

# Arousal and Attention: Self-chosen Stimulation Optimizes Cortical Excitability and Minimizes Compensatory Effort

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## Abstract

■ Cortical excitability is assumed to depend on cortical arousal level in an inverted U-shaped fashion: Largest (optimal) excitability is usually associated with medium levels of arousal. It has been proposed that under conditions of low arousal, compensatory effort is exerted if attentional demands persist. People tend to avoid this resource-consuming top-down compensation by creating or selecting environmental conditions that provide sufficient bottom-up stimulation. These assumptions were tested in an attention-demanding dual-task situation: We combined a simulated driving task to induce three different arousal levels by varying stimulation (high vs. low vs. self-chosen) with a visual two-stimulus paradigm to assess cortical excitability by the initial contingent negative variation (iCNV) component of the event-related potential. Additionally, we analyzed the oscillatory power of the beta2 band of the

electroencephalogram at anterior frontal sites, which is assumed to reflect low-arousal compensatory activity. The iCNV amplitude differed in all three arousal conditions as expected: It was highest in the condition of self-chosen stimulation and lowest in the low- and high-arousal conditions. Additionally, in the low-arousal condition, anterior frontal beta2 power was found to be significantly higher than in the other two conditions and correlated positively with subjective strain. This pattern of results suggests that subjects select medium levels of stimulation which optimize cortical excitability under attentional demand conditions. The elevated fronto-central beta2 power in the low-stimulation condition may indicate the involvement of the anterior cingulate cortex in compensating for reduced arousal by top-down stimulation of the noradrenergic arousal system. ■

## INTRODUCTION

Hull (1943) proposed that people generally strive for an optimal level of arousal. It has often been assumed, but not tested explicitly, that a certain level of arousal is necessary for the optimal availability of attentional resources. This study attempted to shed some light on that issue by investigating if people optimize their arousal and resource availability, as expressed by the level of cortical excitability, when they are allowed to select the level of stimulation.

Since Yerkes and Dodson (1908), the relationship between arousal and performance has been repeatedly described as an inverted U-shaped function. The early concept of arousal was one-dimensional: Arousal was assumed to reflect the general state of activity of the central nervous system ranging from deep sleep to excitement (Hebb, 1955). Hebb (1955) was also one of the first who ascribed a basic attentional function to arousal, modulating the processing of sensory input.

Both ideas are reflected in current, more elaborated views of arousal, which hold that “general arousal” is (a) supported by several distinct arousal systems that are, in turn, influenced by both external and internal factors, and (b) a prerequisite for, and a modulator of, the activation of specific attentional, cognitive, and motor systems (Pfaff, 2006; Garey et al., 2003).

General arousal appears to be reflected by the tonic cortical negativity (TCN), with stronger negativity related to higher arousal (Bechtereva, 1974; O’Leary & Goldring, 1964). Results of Hoffmann, Bonato, Armitage, and Wimmer (1996) and Rockstroh (1990) have shown that circumstances that strongly influence general arousal, such as sleep deprivation or hyperventilation, correspondingly affect the TCN. Further evidence bearing on the association between arousal and TCN was provided by studies showing that performance varied depending on the preceding level of TCN, with better performance contingent upon larger negativity (Born, Whipple, & Stamm, 1982, 1984; Guttman & Bauer, 1984; Lutzenberger, Elbert, Rockstroh, & Birbaumer, 1982; Bauer & Nirnberger, 1981). Corresponding to the U-shaped arousal–performance relationship, both very low and very high levels of TCN were related to performance

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decrements (Pauli, Schleichert, Bourne, & Birbaumer, 1998; Elbert, 1993; Lutzenberger, Elbert, Rockstroh, & Birbaumer, 1979).

The availability of attentional and cognitive resources is thought to be mediated by the activation of those cortical areas that subserve the respective attentional and cognitive functions. According to current views (Bauer, 1998; Rösler, Heil, & Röder, 1997; Elbert, 1993; Birbaumer, Elbert, Canavan, & Rockstroh, 1990), slow negative cortical potentials, such as the contingent negative variation (CNV), reflect modulatory processes that increase the neural excitability in cortical cell assemblies in order to turn cortical processing modules into attentional or cognitive resources. Thus, the amplitude of such negative potentials like the CNV has been taken to quantify the allocation of processing resources: The higher the amplitude, the more resources have been available and are, in turn, devoted to meeting the demands of a given task. This relation is supported by studies showing that a reduction of available attentional resources by means of distraction leads to a decrease of the CNV amplitude (Tecce & Scheff, 1969; McCallum & Walter, 1968). It is also supported by evidence showing a link between interindividual differences in cognitive processing efficiency and slow cortical potential amplitudes (Lamm, Bauer, Vitouch, & Gstättnner, 1999), as well as by findings of a strong association between cognitive load and the amplitude of slow negative potentials (Trimmel & Poelzl, 2006; Pleydell-Pearce, McCallum, & Curry, 1995; McCallum, Cooper, & Pocock, 1988). Also, findings of different negative potential topographies for different tasks (Pleydell-Pearce, 1994; McCallum et al., 1988) support the claim that slow negative potential shifts reflect cortical activation in preparation for, or response to, task demands.

Tecce (1972) proposed a relationship between arousal and cortical excitability (i.e., resource availability) similar to the one between arousal and performance discussed above: He showed an inverted U-shaped relationship between the level of arousal and the amplitude of the initial component of the CNV (iCNV), which reflects cortical excitability (Nagai et al., 2004; Aeschbach et al., 1999; Birbaumer et al., 1990; Elbert & Rockstroh, 1987; Loveless, 1975). The iCNV is regularly elicited in forewarned choice reaction time tasks (two-stimulus, or S1–S2, paradigm) and is largest over prefrontal sites. The inverted U-shaped relationship between general arousal and the iCNV amplitude as an index of cortical excitability has been explained by the assumption that a certain level of TCN is optimal for further phasic increases in excitation of pyramidal cells of the cortex (i.e., large iCNV). Increases of arousal beyond this medium level, however, are assumed to lead to supraoptimal levels of TCN, which are associated with reduced phasic excitability of cortical neurons (i.e., small iCNV) (Birbaumer et al., 1990; Pirch, 1980; Knott & Irwin, 1968).

Cortical excitability, as indicated by the iCNV amplitude, has been shown to be affected by external and inter-

nal stimulation such as variations in brightness (Higuchi, Watanuki, Yasukouchi, & Sato, 1997; Deguchi & Sato, 1992), olfactory stimulation (Hiruma, Yabe, Sato, Sutoh, & Kaneko, 2002), psychotropic drugs (Janssen, Mattie, Plooij-Van Gorsel, & Werre, 1978; Kopell, Wittner, Lunde, Wolcott, & Trinklenberg, 1974), physical effort (Kamijo et al., 2004), self-regulation using biofeedback (Ikemi, 1988; Lutzenberger et al., 1982), and sleep deprivation (Naitoh, Johnson, & Lubin, 1971).

After showing that attentional performance can be maintained to a certain degree under low-arousal conditions, the view of a passive correlative link between arousal and performance was challenged. An effortful top–down mechanism for low-arousal compensation was postulated. This mechanism is supposed to counteract performance decrements due to suboptimal arousal (Robertson & Garavan, 2004; Brocke, Tasche, & Beauducel, 1996; Hockey, 1986; Mulder, 1986; Eysenck & Eysenck, 1985; Sanders, 1983; Eysenck, 1982; Pribram & McGuinness, 1975).

Effortful top–down compensation for low arousal is required in monotonous vigilance tasks, which are characterized by continuous attentional demands and by low environmental and cognitive stimulation. Despite this cognitive “underload,” vigilance tasks are generally rated as very strenuous, which has been attributed to the effort subjects exert to compensate for low stimulation (Helton et al., 2005; Grier et al., 2003; Davies & Parasuraman, 1982). This effortful top–down compensation can be temporally improved by incentives but fails with increasing compensation difficulty, for example, after prolonged sleep deprivation, despite attractive rewards (Horne & Pettitt, 1985). Accordingly, people typically tend to adopt the following behavioral strategy to avoid performance decrements due to suboptimal arousal: At first, as already postulated by Hull (1943), people try to seek out environments or tasks providing optimal stimulation for (effortless) bottom–up arousal regulation (see also Fiske & Maddi, 1961; Hebb, 1955; Leuba, 1955). If this is impossible in attention-demanding tasks, a top–down mechanism seems to be invoked for low-arousal compensation (Foucher, Otzenberger, & Gounot, 2004; Murrell, 1967, 1969; French, Hernandez-Peon, & Livingston, 1955).

Early electrophysiological studies located the neural substrate of cortical arousal regulation in the reticular formation, thought to exert bottom–up control over the arousal level of the entire cortex via widespread unspecific projections (Lindsley, 1960; Moruzzi & Magoun, 1949). However, the notion of a unitary arousal system had to be abandoned in favor of several neurochemically distinct arousal systems ascending from different subcortical regions (Jones, 2003; McCormick et al., 2003; Robbins, 1997; Robbins & Everitt, 1995).

Presently, the noradrenergic arousal system (NAS), arising from the locus coeruleus (LC), constitutes the neuromodulatory system, whose influence on arousal in awake mammals is best understood. Activity

in the noradrenergic system causes higher responsiveness to input together with reduced spontaneous activity in neurons of its target areas (thalamus, cortex, and cerebellum). That is, noradrenergic projections of the LC improve the signal-to-noise ratio in their target zones (Woodward, Moises, Waterhouse, Yeh, & Cheun, 1991; Foote, Freedman, & Oliver, 1975). In studies with awake animals, low tonic LC firing rates have been shown to be associated with states of low arousal (Rajkowski, Kubiak, & Aston-Jones, 1994; Aston-Jones, Chiang, & Alexinsky, 1991; Aston-Jones & Bloom, 1981). In contrast, during focused attentiveness reflected by accurate task performance, LC neurons fire tonically at a moderate rate. An increase of the tonic activity of LC neurons up to high firing rates is accompanied by an increase in responses to task-irrelevant stimuli, which can be interpreted as an increase in distractibility and a reduction in selective attention (Aston-Jones & Cohen, 2005a; Aston-Jones, Rajkowski, & Cohen, 2000). These relationships between tonic LC activity and performance may be interpreted as a neuronal mechanism underlying the inverted U-shaped relation between arousal and selective attention (see also Berridge & Waterhouse, 2003; Posner, 1993).

The thalamus and the medial prefrontal cortex (mPFC), including the anterior cingulate cortex (ACC), are further components of the NAS. The mPFC has bidirectional connections to the LC (Heidbreder & Groenewegen, 2003) and to parts of the thalamus (Lapiz & Morilak, 2006; Paus, 2001; Yingling & Skinner, 1975). Bidirectional connections have been reported between ACC and the LC as well as between ACC and parts of the thalamus (Aston-Jones & Cohen, 2005b; Buchanan, Thompson, Maxwell, & Powell, 1994). Activity of the NAS has been revealed in tasks requiring the intrinsic maintenance of tonic alertness or arousal (Sturm et al., 1999, 2004; Paus et al., 1997; Kinomura, Larsson, Gulyas, & Roland, 1996). Aston-Jones and Cohen (2005b) propose that ACC exerts top-down control over LC activity in order to adjust arousability for optimal task performance. Increased task-related activity in ACC, the mPFC, and the thalamus, observed in low-arousal conditions, supports the view that these structures subserve effortful compensation for the suboptimal availability of attentional resources (Gilbert, Simons, Frith, & Burgess, 2006; Coull, Jones, Egan, Frith, & Maze, 2004; Portas et al., 1998).

The effortful compensation process has been linked to enhanced power in higher-frequency bands of the spontaneous electroencephalogram (EEG) over frontal brain regions. This was evidenced by pharmaco-EEG studies using benzodiazepines for sedation but requiring their subjects to remain vigilant. In these studies, increased higher-frequency beta activity over frontal regions was found in the range of 19–30 Hz (Connemann et al., 2005; Saletu, Grunberger, & Cepko, 1987), 21–30 Hz (van Lier, Drinkenburg, van Eeten, & Coenen, 2004), and 15–24 Hz (Rockstroh, 1990).

Source localization revealed ACC and the mPFC to be major generators of this increased higher-frequency beta power (Connemann et al., 2005). The assumption that brain structures subserving the top-down regulation of the NAS are involved in generating beta activity receives further support from studies using brain imaging techniques together with EEG recordings: Laufs et al. (2003) utilized functional magnetic resonance imaging to show a positive correlation between activity in ACC and power of the beta2 band (24–30 Hz) during an eyes-open rest condition. Additional indirect support for the notion that increased beta2 activity reflects the involvement of the NAS in low-arousal compensation is provided by a positive correlation between LC activity and beta power between 20 and 35 Hz (Berridge & Foote, 1991).

The aim of this study was to investigate whether different degrees of stimulation (task load) evoke different levels of cortical excitability and whether high cortical excitability can be found under conditions of self-chosen (optimal) stimulation. The second aim was to explore whether frontal beta activity increases during the low-stimulation condition, presumably reflecting compensatory effort.

A computer-simulated driving task was chosen for realizing different levels of stimulation by varying the task demands in a real-life situation. This intrinsically motivating and ecologically valid task requires continuous attention, thereby preventing idiosyncratic compensation strategies such as temporary disengagement during low stimulation.

## METHODS

### Subjects

Thirty-eight healthy subjects (9 men) participated in the experiment. Their mean age was 22.9 years with a range of 19–44 years. The participants were medication-free and had normal or corrected-to-normal vision. All subjects were students of the Dresden University of Technology and received course credits for participation. They gave written informed consent prior to the study.

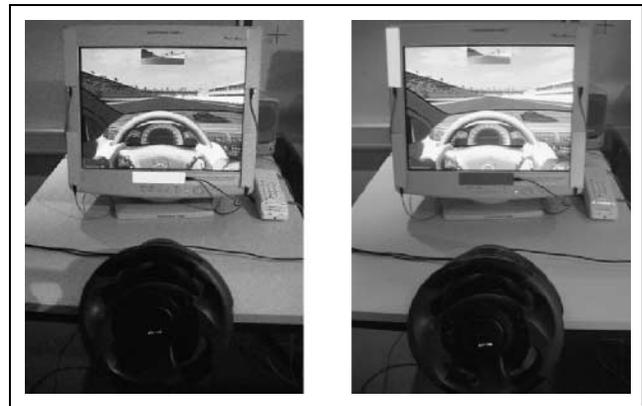
### Procedure and Tasks

We used a dual-task paradigm: The primary task was a simulated driving task in order to produce different states of arousal and cortical excitability, and the secondary task was a forewarned choice reaction time task (S1–S2 paradigm) for determining cortical excitability as indicated by the iCNV. The experiment was conducted with the subjects seated in a sound-attenuated chamber. After finishing the preparations for the psychophysiological measurements, subjects filled out questionnaires. Subsequently, they were instructed about the two ex-

perimental tasks to be done simultaneously. It was emphasized that neither task had priority over the other. The primary task was implemented by using a commercial computer game (“Mercedes World Racing”), which was presented via an IBM-compatible PC and a 21-in. color monitor at a distance of 80 cm. The car was controlled via a force-feedback steering wheel and two foot pedals (brake and accelerator) with an automatic transmission setup. Visual feedback about the current race position (in the high-load condition only) and the gear was given at the left upper corner of the screen. The current speed was shown in the right bottom corner of the screen. The task load of each experimental condition was varied by the task demands of the main task.

The condition with the lowest task demand was realized via a slow-driving condition. In this condition, the subjects drove on a racing car circuit (modeled after the Hockenheimring, Germany) without any competitors and with the first gear working only. The subjects were instructed to keep a speed of 30 km/hr constantly, which was successfully realized with a mean speed (measured successively after 240 sec at five times per condition) of  $M = 29.40$  km/hr ( $SD = 1.52$ ). Driving in the low-load condition was error-free (no significant deviations from the road). For the self-chosen-load condition, we also used a single-driving situation. Here the subjects were free to choose their preferred driving speed and route; they were instructed to drive in a way that felt pleasant to them but still complied with general traffic rules. The driving environment was a hilly scenario with rural roads. The subjects drove alone without gearbox restrictions; no other car was on the roads. The mean speed was 59.08 km/hr ( $SD = 14.40$ ), the mean error rate was 1.34 ( $SD = 1.75$ ). The high-load condition involved the same racing circuit as the low-load condition. Subjects were instructed to win a race against four computer-simulated competitors. The driving speed of the four computer-simulated competitors was adaptive to the speed of the subjects. Thus, the subjects never fully lost track of their opponents, even when committing major driving errors. The subjects’ average speed in the high-load condition was  $M = 101.68$  km/hr ( $SD = 12.81$ ), the mean error rate was 8.42 ( $SD = 5.59$ ). The order of conditions was balanced across subjects. Each task block was followed by a 10-min break, during which the monitor was switched off. The light was dimmed during the task and up-regulated to normal during the break.

The secondary task began 5 min after the driving simulation had started. Both warning (S1) and imperative (S2) stimuli were presented via LCD lamps ( $3 \times 8$  cm<sup>2</sup>) attached to the monitor frame (see Figure 1). S1 was presented via a red lamp placed in the middle of the lower monitor frame, S2 was presented via one of four light blue lamps: two on either side of the monitor frame in the upper and lower corner, respectively. Subjects



**Figure 1.** Testing condition with S1 (left) and S2 (right).

were instructed to respond as fast as possible to the appearance of S2 by pressing one of two buttons corresponding to the side of S2 presentation (left or right). The buttons were located at the rear of the steering wheel and were to be pressed with the left or right forefinger without changing hand position on the wheel. All stimuli were presented for 200 msec; the fixed interval between onset of S1 and S2 was 4.2 sec; the intertrial interval was 12 sec. S2 occurred at each of the four locations with equal probability; the order of presentation varied randomly.

### Subjective Measures

After each experimental condition, the German version of the NASA-Task Load Index (NASA-TLX) was administered to assess subjective workload imposed by this condition (Hart & Staveland, 1988). This self-report questionnaire comprises six rating scales, each representing one dimension of perceived workload: mental demands, physical demands, temporal demands, performance level, frustration, and effort. As total score, the simple, nonweighted average of the six NASA-TLX subscales was calculated as proposed by Nygren (1991) and Byers, Bittner, and Hill (1989).

Likewise, the Short Questionnaire for Current Strain (KAB) (Mueller & Basler, 1992) was administered after each experimental condition to measure current subjective strain due to the driving task. This self-report questionnaire includes eight pairs of adjectives on a 6-point Likert-type rating scale describing opposite endpoints of different strain dimensions (e.g., stressed vs. relaxed; languid vs. fresh).

### EEG Recordings and Preprocessing

EEG activity was recorded using a Synamp DC-amplifier (Neuroscan). Twenty-eight nonpolarizable Ag/AgCl electrodes were placed according to the standard 10–20 system (Fp1, Fp2, AF3, AF4, F7, F3, Fz, F4, F8, FC1,

FC2, T7, C3, Cz, C4, T8, CP1, CP2, P7, P3, Pz, P4, P8, PO7, PO8, O1, O2) and recorded against the average activity at both mastoids (A1, A2) as reference. An additional pair of electrodes was placed vertically above and below the left eye to record the vertical electrooculogram. The ground electrode was placed on the forehead, and an additional electrode was placed on the neck for recording muscle activity. Furthermore, two electrodes were used to record the electrocardiogram. All electrode impedances were kept below 5 k $\Omega$  at 5 Hz. Signals were sampled at 500 Hz and passed through a 0–30 Hz band-pass filter. Data were recorded continuously and stored for off-line analysis.

Before data analysis, drifts were compensated by subtracting a correction signal. This correction signal was computed via Piecewise Cubic Hermite Interpolating Polynomial (PCHIP), which was optimized by averaging data across 30-sec segments. Further, data were repeatedly band-pass-filtered (12–40 Hz) for elimination of low frequencies and residual 50-Hz artifacts. Independent component analysis (ICA; Infomax) was used to remove artifacts due to eye blinks and heartbeat. The activity at the neck electrode was used for allocating muscle activity to ICA components by visual inspection. All components with activity similar to the one at the neck electrode were excluded from further analysis. In a second step, the ICA components with maximal variance at AF3, AF4, Fz, F3, or F4 electrodes were selected for further analysis to exclude activity outside the fronto-central cluster. At last, the power density was measured in a range from 18 to 30 Hz.

For event-related potential analysis, data of each epoch were referred to a 500-msec pre-S1 baseline. Each trial was visually inspected and excluded if there were remaining artifacts. The iCNV was quantified by computing mean amplitudes via successive averaging (Rockstroh, Elbert, Canavan, Lutzenberger, & Birbaumer, 1989) in a latency window of 900–1300 msec after onset of S1.

For EEG power analysis, activity was averaged across artifact-free intertrial time windows of 7500 msec (2250 msec after S2 onset) from the last 5 min of each experimental condition. For computing EEG power in the resting period, activity during artifact-free 2-min epochs from the second half of each break period was averaged. EEG power spectra were computed with fast Fourier transformation of the autocorrelation function of each segment over 1-sec epochs (50% overlap, Hann windows, mean- and trend-corrected). The power values of AF3, AF4, Fz, F3, and F4 electrodes were averaged and the sum of the power density from 18 to 30 Hz was used for statistical analysis.

## Statistical Analyses

Subjective ratings (NASA-TLX and KAB) and electrophysiological data (mean iCNV amplitudes and beta2 power) were subjected to a general linear model analysis of var-

iance for repeated measures with Greenhouse–Geisser correction for violations of sphericity to test the effects of task conditions, with  $p$  values less than .05 considered significant. Simple contrasts were used for pairwise comparisons. The low-load condition was the reference category for beta2 power contrast testing. For all other contrasts, the self-chosen-load condition was used as reference.

## RESULTS

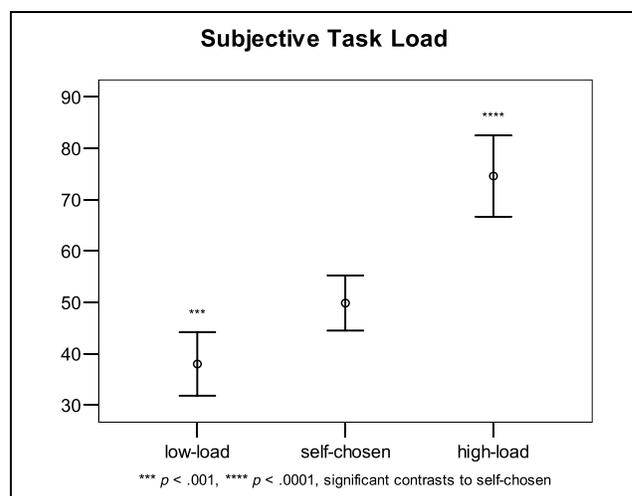
### Behavioral Measures

In the secondary task, reaction time showed a main effect of condition. The shortest reaction times ( $M = 572.56$  sec,  $SD = 105.78$ ) occurred in the low-load condition. They differed significantly from the self-chosen-load condition [ $M = 632.65$  sec,  $SD = 113.26$ :  $F(1, 35) = 34.50$ ,  $p < .001$ ,  $\epsilon = .496$ ]. Reaction times were longest in the high-load condition ( $M = 681.57$  s,  $SD = 128.07$ ), which also differed significantly from the self-chosen-load condition [ $F(1, 35) = 7.98$ ,  $p < .01$ ,  $\epsilon = .186$ ]. No time-on-task-effects were found in any condition. The mean error rate (missing responses to S2) differed significantly between the self-chosen-load ( $M = 0.86$ ,  $SD = 1.29$ ) and the high-load condition [ $M = 3.51$ ,  $SD = 4.49$ :  $F(1, 35) = 12.58$ ,  $p < .001$ ,  $\epsilon = .270$ ]. No significant difference in error rate was found between the self-chosen-load condition and the low-load condition ( $M = 0.49$ ,  $SD = 0.70$ ).

### Subjective Measures

#### NASA-Task Load Index

As expected, the total score of the NASA-TLX showed a main effect of condition: [ $F(1.62, 58.26) = 52.01$ ,  $p < .001$ ,  $\epsilon = .591$ ; see Figure 2]. The highest score was



**Figure 2.** NASA-TLX total scores and 95% confidence intervals for the three task conditions.

found in the high-load condition ( $M = 74.61, SD = 24.04$ ), which was significantly different from the self-chosen-load condition [ $M = 49.86, SD = 16.36; F(1, 36) = 37.13, p < .0001, \epsilon = .508$ ]. The lowest NASA-TLX score was found in the low-load condition ( $M = 38.00, SD = 18.67$ ), with a significant difference to the self-chosen-load condition [ $F(1, 36) = 20.39, p < .001, \epsilon = .362$ ].

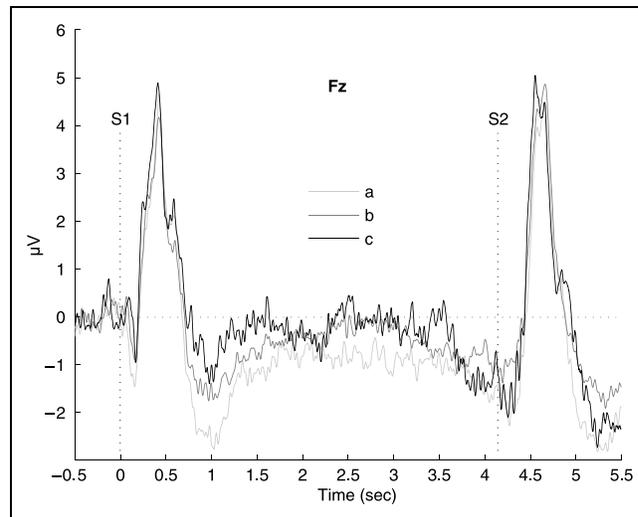
### Short Questionnaire for Current Strain

A main effect of condition (pre-experimental baseline and three task conditions) on the KAB score was found [ $F(2.53, 91.06) = 19.92, p < .001, \epsilon = .356$ ]. The highest subjective strain turned out to be reported after the condition with the lowest task load ( $M = 29.11, SD = 3.45$ ) (see Figure 3). Simple contrasts showed that the subjective strain reported after this condition was significantly higher than after the self-chosen-load condition [ $M = 22.43, SD = 5.63; F(1, 36) = 43.39, p < .001, \epsilon = .547$ ]. Further, lower subjective strain, as compared to the low-load condition, was reported at baseline ( $M = 21.41, SD = 6.57$ ) and after the high-load condition ( $M = 23.43, SD = 6.60$ ). The KAB scores related to the latter two conditions did not differ significantly from the score reported after the self-chosen-load condition.

### Electrophysiological Data

#### Initial Contingent Negative Variation

The iCNV amplitude showed a significant main effect of condition at position Fz [ $F(1.61, 56.21) = 4.71, p = .019, \epsilon = .119$ ] (see Figure 4). The largest amplitude was found in the self-chosen-load condition ( $M = -2.14 \mu V, SD = 2.03$ ). In comparison, significant smaller amplitudes were found in the high-load [ $M = -1.37 \mu V, SD = 2.10, F(1, 35) = 4.412, p = .043, \epsilon = .112$ ] and low-load

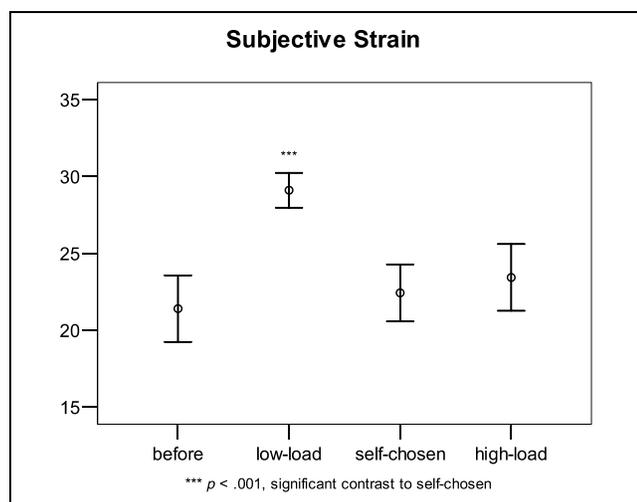


**Figure 4.** Grand means of evoked potentials at position Fz between S1 and S2 for all three conditions. Onsets of S1 and S2 are marked by vertical dotted lines. Line a shows the significant larger iCNV amplitude in the self-chosen-load condition (at 900–1300 msec). Line b refers to the high-load condition and line c to the low-load condition.

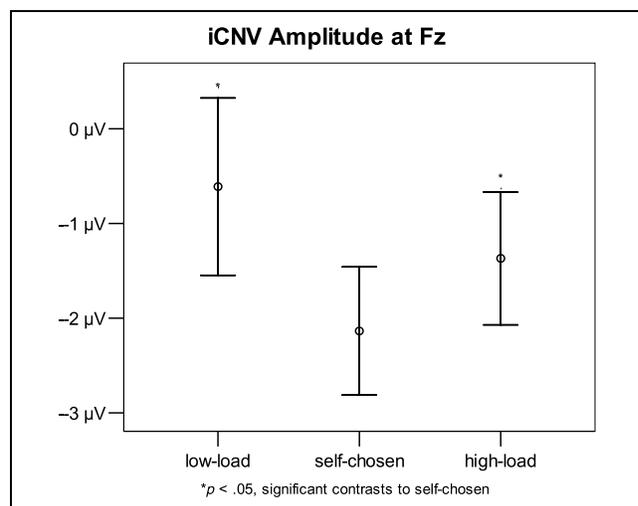
conditions [ $M = -0.61 \mu V, SD = 2.81, F(1, 35) = 6.784, p = .013, \epsilon = .162$ ] (see Figures 4 and 5).

#### Beta2 Power

A significant main effect of condition (three tasks and rest) was found for beta2 power in the anterior frontal cluster [ $F(1.75, 56.06) = 4.648, p = .017, \epsilon = .127$ ]. As expected, significantly enhanced beta2 power was found in the low-load condition ( $M = 0.445 \mu V^2, SD = 0.446 \mu V^2$ ) as compared to both the self-chosen-load condition [ $M = 0.237 \mu V^2, SD = 0.198 \mu V^2, F(1, 32) = 6.783, p = .014, \epsilon = .175$ ] and the high-load condition



**Figure 3.** KAB total scores and 95% confidence intervals at baseline and after the three task conditions.



**Figure 5.** Mean and 95% confidence intervals of iCNV amplitude ( $\mu V$ ) at the three task conditions.

[ $M = 0.268 \mu\text{V}^2$ ,  $SD = 0.172 \mu\text{V}^2$ ,  $F(1, 32) = 5.142$ ,  $p = .030$ ,  $\epsilon = .138$ ], as well as compared to rest [ $M = 0.272 \mu\text{V}^2$ ;  $SD = 0.246 \mu\text{V}^2$ ,  $F(1, 32) = 5.154$ ,  $p = .030$ ,  $\epsilon = .139$ ] (see Figure 4). Thus, the characteristic of the anterior frontal beta2 power is in accordance with the ratings of subjective strain (Figure 6).

## DISCUSSION

This study aimed to determine (1) if the level of arousal that people choose if free to do so will lead to an optimal availability of attentional resources, expressed by high cortical excitability, and (2) if suboptimal arousal is compensated for by additional effortful brain activity. Resource availability, neurophysiologically expressed by the level of excitability in assemblies of cortical neurons, was probed by a standard two-stimulus (S1–S2) choice reaction time paradigm under three different conditions of stimulation: high, low, and self-chosen. The initial component of the CNV, an event-related potential typically elicited in S1–S2 paradigms, was used to quantify neural excitability at fronto-cortical sites. Additional compensatory effort in low-arousal conditions was assumed to be reflected by the power of the spontaneous EEG in the beta2 frequency range.

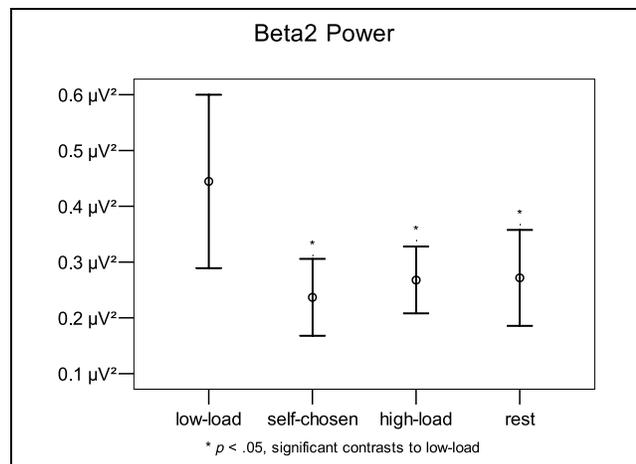
Cortical excitability was expected to be higher in the condition with self-chosen stimulation than in conditions with high, or low, stimulation. Our results support this hypothesis: The largest iCNV amplitude was found in the condition with self-chosen stimulation. Smaller amplitudes found under low- and high-stimulation conditions fit the inverted U-shaped relationship between iCNV and arousal level proposed by Elbert (1993) and Tecce (1972). These results also support Hull's (1943) assumption of an innate drive for seeking a stimulation (i.e., arousal) level that optimizes attentional responsiveness.

In case of low external stimulation, it is reasonable to assume that sufficiently motivated people strive for

counteracting an impending performance decrease due to suboptimal arousal by means of an effortful top-down mechanism. This top-down regulation is invoked only if external or internal stimulation cannot be increased (Collet, Petit, Priez, & Dittmar, 2005). As suggested by related research (Smit, Droogleever Fortuyn, Eling, & Coenen, 2005; Kiroy, Warsawskaya, & Voynov, 1996; Belyavin & Wright, 1987), we assumed that elevated beta2 power at frontal sites reflected top-down low-arousal compensation. Our results confirmed this assumption: In comparison to self-chosen and high-stimulation levels, frontal beta2 power was significantly higher in the low-stimulation condition. Although this condition imposes the least task load, as reflected in the NASA-TLX ratings, it still requires continuous allocation of attention. The lower beta2 power during the rest condition indicates an environment more arousing than expected. The reason could be the enhanced environmental brightness level and the cognitive demands of filling out the questionnaires. The remaining interval after the fill-out was probably too short to be de-arousing down to a point of uncomfortable low arousal that needed effortful compensation. Therefore, the abovementioned findings of Laufs et al. (2003) of enhanced beta2 (24–30 Hz) power in a state of wakeful rest may be closer related to our low-stimulation condition, rather than to our rest condition.

The interpretation of fronto-central beta2 activity as the expression of an effortful top-down regulation mechanism receives additional support from the subjective reports of high strain elicited by the low-arousal condition. Thus, our data suggest that this kind of compensatory activity is effortful and, therefore, is exclusively connected to low-arousal situations having subjectively relevant consequences, such as a performance decrease due to a failure to meet attentional task demands. These anticipated consequences provide the motivation for exerting this additional compensatory effort if, and only if, bottom-up arousal regulation is insufficient. Thus, we also found support for Hull's (1943) claim that people are motivated to avoid the need for effortful compensation by seeking appropriate stimulation whenever possible.

In the Introduction section (see above), we presented arguments for the likely involvement of the NAS in arousal regulation including top-down compensation in suboptimal arousal conditions. Assuming that elevated beta2 power reflects higher activity in underlying neural structures (Papanicolaou, Loring, Deutsch, & Eisenberg, 1986; Birbaumer, Elbert, Lutzenberger, Rockstroh, & Schwarz, 1981) and considering the abovementioned results of Laufs et al. (2003) and Berridge and Foote (1991), which revealed correlations of EEG beta power with activity in parts of the NAS, the increased fronto-central beta2 power in the low-arousal condition may be interpreted as a correlate of compensatory NAS activity. We assume that this increased fronto-central beta2



**Figure 6.** Mean and 95% confidence intervals of beta2 power ( $\mu\text{V}^2$ ) at rest and the three task conditions.

power reflects higher activity in the mPFC and in ACC—structures that have been shown to be involved in the top-down regulation of arousal and alertness (Mottaghy et al., 2006; Foucher et al., 2004). Accordingly, the low beta2 power in the self-chosen-stimulation condition suggests low activity of the mPFC and ACC. This conclusion allows for a new interpretation of the assumption—originally put forward by Posner and Petersen (1990) and later confirmed by Lawrence, Ross, Hoffmann, Garavan, and Stein (2003)—of a negative correlation between ACC activity and performance level in sustained-attention tasks. Based on our results, it may be conjectured that low ACC activity and concomitant good performance can be ascribed to an optimal arousal level, at which no compensatory activity is necessary and which thus enables the optimal availability of attentional resources.

This kind of interpretation is indirectly supported by our finding that the iCNV amplitude, which is assumed to index the phasic resource availability of ACC, was largest at the self-chosen (and supposedly optimal) arousal level. This interpretation gets further support by findings of greater ACC activity (Grady, Springer, Hongwanishkul, McIntosh, & Winocur, 2006) and lower iCNV amplitudes (Dirnberger et al., 2000; Zappoli et al., 1988) in older compared to young people. Future studies that simultaneously apply functional brain imaging and EEG will enable testing these conjectures about the activity of the NAS at different arousal levels. Furthermore, the use of suitable single-task paradigms should allow for the evaluation of performance across arousal levels without ambiguities arising from dual-task methodology.

In sum, this study showed that there is a motivation to seek a stimulation level that enables optimal reactivity to attentional demands. Thus, our results support the assumption of a tendency for searching an optimal arousal level; they also confirm the assumed preference for varying external stimulation over effortful top-down compensation. However, effortful top-down regulation is characteristic for situations combining attentional requirements with inadequate external stimulation. We propose that low-arousal compensation is accomplished by the NAS and is, on the cortical level, reflected by elevated anterior frontal beta2 activity. It may be speculated that the higher compensatory ACC activity is the reason for the reduced availability of attentional resources (reduced iCNV amplitude) in situations with suboptimal external stimulation. This is in line with the inverted U-shaped relationship between CNV amplitude and arousal proposed by Tecce (1972).

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