

# Effects of mood on the speed of conscious perception: behavioural and electrophysiological evidence

Christof Kuhbandner,<sup>1,\*</sup> Simon Hanslmayr,<sup>2,\*</sup> Markus A. Maier,<sup>3</sup> Reinhard Pekrun,<sup>1</sup> Bernhard Spitzer,<sup>2</sup> Bernhard Pastötter,<sup>2</sup> and Karl-Heinz Bäuml<sup>2</sup>

<sup>1</sup>Department of Psychology, University of Munich, Germany, <sup>2</sup>Department of Experimental Psychology, Regensburg University, Germany, and <sup>3</sup>Department of Psychology, Stony Brook University, USA

**When a visual stimulus is quickly followed in time by a second visual stimulus, we are normally unable to perceive it consciously. This study examined how affective states influence this temporal limit of conscious perception. Using a masked visual perception task, we found that the temporal threshold for access to consciousness is decreased in negative mood and increased in positive mood. To identify the brain mechanisms associated with this effect, we analysed brain oscillations. The mood-induced differences in perception performance were associated with differences in ongoing alpha power (around 10 Hz) before stimulus presentation. Additionally, after stimulus presentation, the better performance during negative mood was associated with enhanced global coordination of neuronal activity of theta oscillations (around 5 Hz). Thus, the effect of mood on the speed of conscious perception seems to depend on changes in oscillatory brain activity, rendering the cognitive system more or less sensitive to incoming stimuli.**

**Keywords:** emotion; consciousness; brain oscillations; affective states; visual masking

The ability to extract visual information from the environment with a fast perceptual speed should be advantageous for an organism, particularly if a situation is experienced as highly negative. However, there seems to exist a temporal limit for the conscious perception of a stimulus. Numerous studies using visual masking techniques have shown that a stimulus fails to reach consciousness when it is too quickly followed in time by a masking stimulus, indicating that conscious perception requires a minimum amount of time for stimulus processing (for reviews, see Breitmeyer, 1984; Enns and Di Lollo, 2000). This temporal limit for access to consciousness is generally explained by the assumption that conscious perception presupposes a comparison between (1) ascending stimulus-induced low-level activity and (2) descending high-level activity representing a perceptual hypothesis (e.g. Grossberg, 1995; Lamme and Roelfsema, 2002). Presenting a second stimulus before a match is reached disrupts the integration between bottom-up inputs and top-down signals, as the second stimulus replaces the activity generated by the target stimulus in early visual processing areas (Di Lollo *et al.*, 2000).

On the other hand, there are numerous anecdotal accounts of people threatened with mortal danger reporting

a dramatically increased speed of conscious perception in such highly emotional situations. For instance, Noyes and Kletti (1976) found that people who survived a life-threatening experience described an increased speed of perception and an apparent slowing down of time during the experience. This finding suggests that affective states may influence the time required to form a conscious percept. Also, previous research has shown that highly arousing emotional stimuli are detected quickly and prioritized for attentive processing (e.g. Öhman *et al.*, 2001; Anderson, 2005). However, direct evidence is lacking on the influence of mood on the speed of conscious perception, independent of the emotional content of the stimuli.

Although mood effects on the speed of conscious perception have not been examined, it is well established that mood modulates the general style of processing information [for reviews, see Clore and Huntsinger (2007) and Fiedler (2001)]. Negative mood promotes a bottom-up driven processing style by focusing processing on incoming information and limiting the number of activated concepts in memory. For instance, it has been demonstrated that individuals in negative moods focus more on local stimulus features of perceptual experience at the expense of gist (e.g. Gasper and Clore, 2002), show an enhanced ability to identify targets in a rapid visual sequence (e.g. Jefferis *et al.*, 2008) and are less likely to activate concepts in memory associated with given stimuli (e.g. Bäuml and Kuhbandner, 2007; Storbeck and Clore, 2008). In contrast, positive mood promotes a top-down driven processing style characterized

Received 17 June 2008; Accepted 17 February 2009

Advance Access publication 7 April 2009

This work was supported by a grant of the institutional strategy LMUexcellent within the framework of the German Excellence Initiative.

Correspondence should be addressed to Christof Kuhbandner, Department of Psychology, University of Munich, Munich, Germany. E-mail: christof.kuhbandner@psy.lmu.de.

\*These authors contributed equally to this work.

by strong and more widespread activation of stored knowledge, at the cost of weaker bottom-up inputs. For instance, individuals in positive moods have been shown to process incoming information in a global manner at the expense of local details (e.g. Fredrickson and Branigan, 2005), to use schemas and stereotypes to fill in blanks during information processing (e.g. Bodenhausen, 1993; Bless *et al.*, 1996), to activate unusual concepts associated with given stimuli (e.g. Bolte *et al.*, 2003) and to reactivate intentionally forgotten memories (Bäuml and Kuhbandner, 2009).

It can be assumed that mood-induced differences in processing style also affect the time required to form a conscious percept. By inducing a bottom-up driven processing style, negative mood should decrease the time needed for achieving a match between bottom-up inputs and top-down signals due to strong stimulus-induced bottom-up activity and reduced interference from inappropriate higher-level concepts. In contrast, by inducing a top-down driven processing style, positive mood should increase the time required to form a stable match between low-level and high-level activity due to weak bottom-up activity and enhanced interference, thus slowing down conscious perception.

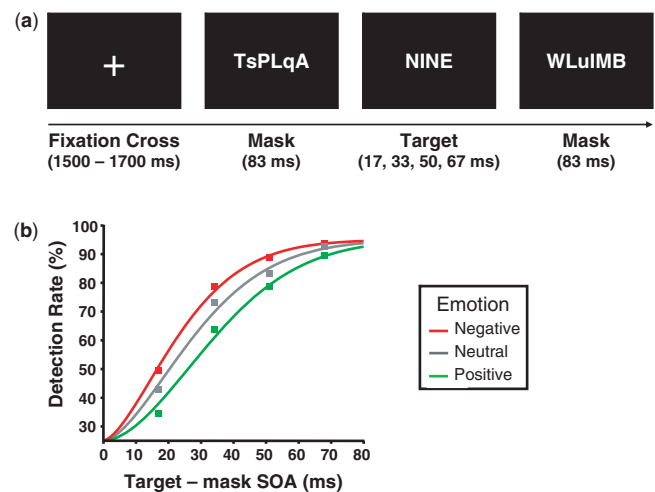
On a neurophysiological level, the effect of mood on conscious perception may be associated with mood-induced alterations in the general brain state. Several studies suggest that the amplitude of ongoing activity in the alpha frequency range (around 10 Hz) modulates the way incoming information is processed (Ray and Cole, 1985; Klimesch *et al.*, 2007). While a decrease in alpha activity enhances the processing of incoming stimuli and facilitates visual perception, an increase in alpha activity enhances the processing of representations stored in memory and impairs visual perception (Ergenoglu *et al.*, 2004; Hanslmayr *et al.*, 2005, 2007; Thut *et al.*, 2006). Thus, mood may affect conscious perception by inducing changes in the alpha activity, rendering the cognitive system more or less sensitive to incoming stimuli. Such a finding would not only explain the effects of mood on conscious perception, but also clarify the above-cited findings that affective states modulate the style of processing by inducing predominantly stimulus-driven processing during negative mood and predominantly knowledge-driven processing during positive mood [for a review, see Fiedler (2001)].

If mood influences the formation of a conscious percept, then mood should also affect the global coordination of neuronal activity after stimulus presentation. It has been proposed that conscious perception is associated with a synchronization of neuronal activity in early sensory areas and higher cortical areas (Dehaene *et al.*, 2006; Lamme, 2006). Whereas unperceived stimuli induce synchronization in local neuronal assemblies (e.g. Dehaene *et al.*, 1998; Melloni *et al.*, 2007), conscious perception additionally requires long-range synchronization between distant neuronal assemblies (e.g. Rodriguez, 1999; Melloni *et al.*, 2007).

Accordingly, mood-induced variations in the speed of conscious perception may also be accompanied by changes in the amount of stimulus-induced long-range synchronization after the presentation of a stimulus.

The aim of the present study was to investigate whether the affective state of an individual affects the speed of conscious perception. Additionally, we sought to determine the brain mechanisms associated with possible mood effects by analysing brain oscillations. To examine the time required to form a conscious percept as a function of mood, we varied the delay between the onset of a target stimulus and the onset of a subsequent mask, referred as the stimulus onset asynchrony (SOA), in a visual perception task (Figure 1a). At very short SOAs, conscious perception is usually absent. With increasing SOA, the ability to detect a target increases until it is clearly visible at longer SOAs (Breitmeyer, 1984; Enns and Di Lollo, 2000). To examine the influence of mood, we induced a positive, negative, or neutral mood state by presenting different film clips directly before participants performed the perception task. It is well known that watching these film clips is a highly effective method to induce intense mood states (Rottenberg *et al.*, 2007).

To analyse brain oscillations, we recorded electroencephalographic (EEG) signals of the participants while they performed the perception task. To determine whether the effect of mood on perception is associated with alterations in the general brain state, we analysed ongoing neuronal activity before a stimulus was presented. Additionally, we analysed brain oscillations after stimulus presentation. This was done to determine whether mood indeed affected the ability to consciously perceive rapidly masked stimuli.



**Fig. 1** Stimuli and behavioural results. (a) Example of one experimental trial. After the presentation of a fixation cross, the following three visual stimuli appeared successively, centred on the same screen location: a random-letter-string mask, a number word and another mask. The presentation duration of the number word was systematically varied. Subjects were told to press one of four buttons to indicate which number-word they saw. (b) The mean percentage of correct responses is plotted for the four different target durations in each of the three mood conditions. The lines represent the psychometric Weibull functions for the three mood conditions.

As conscious perception is associated with a synchronization of neuronal activity in early sensory areas and higher cortical areas, we expected to find differences in large-scale synchronization after stimulus presentation. In the masked visual perception task used in the present study, one out of four number words had to be detected. Accordingly, the process of perceiving a presented stimulus required the comparison of the activity generated by a stimulus with a working memory template containing the four possible number words. As working memory processes are commonly associated with oscillations in the theta frequency (Sarnthein *et al.*, 1998; Raghavachari *et al.*, 2001), long-distance synchronization should be mainly found in the theta frequency range.

## METHOD

### Participants and design

Thirty-nine neurologically normal undergraduate students (27 females;  $M$  age = 23.2 years,  $s.d.$  = 3.2) at the University of Munich participated in the experiment. Thirteen participants were randomly assigned to each of three mood conditions (positive, negative and neutral).

### Materials and procedure

All stimuli were presented in white on a black background at the centre of the computer screen (70 Hz refresh) using ERTS software (Experimental Run Time System, Version 3.18, 1996, J. Beringer, Germany). Each trial started with a fixation cross displayed in the middle of the screen with a random duration of 1300–1700 ms. Thereafter, a mask consisting of a random-letter-string (e.g. TsPlqA) was presented for 83 ms. After the mask, a target stimulus was shown at the same screen location, which was one out of four possible four-letter number words, 'EINS' (one), 'VIER' (four), 'ACHT' (eight) and 'NEUN' (nine). After the target, a random-letter-string mask was presented again for 83 ms. The duration of the target could take one out of four values, leading to SOAs of 17, 33, 50 and 67 ms. The participants were instructed to give their response as fast as possible after the onset of the second mask by pressing one of four buttons with their dominant hand, indicating which target number they had perceived. The sequence of number words and SOAs was randomized. Each participant performed 160 trials, 40 trials per SOA (for similar methods, see Dehaene *et al.*, 1998; Sergent and Dehaene, 2004).

To induce a mood state, a positive, negative or neutral film clip was presented directly before participants started the perception task. The clips were drawn from a set of standardized emotional film stimuli developed to reliably elicit emotional states in the laboratory (Rottenberg *et al.*, 2007). The positive film clip (2 min 31 s) was a comedy segment from the commercial movie 'When Harry met Sally.' The negative film clip (2 min 51 s) depicted a death scene from the commercial movie 'The Champ.' The positive and negative film clips were comparable regarding

unemotional characteristics (e.g. length, presence of human figures, picture motion and complexity; see Rottenberg *et al.* (2007), for a detailed description). The neutral film clip ('Sticks'; 2 min 30 s) presented a dynamic display of geometric shapes and has been shown to elicit a neutral affective state characterized by low levels of positive and negative emotions.

Psychometric (Weibull) functions were fitted using the Psignifit software package (Wichmann, 2001a) to determine the threshold SOA at the mid-point of the best fitting Weibull function ( $F^{-1}_{0.5}$ ). For statistical comparisons, Monte-Carlo tests (Wichmann, 2001b) based on 10,000 simulations were used.

### EEG recording and analyses

The EEG was recorded from 30 Ag–AgCl electrodes positioned according to the extended 10–20 system. The EEG signals were recorded against a reference electrode placed at FCz and were later re-referenced against a common average reference. The vertical and the horizontal electrooculogram (EOG) were recorded from two additional channels to control for eye movements and blinks. Sampling rate was 200 Hz. Impedances of all channels were kept below 10 kOhm. Prior to data analysis, EEG data were corrected for EOG artefacts.

The data was filtered in a time-window of 1 s prestimulus to 1 s poststimulus and a frequency range of 4–30 Hz. Time-frequency resolution was set to 25 ms and 2 Hz. All statistical comparisons regarding the effects of mood on ongoing EEG activity were computed for the prestimulus interval ranging from –500 ms prior stimulus presentation to stimulus onset. Prior to statistical comparisons, the time frequency data were collapsed over the prestimulus interval (–500 ms to 0 ms), and alpha power was pooled for a frequency range of 7–12 Hz. In order to account for the high variance in alpha power between the participants, all power values were calculated as percent change according to a resting condition (eyes open), which was recorded before the experiment started and before the participants watched the film clips. No difference in this baseline condition was observed between the three experimental groups,  $F(2, 36) = 0.039$ ,  $P = 0.96$ . Prior to statistical analysis, the power values were pooled over the electrode sites in order to obtain four locations: Frontal (electrodes: Fp1, Fp2, F3, F4, F7, F8 and Fz); central (electrodes: FC3, FC4, FCz, C3, Cz and C4), parietal (electrodes: O1, O2, Oz, P7, P8, P3, P4, Pz, CP3, CP4 and CPz) and temporal (electrodes: FT7, FT8, TP7, TP8, T7 and T8).

To analyse large-scale synchronization across recording sites, we calculated the phase locking value (PLV) for each electrode pair in the time window of 1 s prior stimulus presentation to 1 s after stimulus presentation. In order to exclude phase-coupling due to a common underlying source, the raw EEG data was transformed into the current source density (CSD) profiles prior to PLV calculation. The CSD

represents the second spatial derivative of the voltage distribution in the tissue and is implicitly reference free. Several prior studies have shown that such an approach largely diminishes the contribution of volume conduction (e.g. Lachaux *et al.*, 1999). The PLV is a measure of phase coupling between two electrodes and ranges from 0 (no phase coupling) to 1 (perfect phase coupling; Lachaux *et al.*, 1999). Prior to statistical analysis, the PLV values were baseline corrected and transformed into a synchronization index (SI). The SI represents the percent change of the poststimulus PLV compared with a prestimulus baseline (−500 to −100 ms). To determine the frequency bands that were most reactive to the differences between the latencies (17 ms vs 67 ms), the grand averages of SI were calculated for all electrode pairs (495; see Figure 3a).

For statistical comparisons, non-parametric Wilcoxon tests were calculated for each electrode pair ( $P$  level set to 0.01). To account for multiple testing, a randomization procedure based on 5000 permutation runs was carried out, which was already used in several other studies (Hanslmayr *et al.*, in press, 2007). To evaluate the effects of emotion on phase-synchronization, we first calculated the SI for those electrode pairs that exhibited significant differences between the two latencies (17 ms vs 67 ms). Thereafter, a non-parametric Mann–Whitney test was carried out to compare the mean theta SI (0–500 ms) between the positive and the negative mood conditions.

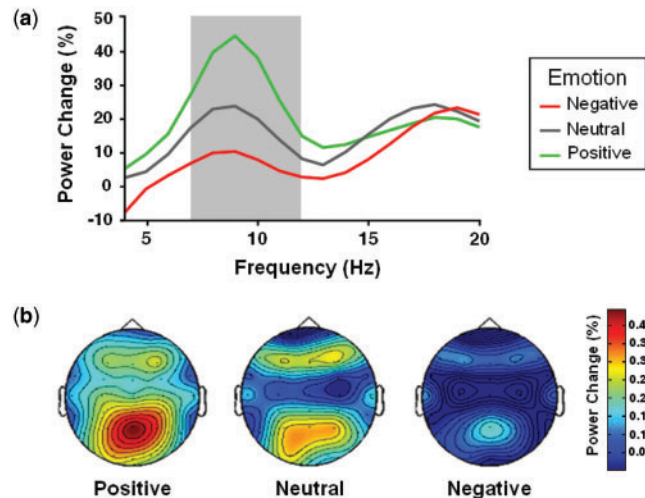
## RESULTS

### Behavioural results

As can be seen in Figure 1b, perception performance varied depending on the mood state induced before the task. To determine the threshold for the access to consciousness for each mood condition, separate psychometric (Weibull) functions were fitted to the data (Wichmann, 2001a). The estimated threshold SOA was shortest in the negative mood condition (22 ms), middle in the neutral mood condition (27 ms) and longest in the positive mood condition (33 ms). Pair-wise Monte-Carlo tests (Wichmann, 2001b) confirmed that the Weibull functions for both the negative and the positive mood conditions were significantly different from the neutral mood condition ( $P < 0.025$ ,  $P < 0.005$ , respectively). Thus, the affective state influenced the time required to form a conscious percept, thereby reducing the threshold duration for conscious perception during negative mood and increasing the threshold duration during positive mood.

### EEG results

As shown in Figure 2a, differences between mood conditions were most evident in the alpha frequency band (7–12 Hz). To determine whether mood affected ongoing alpha activity, a 3 (mood: positive, negative, neutral)  $\times$  4 (location: frontal, central, parietal and temporal) analysis of variance (Greenhouse–Geisser corrected) was conducted. The analysis

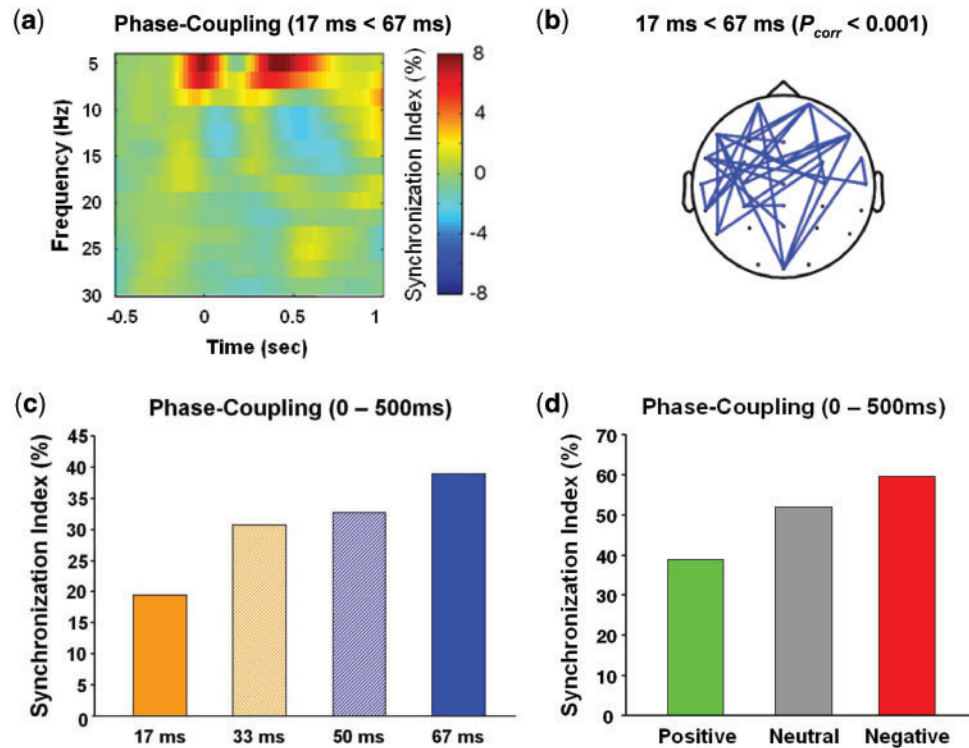


**Fig. 2** Alpha activity in the prestimulus interval. (a) Frequency plot of power for electrode Pz as an example. The y-axis indicates the percent change relative to the resting condition. Differences between mood conditions were most evident in the alpha frequency range. The grey bar indicates the frequency window used for statistics. (b) Scalp maps for the three mood conditions. The colour indicates the increase in alpha power. The maps show that prestimulus alpha power was lowest in negative mood, middle in neutral mood and highest in positive mood. Differences were strongest at occipital electrode sites, indicating that mood effects were largely restricted to visual processing areas.

revealed a main effect of mood,  $F(2, 36) = 3.98$ ,  $P < 0.05$ . Additional linear contrast analysis showed that alpha power increased linearly from negative to positive mood induction,  $F(1, 36) = 7.69$ ,  $P < 0.01$ , indicating that ongoing relative alpha power was lowest in negative moods, middle in neutral moods and highest in positive moods. Differences in alpha power were evident across multiple electrodes and highest at parietal and occipital recording sites (Figure 2b), as indicated by a significant interaction between the factors of mood and location,  $F(6, 108) = 2.92$ ,  $P < 0.05$ . The interaction revealed that mood effects were largely restricted to visual processing areas. These results indicate that the effect of the affective state on perception is associated with changes in ongoing alpha activity, which is known to facilitate or restrict the entering of external stimuli into the cognitive system.

Next, we analysed the synchronization of neuronal activity after stimulus presentation. To determine whether large-scale synchronization in the theta range generally discriminated between perceived and unperceived stimuli, we first analysed phase synchronization of induced oscillations across all electrodes and frequency ranges for short (mainly unperceived) and long (mainly perceived) target durations independent of the affective state. As can be seen in Figure 3a and b, differences in synchronous activity between short and long-target durations were mainly found in the theta frequency range, and mean phase synchrony was highly different depending on target duration. Long-target durations elicited significantly stronger theta phase coupling than the short target duration in the time window 0–500 ms





**Fig. 3** Phase synchrony during stimulus processing. (a) The difference in phase synchronization between short (mainly unseen) and long (mainly seen) target durations is plotted. The time-frequency plot shows that the strongest differences were observed in the theta frequency range (4–8 Hz). (b) The scalp map shows that significantly increased phase coupling was mainly found between occipital, parietal and frontal electrode pairs. (c) Phase-coupling for those electrode pairs that exhibited a significant difference between long and short-target durations is shown. Phase synchrony increases linearly with increasing target duration. (d) Phase synchronization in the positive, neutral and negative mood conditions is plotted for the same electrode pairs. Phase synchrony was strongest in the negative mood condition and weakest in the positive mood condition.

after the presentation of a stimulus ( $P_{corr} < 0.001$ ; see ‘Methods’ section). The increase in phase-synchronization of theta oscillations was mainly found between frontal, temporal and occipital electrode sites (Figure 3b). Linear contrast analysis revealed that the theta phase-coupling between these electrode sites increased linearly with target duration,  $F(1, 38) = 107.28$ ,  $P < 0.001$ . These results suggest that conscious perception may be related to the coordination between activity generated by a stimulus and activity of descending high-level representations held active in working memory.

In the next step, we examined whether the amount of phase coupling was modulated by the mood state by analysing the difference in theta synchronization between the negative and positive mood conditions. Because a two-way ANOVA with the factors SOA (17, 33, 50 and 67 ms) and MOOD (positive, neutral, negative) revealed no significant interaction,  $F(6, 108) = 0.85$ ,  $P > 0.50$ , we collapsed the phase coupling values across the four SOA conditions. As can be seen in Figure 3d, synchronization was highest in the negative, moderate in the neutral and lowest in the positive mood condition. To compare the mean theta synchronization (0–500 ms) between the positive and the negative mood condition, a non-parametric Mann–Whitney test was carried out. The analysis yielded a significant difference,

$z = 2.18$ ,  $P < 0.05$ . The effect of mood thus mimicked the effect of target duration on the amount of global synchronization, with negative mood increasing and positive mood decreasing phase-coupling. These results suggest that the mood-induced enhanced or restricted entering of external stimuli into the cognitive system determined the ability to consciously perceive masked stimuli.

## DISCUSSION

The results of the present study indicate that mood has a strong influence on our conscious perception of external stimuli. By applying psychometric analysis to the behavioural data from a masked visual perception task, we have shown that the temporal threshold to perceive a visual stimulus is increased after positive mood induction and decreased after negative mood induction. From an evolutionary view, such an effect may be highly adaptive. In threatening situations, for example, high-perceptual speed is advantageous as fast extraction of critical information from the environment is a beneficial quality (Öhman et al., 2000). In contrast, positive mood usually signals safe situations wherein fast and accurate monitoring of the external world is not necessary, implying that we can impose our internalized representations derived from past experiences on our perception of the environment (Fredrickson, 2001).

Such an interpretation is consistent with the assumption that affective states modulate perception by inducing a bottom-up style of processing information in negative moods and by enhancing the processing of top-down representations in positive moods (Fiedler, 2001). In the present study, an increase of alpha power above baseline levels was observed for all conditions (Figure 2a), whereby the lowest increase occurred after negative mood induction and the highest increase occurred after positive mood induction. A number of previous studies using several different methodologies have demonstrated that high-alpha power over posterior recording sites inhibits cortical excitability to visual stimulation. For example, TMS studies showed that high levels of alpha power inhibit cortical responses to TMS pulses (Romei *et al.*, 2008a, b; Sauseng *et al.*, in press). Similarly, other studies reported high-alpha power to be negatively related to the perception of shortly presented stimuli (Ergenoglu *et al.*, 2004; Hanslmayr *et al.*, 2005, 2007; Thut *et al.*, 2006). Investigations of the relation of alpha oscillations to spatial shifts of attention have shown that an increase in alpha power beyond baseline levels index the inhibition of distracting visual information (Kelly *et al.*, 2007; Rihs *et al.*, 2007). Together, these findings have led to the hypothesis that alpha oscillations represent an active top-down driven filter mechanism by regulating excitation and inhibition of the cortex (Klimesch *et al.*, 2007). Our results thus suggest that mood induction regulates the gain of visual processing areas, with negative mood facilitating and positive mood inhibiting bottom-up processing.

Several studies indicate that emotional states are also associated with differences in prefrontal alpha activity, with increased left-sided activation (i.e. lower alpha power) during the experience of positive approach emotions and increased right-sided activation during the experience of negative withdrawal emotions (e.g. Davidson *et al.*, 1990; Tomarken *et al.*, 1990). In the present study, no differences in prefrontal alpha activity were observed between the positive and the negative mood condition. As the aim of our study was to manipulate the valence of a mood state, this finding is in line with recent research suggesting that emotions may be lateralized according to the concepts of approach and avoidance, rather than valence (e.g. Davidson, 2004). Interestingly, several studies indicate that inducing approach or avoidance states by the enactment of approach or avoidance behaviour can also influence cognitive processing (e.g. Förster *et al.*, 2006). Thus, one line of interesting future research may be to determine the influence of differences in approach-withdrawal tendencies (and in the associated emotions) on the speed of conscious perception and to examine the relationship between prefrontal alpha asymmetry and perceptual encoding.

Current perception theories indicate that conscious perception emerges from the integration of stimulus-induced bottom-up inputs and concept-driven top-down signals representing a perceptual hypothesis (Di Lollo *et al.*, 2000;

Lamme and Roelfsema, 2002; Dehaene *et al.*, 2006). From the perspective of these theories, a change in processing style should affect the speed of conscious perception by influencing the ease of achieving a match between ascending low-level activity and a top-down perceptual hypothesis held active in working memory. On a neurophysiological level, such a match is assumed to be accompanied by long-range synchronization of neuronal activity. To examine whether mood affected this global coordination of neuronal activity, stimulus-induced synchronization between different brain areas was examined. In EEG data, such a match should mainly be observed in the theta frequency range as synchronization in this frequency band is closely related to working memory processes (Sarnthein *et al.*, 1998; Raghavachari *et al.*, 2001). Our results indicate that items which were presented above perception threshold (67 ms) induced stronger phase-coupling between electrodes across widely distributed regions of the brain than items that were presented below threshold (17 ms). Moreover, phase-coupling between the same electrode pairs was modulated by mood; negative mood induced stronger phase-coupling than positive mood. These results suggest that mood modulates the network that synchronizes in the theta frequency range in order to promote conscious perception.

The present study addressed the question of whether affective states influence the speed of conscious perception, independent of the emotional content of incoming stimuli. In contrast, several previous studies addressed the question of whether emotional stimuli are detected quickly and prioritized for conscious processing, independently of people's affective state. For instance, using a visual search task Öhman *et al.* (2001) demonstrated that fearful stimuli are detected faster than neutral stimuli. Using an attentional blink task, Anderson and Phelps (2001) showed that the impairment typically found in conscious perception for stimuli presented shortly after a preceding stimulus is substantially alleviated for negative stimuli. Interestingly, whereas it was initially assumed that these effects are driven by valence with a prioritization of negative information, recent research suggests that rather the arousal value of a stimulus is most predictive of prioritized processing (e.g. Keil and Ihssen, 2004; Anderson, 2005). Even more pertinent to the present study, Maljkovic and Martini (2005) showed that the speed of stimulus processing is enhanced for highly arousing stimuli in a Rapid Serial Visual Presentation Task. The findings of the present study indicate that differences in valence predict the speed by which neutral stimuli are perceived. However, the role of arousal at the emotional content level of a stimulus suggests that differences in arousal states may also affect the perceiving of neutral stimuli. Indeed, a recent study examined the effect of mood on the ability to identify targets in a rapid visual sequence by manipulating both valence and arousal (Jefferies *et al.*, 2008). Individuals with negative affect and low arousal showed a reduction of attentional blink

effects. However, attentional blink effects were strongest for individuals with negative affect and high arousal. One avenue for interesting future research will thus be to determine the role of arousal in the ability to perceive masked neutral stimuli.

Taken together, the results of this study demonstrate that negative mood can speed up and positive mood can slow down the formation of a conscious percept. The finding that these effects are associated with mood-induced changes in ongoing alpha activity suggests that the effect of mood on perception is based on mood-induced changes in the way information is processed, with negative mood facilitating bottom-up processing and positive mood top-down processing. Thus, mood may have a stronger influence on how we perceive the world than was previously believed.

## REFERENCES

- Anderson, A.K. (2005). Affective influences on the attentional dynamics supporting awareness. *Journal of Experimental Psychology: General*, 134, 258–81.
- Anderson, A.K., Phelps, E.A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, 411, 305–9.
- Bäumel, K.-H., Kuhbandner, C. (2007). Remembering can cause forgetting—but not in negative moods. *Psychological Science*, 18, 111–5.
- Bäumel, K.-H., Kuhbandner, C. (2009). Positive moods can eliminate intentional forgetting. *Psychonomic Bulletin and Review*, 16, 93–8.
- Bless, H., Clore, G.L., Schwarz, N., Golisano, V., Rabe, C., Wolk, M. (1996). Mood and the use of scripts: does a happy mood really lead to mindlessness? *Journal of Personality and Social Psychology*, 71, 665–79.
- Bodenhausen, G.V. (1993). Emotions, arousal, and stereotypic judgments: a heuristic model of affect and stereotyping. In: Mackie, D., Hamilton, D., editors. *Affect, cognition, and stereotyping: interactive processes in group perception*. New York: Academic Press, pp. 13–37.
- Bohle, A., Goschke, T., Kuhl, J. (2003). Emotion and intuition: effects of positive and negative mood on implicit judgments of semantic coherence. *Psychological Science*, 14, 416–21.
- Breitmeyer, B.G. (1984). *Visual Masking: An Integrative Approach*. New York: Oxford University Press.
- Clore, G.L., Huntsinger, J.R. (2007). How emotions inform judgment and regulate thought. *Trends in Cognitive Sciences*, 11, 393–9.
- Davidson, R.J. (2004). What does the prefrontal cortex “do” in affect: perspectives on frontal EEG asymmetry research. *Biological Psychology*, 67, 219–33.
- Davidson, R.J., Ekman, P., Saron, C., Senulis, J., Friesen, W.V. (1990). Approach/withdrawal and cerebral asymmetry: emotional expression and brain physiology, part I. *Journal of Personality and Social Psychology*, 58, 330–41.
- Dehaene, S., Changeux, J.P., Naccache, L., Sackur, J., Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, 10, 204–11.
- Dehaene, S., Naccache, L., LeClecq, H.G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P.-F., Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature*, 395, 597–600.
- Di Lollo, V., Enns, J.T., Rensink, R.A. (2000). Competition for consciousness among visual events: the psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General*, 129, 481–507.
- Enns, J.T., Di Lollo, V. (2000). What’s new in visual masking? *Trends in Cognitive Sciences*, 4, 345–52.
- Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, 20, 376–83.
- Fiedler, K. (2001). Affective states trigger processes of assimilation and accommodation. In: Martin, L.L., Clore, C.L., editors. *Theories of Mood and Cognition: A User’s Guidebook*. Mahwah, NJ: Erlbaum, pp. 86–98.
- Förster, J., Friedman, R., Özsel, A., Denzler, M. (2006). Enactment of approach and avoidance behavior influences the scope of perceptual and conceptual attention. *Journal of Experimental Social Psychology*, 42, 133–46.
- Fredrickson, B.L. (2001). The role of positive emotions in positive psychology: the broaden-and-build theory of positive emotions. *American Psychologist*, 56, 218–26.
- Fredrickson, B.L., Branigan, C. (2005). Positive emotions broaden the scope of attention and thought-action repertoires. *Cognition and Emotion*, 19, 313–32.
- Gasper, K., Clore, G.L. (2002). Attending to the big picture: mood and global versus local processing of visual information. *Psychological Science*, 13, 34–40.
- Grossberg, S. (1995). The attentive brain. *American Scientific*, 83, 438–49.
- Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C.S., Bäumel, K.-H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage*, 37, 1465–73.
- Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters*, 375, 64–8.
- Hanslmayr, S., Spitzer, B., Bäumel, K.-H. (in press). Brain oscillations dissociate between semantic and non-semantic encoding of episodic memories. *Cerebral Cortex*.
- Jefferies, L.N., Smilek, D., Eich, E., Enns, J.T. (2008). Emotional valence and arousal interact in the control of attention. *Psychological Science*, 19, 290–5.
- Keil, A., Ihssen, N. (2004). Identification facilitation for emotionally arousing verbs during the attentional blink. *Emotion*, 4, 23–35.
- Kelly, S.P., Lalor, E.C., Reilly, R.B., Foxe, J.J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *Journal of Neurophysiology*, 95, 3844–51.
- Klimesch, W., Sauseng, P., Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, 53, 63–88.
- Lachaux, J.P., Rodriguez, E., Martinerie, J., Varela, F.J. (1999). Measuring phase synchrony in brain signals. *Human Brain Mapping*, 8, 194–208.
- Lamme, V. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, 10, 494–501.
- Lamme, V.A., Roelfsema, P.R. (2002). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 14, 1044–53.
- Maljkovic, V., Martini, P. (2005). Short-term memory for scenes with affective content. *Journal of Vision*, 5, 215–29.
- Melloni, L., Molina, C., Pena, M., Torres, D., Singer, W., Rodriguez, E. (2007). Synchronization of neural activity across cortical areas correlates with conscious perception. *Journal of Neuroscience*, 27, 2858–2865.
- Noyes, R., Kletti, R. (1976). Depersonalization in the face of life-threatening danger: a description. *Psychiatry*, 39, 19–27.
- Öhman, A., Flykt, A., Esteves, F. (2001). Emotion drives attention: detecting the snake in the grass. *Journal of Experimental Psychology: General*, 130, 466–78.
- Öhman, A., Flykt, A., Lundqvist, D. (2000). Unconscious emotion: evolutionary perspectives, psychophysiological data and neuropsychological mechanisms. In: Lane, R.D., Nadel, L., editors. *Cognitive Neuroscience of Emotion*. New York: Oxford University Press, pp. 296–327.
- Raghavachari, S., Kahana, M.J., Rizzuto, D., et al. (2001). Gating of human theta oscillations by a working memory task. *Journal of Neuroscience*, 21, 3175–83.
- Ray, W.J., Cole, H.W. (1985). EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. *Science*, 228, 750–2.

- Rihs, T.A., Michel, C.M., Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *European Journal of Neuroscience*, 25, 603–10.
- Rodriguez, E., George, N., Lachaux, J.P., Martinerie, J., Renault, B., Varela, F.J. (1999). Perception's shadow: long-distance synchronization of human brain activity. *Nature*, 397, 430–3.
- Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., Thut, G. (2008a). Spontaneous fluctuations in posterior alpha-band EEG activity reflect variability in excitability of human visual areas. *Cerebral Cortex*, 18, 2010–18.
- Romei, V., Rihs, T., Brodbeck, V., Thut, G. (2008b). Resting electroencephalogram alpha-power over posterior sites indexes baseline visual cortex excitability. *Neuroreport*, 19, 203–8.
- Rottenberg, J., Ray, R.R., Gross, J.J. (2007). Emotion elicitation using films. In: Coan, J.A., Allen, J.J.B., editors. *The Handbook of Emotion Elicitation and Assessment*. New York: Oxford University Press, pp. 9–28.
- Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G.L., von Stein, A. (1998). Synchronization between prefrontal and posterior association cortex during working memory tasks in humans. *Proceedings of the National Academy of Science*, 95, 7092–6.
- Sauseng, P., Klimesch, W., Gerloff, C., Hummel, F.C. (2009). Spontaneous locally restricted EEG alpha activity determines cortical excitability in the motor cortex. *Neuropsychologia*, 47, 284–8.
- Sergent, C., Dehaene, S. (2004). Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. *Psychological Science*, 15, 720–8.
- Simons, D., Chabris, C.F. (1999). Gorillas in our midst: sustained inattention blindness for dynamic events. *Perception*, 28, 1059–74.
- Storbeck, J., Clore, G.L. (2008). The affective regulation of cognitive priming. *Emotion*, 8, 208–15.
- Tomarken, A.J., Davidson, R.J., Henriques, J.B. (1990). Resting frontal brain asymmetry predicts affective responses to films. *Journal of Personality and Social Psychology*, 59, 791–801.
- Thut, G., Nietzel, A., Brandt, S.A., Pascual-Leone, A. (2006). Alpha-band electro-encephalographic activity over occipital cortex indexes visuo-spatial attention bias and predicts visual target detection. *Journal of Neuroscience*, 26, 9494–502.
- von Stein, A., Chiang, C., Koenig, P. (2000). Top-down processing mediated by interareal synchronization. *Proceedings of the National Academy of Science*, 97, 14748–53.
- Wichmann, F.A., Hill, N.-J. (2001a). The psychometric function. I. Fitting, sampling and goodness-of-fit. *Perception and Psychophysics*, 63, 1293–313.
- Wichmann, F.A., Hill, N.-J. (2001b). The psychometric function. II. Bootstrap-based confidence intervals and sampling. *Perception and Psychophysics*, 63, 1314–29.