain Res.* 14 (2002) 370–382.
- [21] D. Strüber, M. Stadler, Differences in top-down influences on the reversal rate of different categories of reversible figures, *Perception* 28 (1999) 1185–1196.