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The physical basis of alpha waves in the electroencephalogram and the origin of the "Berger effect"

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Abstract. Synchronised activity, differing in phase in different populations of neurons, plays an important role in existing theories on the function of brain oscillations (e.g., temporal correlation hypothesis). A prerequisite for this synchronisation is that stimuli are capable of affecting (resetting) the phase of brain oscillations. Such a change in the phase of brain waves is also assumed to underlie the "Berger effect": when observers open their eyes, the amplitude of EEG oscillations in the alpha band (8–13 Hz) decreases significantly. This finding is usually thought to involve a desynchronisation of activity in different neurons. For functional interpretations of brain oscillations in the visual system, it therefore seems to be crucial to find out whether or not the phase of brain oscillations can be affected by visual stimuli. To answer this question, we investigated whether alpha waves are generated by a linear or a nonlinear mechanism. If the mechanism is linear – in contrast to nonlinear ones – phases cannot be reset by a stimulus. It is shown that alpha-wave activity in the EEG comprises both linear and nonlinear components. The generation of alpha waves basically is a linear process and flash-evoked potentials are superimposed on ongoing alpha waves without resetting their phase. One nonlinear component is due to light adaptation, which contributes to the Berger effect. The results call into question theories about brain-wave function based on temporal correlation or event-related desynchronisation.

1 Introduction

Oscillations in the electroencephalogram (EEG) indicate periodic activity of large populations of synchronized neurons, usually called neuronal assemblies, a term coined by Hebb (1949). The formation of such assemblies is observed in various sensory, behavioural, or cognitive states. A number of hypotheses were proposed based on synchronized activity or temporal correlation (Eckhorn et al. 1988; Gray et al. 1989; Rodriguez et al. 1999; Fries et al. 2001; Patel and Balban 2000; Engel et al. 2001). The functional significance of such correlated activity, however, is still being debated (Abbott and Dayan 1999; Shadlen and Movshon 1999).

Berger, quite early in his pioneering work on the human EEG, made the following unexpected observation: when observers opened their eyes, the EEG oscillations in the alpha band (8–13 Hz) decreased in amplitude or disappeared completely. Berger had expected the opposite, namely that sensory stimuli would *evoke* oscillations in the EEG with *larger* amplitudes than those of background activity. He, therefore, initially distrusted the validity of this finding. The robustness of the phenomenon convinced him, however, that it was genuine (Berger 1933). Since Berger's initial observation, the phenomenon was observed by countless scientists and physicians. The "Berger effect" is also called "alpha blocking", a designation which describes the phenomenon without explaining it. Yet another name, "desynchronization", implies that after eye opening, oscillators in the brain get out of phase, a supposition which is still waiting for direct proof. Hence, understanding neural synchronisation and the Berger effect is of critical importance for the development of a theory of sensory and cognitive processing.

The hypotheses regarding temporal correlation and the interpretation of the Berger effect as a desynchronisation of neural activity have one aspect in common: both postulate that stimuli are capable of affecting the phase of brain oscillations. The question of whether or not this is possible is raised here, with alpha waves as an example.

Section 2.1 describes properties of linear and nonlinear oscillators, and how the differences can be used to experimentally classify alpha waves. In Sect. 2.2, experimental data will be analysed according to the linear versus nonlinear concept, and it will be shown that evoked potentials are generated mainly by a linear mechanism.

In Sect. 2.3, experiments are presented which show that after a flash, the sensitivity of the system decreases as manifested by the reduced amplitude of evoked potentials. At

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the same time, alpha amplitudes decrease, which supports the view that alpha amplitudes reflect the adaptation level (sensitivity, gain) of the visual system.

In Sect. 2.4, a model will be presented which comprises the linear as well as the nonlinear components of the alpha-wave- and EVP-generating mechanism, and which is in agreement with the main experimental findings.

2 Results

2.1 Linear systems and nonlinear oscillators

For a functional interpretation of brain waves, a distinction between nonlinear and linear processing is of importance, because it is only in the nonlinear case that a resetting of the phases of brain waves by a stimulus is possible. In the linear case, the signal of a stimulus is merely superimposed onto the ongoing brain wave, the phase of which remains unaffected.

Usually brain waves are considered to be due to self-sustained oscillators which are necessarily nonlinear. Sometimes brain waves have been interpreted as a mere consequence of linear processing, such as band-pass filtering or linear oscillations (van der Tweel 1964; Spekreijse 1966; Lopes da Silva et al. 1974). Linear and nonlinear contributions in brain waves were also demonstrated (Gebber et al. 1999; Stam et al. 1999). An explicit proof of whether the superposition principle holds and whether resetting of the phase by a stimulus is possible has not yet been presented. In particular, the relevance of these topics to functional interpretations has not been taken into account. Therefore, these questions are raised here and experimentally investigated by analysing alpha waves.

Discriminating experimentally between the linear and the nonlinear case in a living brain is not trivial, because the responses to flashes or light steps that activate either linear or nonlinear oscillators can be similar, as can be the frequency- and phase-response characteristics of such oscillators. An experimental paradigm that allows us to discriminate between the two mechanisms is the following: if flashes are presented in different phases of an alpha wave, the responses differ, depending upon whether the behaviour is linear or nonlinear.

Figure 1 shows model calculations for a linear system capable of generating oscillations. It is a simple feedback-loop system (Fig. 1a). If the gain in such a system is sufficiently high, the system acts as a band-pass filter (with low gain it acts as a low-pass filter). Square waves as input evoke overshoots with damped oscillation (Fig. 1b). Input is necessary in order to generate continuous oscillations at the output. If wide-band noise (Fig. 1c) enters such a loop at N in Fig. 1a, the output of the loop is restricted to a relatively narrow frequency band (Fig. 1d). This feedback model is basically a linear system, which means that the flash response is simply superimposed on the noise-induced alpha waves (Fig. 2a–d). In this model, the visually evoked potential is independent of the phase of the ongoing alpha waves at the time when the stimulus is presented. Furthermore, the *phase of the alpha waves* is *not affected* by the flashes (Fig. 2b). In contrast, in self-sustained oscillators like the one described by the *van der Pol* equation (see caption of Fig. 2, van der Pol 1926), the effect of a flash at the input depends upon the phase at which it is presented (Fig. 2e–f). In addition, a *resetting of the phase of the oscillations by the flash is obvious* (Fig. 2f).

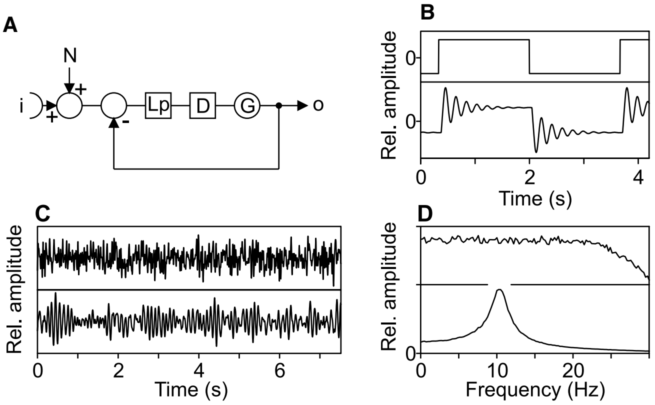

Fig. 1. Feedback loop with band-pass characteristics. Model calculations. **a** Block diagram. Parameters of the elements were selected in such a way that the maximum of the pass band was close to 10 Hz. *i* Signal input, *o* Output, *N* Noise input, *Lp* First order low-pass filter, time constant 1 s, *D* Delay 26 ms, *G* Amplification element, gain 9. **b** Model calculation with square wave as input (*upper part*), resulting output (*lower part*). **c** Noise input (*upper part*), calculated output (*lower part*). **d** Noise input (*upper part*), calculated output (*lower part*), frequency characteristics. These calculations and those of Fig. 6 were carried out with DasyLab (National Instruments Services)

2.2 A modified superposition rule holds for alpha waves and visually evoked potentials

Flashes presented at different phases of alpha waves should allow us to discriminate between the linear and nonlinear oscillator hypotheses. There are excellent experimental data published by Brandt on the effect of pre-stimulus alpha phase activity on the averaged visually evoked potential (Brandt 1997). These data have not yet been analysed with respect to the superposition rule (Brandt was dealing with self-sustained oscillators generating alpha waves only; therefore, he did not consider superposition as an interpretation of his results). Here, Brandt's data are subjected to such an analysis (Fig. 3).

In Figs. 3a and f, data published by Brandt are reproduced. They show two kinds of averaged visually evoked potentials. In one of the experimental paradigms, flashes were presented (at time $t = 0$) as usual, that is randomly at all possible phases of the alpha waves. In this trigger mode, alpha waves cancel each other out, because they are superimposed with randomly variable phases (shown in light blue). What remains is the evoked potential without contribution of alpha waves.

In the second paradigm, flashes were always presented at a particular phase of the alpha waves: either when the alpha waves crossed the zero potential with a positive slope (Fig. 3a in red), or when they crossed it with a negative slope (Fig. 3f). In this trigger mode, alpha waves are superimposed always with the same phase. Therefore, they do

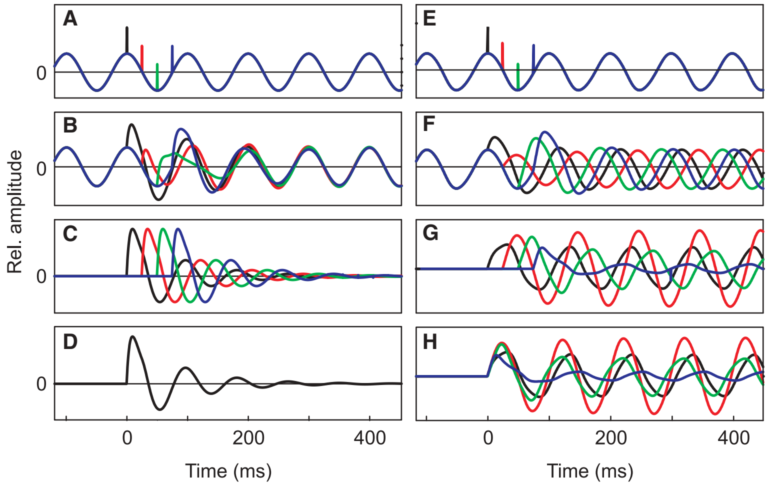

Fig. 2. Comparison of band-pass filter (*feedback loop*) and van der Pol oscillator. Impulses were superimposed at different phases of a sine wave or the spontaneous oscillation of the oscillator, and the responses calculated. Impulses were computed separately and the curves combined in the figures later. **a**–**d** Data from linear feedback loop as in Fig. 1. **a** Input. **b** Responses. **c** Responses with sine wave subtracted. What remains are the impulse responses. The ordinate in (**c**) is magnified by a factor of 1.8 compared to (**b**) **d** The beginning of the impulse responses was shifted to time zero to show that they are identical. **e**–**f** Input and responses of a self-sustained oscillator. The oscillator used was of the *van der Pol* type, and is described by the differential equation $\ddot{y}+\mu(y^2-1)\dot{y}+y=f(t)$. The van der Pol equation describes, for example, circadian rhythms the phase of which can be reset by light flashes. Since all self-sustained oscillators are essentially nonlinear, the superposition rule does not apply to any of them. Whenever the superposition rule is verified in a particular system, all self-sustained oscillators are excluded. The parameter μ was set to 0.5 in the model calculation. The conclusions drawn do not critically depend upon the actual value of μ. μ is a constant that affects how nonlinear the system is. For $\mu=0$ the system is just a linear oscillator, for $\mu>1$ the oscillations no longer are sine waves but highly nonlinear sweep oscillations. **e** The spontaneous oscillation of the loop with superimposed impulses (not to scale). **f** Responses of the oscillator. **g** Here, the oscillation was subtracted from the output signal. **h** The beginning of each impulse response was shifted to time zero to illustrate the different shapes of the impulse responses

not cancel but appear in full amplitude, as can be seen easily before flash presentation.

To test the superposition rule, we have to find out whether the evoked potentials after the flash, as shown in red in Figs. 3a and f, correspond to the superposition of (1) alpha waves and (2) evoked potential without contribution of alpha waves, as shown in blue in Fig. 3a and f.

The alpha waves after the flash can be represented simply by extrapolating the alpha waves before flash presentation, as shown in black in Fig. 3b and g. (Actually, the black curve was obtained by rotating the red part of the alpha-wave curve in Fig. 3b and g through 180° around the origin of the coordinate system, a procedure which corresponds to an extrapolation.) We now have to add (superimpose) the black and the blue curves in Fig. 3b and g; the result is the green curves in Fig. 3c and h. Here only the time after flash presentation is shown. If the superposition law holds, the green curves should coincide with the measured evoked potentials shown in red in Fig. 3a and f, and redrawn on an expanded scale in Fig. 3c and h, respectively.

As can be seen at the first maximum or the first minimum after the flash (both marked with asterisks), the prediction and response initially coincide. From then on, the two functions diverge more and more, such that the amplitude of the prediction (green) is always too large. This result shows that the feedback loop (Fig. 1a) is not a sufficient model for the response to light stimuli presented at different alpha phases, because according to this loop, the predictions in Fig. 3c and h and the measured data should coincide. There is, however, an easy way to obtain coincidence between the two: we simply have to assume that the amplitude of alpha waves after flash presentation does not stay more or less constant (as assumed in the prediction, black in Fig. 3c and h), but that the amplitude decays over time, as shown in Fig. 3d and i (dark blue). Measured data and predictions under this assumption are identical (Fig. 3e and j).

The decay of the alpha waves after the flash (Fig. 3d, i) was determined as follows: the difference between the amplitudes of the green and the red functions at the inflection points of the alpha waves in Fig. 3c and h was measured. These differences were subtracted from the alpha-wave maxima and minima to obtain the maxima and minima of the blue functions in Fig. 3d and i. The remaining parts of these functions were then interpolated by sine waves, to produce the damped oscillations shown in Figs. 3d and i (blue). Superposition of the mean evoked potentials (light blue in Figs. 3b and g) on these damped oscillations leads to the green dotted functions in Fig. 3e and j, which conform closely to the measured data as shown in red.

When the data from the four additional observers cited in Brandt's paper were analysed with the same method, the measured and predicted data were found to practically coincide (Fig. 4).

We have to conclude from this analysis that there is superposition, but the superposition rule in alpha waves and evoked potentials does not hold in the strict sense. We

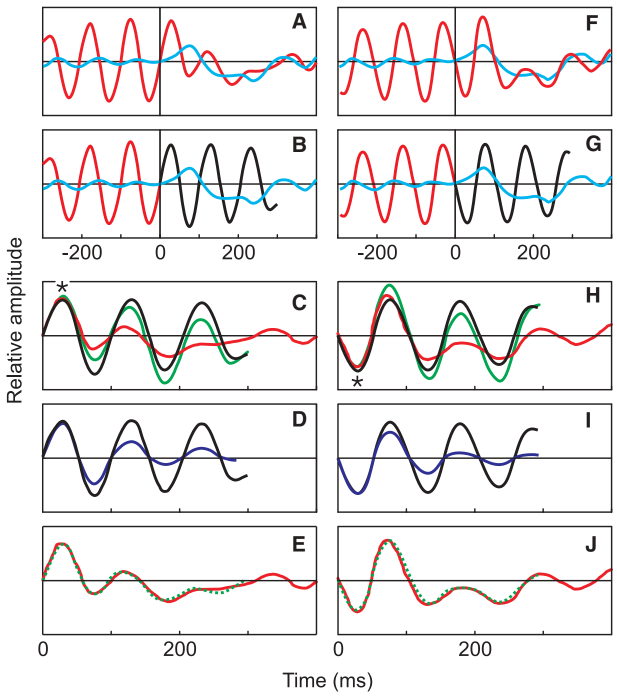

Fig. 3. Verification that a modified superposition rule holds in the human electroencephalogram for alpha waves and visually evoked potentials. **a**, **f** Data from Brandt (1997). The *light blue lines* show the potential evoked by flashes that were presented randomly in time. *Red lines* are evoked potentials in response to flashes presented at two different phases of the spontaneous alpha waves, either when they crossed the zero line with positive (**a**) or with negative slope (**f**). **b**, **g** Extrapolation of the alpha waves after time $t = 0$ (*black*, details are described in the text). **c**, **h** Alpha wave (*black*, from **b**, **g**) measured evoked potential (*red*, from **a**, **f**) and prediction (*green*). **d**, **i** Alpha wave (*black*, from **b**, **g**) and an alpha wave that decays with time after the flash (*dark blue*), as used for the new prediction. **e**, **f** Measured evoked potentials (*red*, from **a**, **f**) and new prediction (*dotted green*)

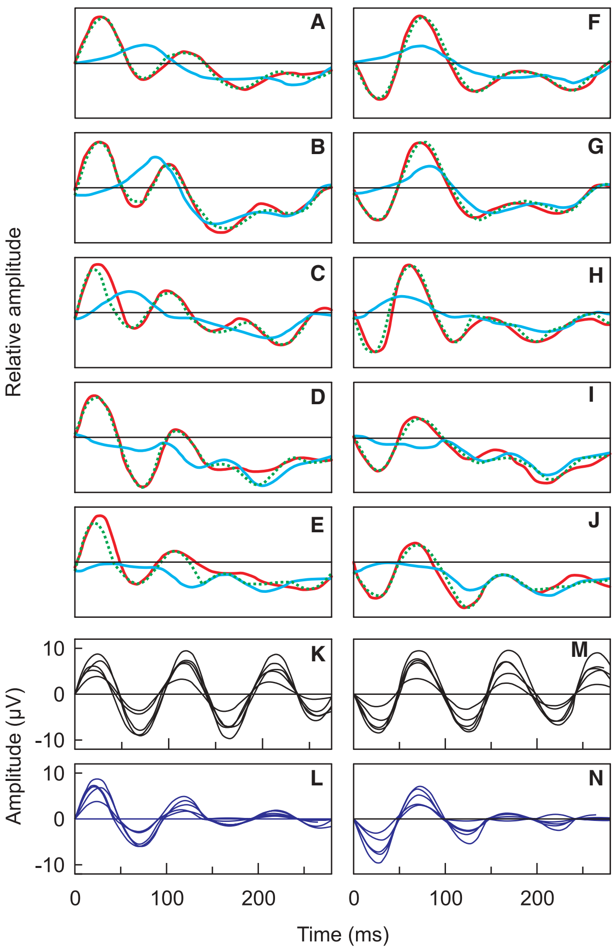

Fig. 4. Measured and predicted-evoked potentials from five subjects (**a**–**j**), alpha waves as extrapolated from the time before flash presentation (**k**, **m**), and alpha waves with declining amplitudes after the flash (**l**, **n**). **a**, **f** Data from Fig. 3e and j. **b**–**e** and **g**–**j** Equivalent data from the four other subjects published by Brandt (1997). **k**, **m** Data equivalent to those of Fig. 3d, i (*black*), from all observers in the paper by Brandt. **l**, **n** Alpha waves with declining amplitudes such as were used to arrive at the predictions shown in (**a**)–(**e**) and (**f**)–(**j**)

obtain coincidence with the measured data only by assuming that the alpha-wave amplitude decreases after a flash. But is this assumption justified? That it indeed happens is verified in an independent experiment, which will now be described.

2.3 Light adaptation contributes to the Berger effect

It is well known that when exposed to light stimulation, the visual system adapts. As a consequence, the evoked potential after a second flash is smaller than that following the first flash (shown in Fig. 5a, c). If alpha waves and evoked potentials are generated by the same neuronal structures, as implied by the model in Fig. 1, we expect that not only evoked potentials should be reduced due to light adaptation but alpha waves as well.

In order to check the prediction that alpha waves decrease after a flash we measured the time course of alpha-wave amplitudes following a flash. We confined our analysis to recordings from the occipital cortex (electrode position Oz) and did not consider other components of the alpha frequency range, such as lateral posterior alpha or left and right mu, for the following reasons:

1. We were interested in cortical areas of the *visual system* which are in the occipital region.
2. Makeig et al. (2002) have shown that power spectra with maxima around 10 Hz in unaveraged EEG and averaged event-related potential (ERP) data have similar topographies in the occipital region, suggesting that EEG and ERP are generated by the same neuronal substrate.
3. The same authors have shown by multiple component analysis that the scalp topography of EEG and ERP in the 10-Hz frequency range is consistent with the assumption that the recorded signals are generated in compact cortical regions.
4. The behaviour of alpha amplitudes after a flash is qualitatively similar in all nine observers investigated, although different quantitatively as far as alpha-wave amplitude is concerned (Fig. 5e, f).

The results of the experiments are shown in Fig. 5. In Fig. 5a, an evoked potential is shown following a flash. In

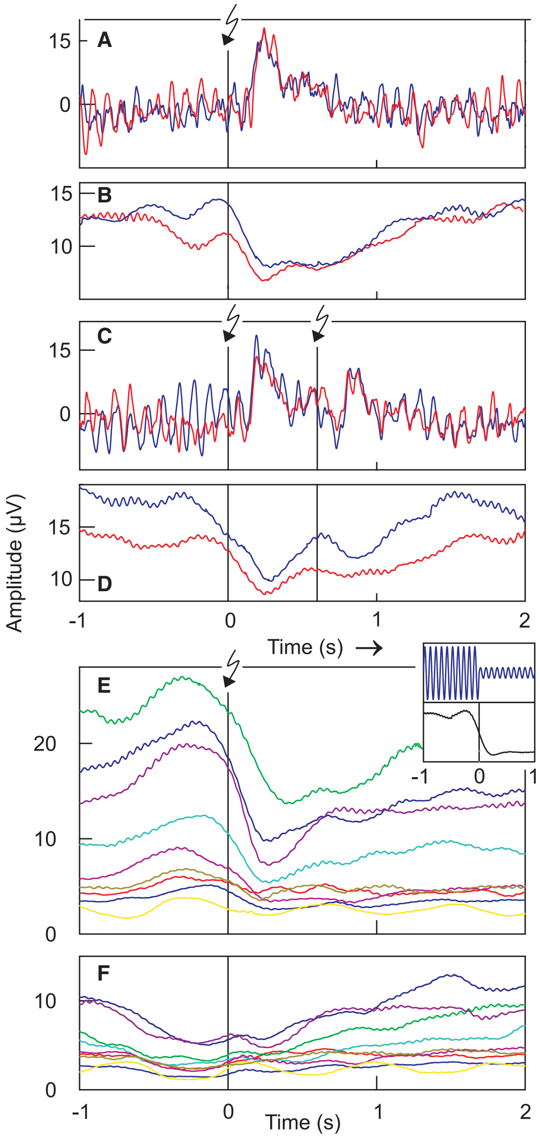

Fig. 5. Visually evoked potentials and time course of alpha-wave amplitudes after flash and double flash. **a** Evoked potentials in response to a single flash. Tracks in red and blue were recorded at different times. **b** Alpha-wave amplitudes in a time window from 1 s before to 2 s after a single flash. *Red* in **a** and **b**, average of $n = 64$ flash presentations, *blue*: average of $n = 51$ flash presentations. **c**, **d** as in (**a**, **b**), but with double flashes (for details see Appendix). *Red*: $n = 56$, *blue*: $n = 62$. **e** Alpha-wave amplitudes as in (**b**), from nine different observers. Here, alpha waves were selected, the amplitudes of which were in the highest third of all records in the time window 500 ms before the flash. **f** As in (**a**). Here, however, alpha waves were selected, the amplitudes of which were in the lowest third in the time window, 500 ms before the flash. In these measurements, the number of samples n was between 50 and 65 for the different curves

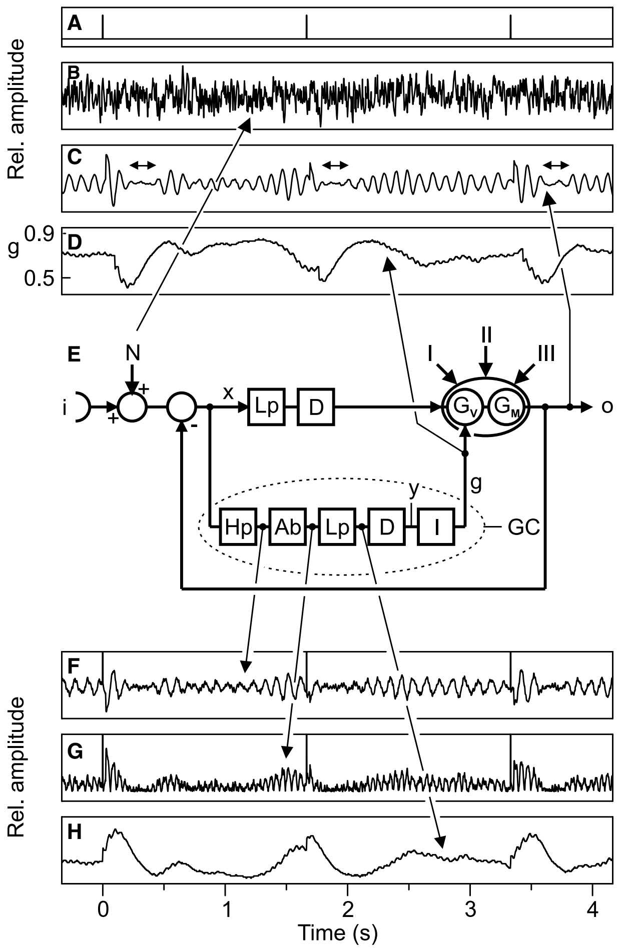

Fig. 6. Feedback-loop system as in Fig. 1, but with an additional loop GC for gain control, model calculations. **a**–**d** and **f**–**h**, time course of functions at different points in the loop as defined in the block diagram (**e**). **e** Block diagram of the loop: *i* Input, *o* Output of the loop. *Lp* Low-pass filter, upper limit frequency 1 Hz, *D* Delay, in upper branch 26 ms, *Gv* and *Gm* Gain element. Gv is the variable gain, which can vary from 0 to 1 and is controlled by the gain control loop GC. Gm is the fixed main gain, which is 12. *GC* Gain control loop with *Hp* High-pass filter, time constant 300 ms, *Ab* Element that calculates the absolute value. *Lp* Low-pass filter, time constant 1 s. *D* Delay, 50 ms, *I* Element that transforms the value y into a value g according to the equation $g = -x + 1$

Fig. 5b, the alpha-wave amplitudes are shown. As can be seen, alpha amplitudes do indeed decrease after the flash, and the decrease occurs within 200 ms, as postulated in Fig. 3d, i and Fig. 4i, n. The alpha amplitude signals in Fig. 5b also include some contribution from the evoked potentials. By comparing alpha amplitudes and amplitudes of evoked potentials in Fig. 3a and f, it becomes clear, however, that the contribution of the evoked potentials is comparatively small, at least in this experiment.

Data from nine observers are shown in Fig. 5e and f. It turned out that the results are easier to interpret if they are separated according to alpha-wave amplitude in the time window 500 ms before the flash. Figure 5e, f show the time course of alpha-wave amplitude before and after the flash. The alpha waves presented in Fig. 5e had amplitudes in the time window 500 ms before the flash that were in the highest third of all records, whereas those in Fig. 5f belonged to the lowest third. In Fig. 5e, it can be seen that the larger the absolute alpha amplitude, the larger the absolute decrease in the alpha amplitude. Figure 5f shows that no decay of the alpha amplitude can be observed if low alpha amplitudes are selected for the analysis. The fact that on average the decrease (Fig. 5e) starts before the flash is a consequence of the band-pass filter used to isolate the alpha band (inset).

2.4 The alpha-wave generating mechanism is partly nonlinear because of a gain control element

As we have seen, the kind of loop shown in Fig. 1a is not appropriate to model the data, because in this loop the gain is constant and after a flash, neither the response to a second flash nor alpha-wave amplitudes are reduced, a consequence contradicted by the experimental results (Fig. 5). A modification of the loop in Fig. 1a can correct this problem. The solution is illustrated in Fig. 6e. The loop in Fig. 1a is extended by an additional channel GC, the function of which is to control the gain as a function of the signal x in the loop. If the signal x is transiently increased by a flash, the gain in the loop must be reduced transiently. To achieve this, the signal x is first high-pass filtered (Hp, because only changes in x are supposed to generate an effect, and slow DC drifts will be suppressed by the high-pass filter), then the absolute value of the signal is taken (Ab), the resulting signal is low-pass filtered to acquire a temporal average, and some delay (D) is also introduced. Finally, the resulting signal y is transferred to $g = -y + 1$. The latter transformation has the consequence that the gain g becomes smaller as x increases (Kirschfeld 1991). Figure 6 illustrates in some detail how such a loop works if impulses are presented at its input, and if noise is also added. It is obvious that after a flash, the gain in the mean transiently decays to a lower level (Fig. 6d), as do the alpha-wave amplitudes (double arrows in Fig. 6c).

The gain-control mechanism makes the whole system nonlinear. In this context, two questions have to be considered. (1) Does the nonlinearity transform the system into a self-sustained, nonlinear oscillator? (2) Is the superposition principle no longer valid, due to the nonlinearity?

As can be seen in Figs. 3c and h, the gain-control mechanism is relatively slow compared to the alpha-wave oscillation frequency: the first maximum (asterisk in Fig. 3c) or minimum (in Fig. 3h) after the flash is not yet reduced, the second peaks and troughs are diminished by some 25%, and it takes more than 200 ms to arrive at the minimal alpha-wave amplitudes. In contrast, the parabolic nonlinear term ($y^2 - 1$) in the *van der Pol* equation (caption of Fig. 2) always has to act immediately in order to create spontaneous oscillations. The consequence of the slow gain control mechanism is that the system (Fig. 6) is not a self-sustained oscillator. There is no oscillation at the output without input.

Figure 7 illustrates the finding that the superposition remains valid with the functions and parameters used in such a feedback loop in spite of the nonlinear gain-control mechanism. Figure 7a and b shows the input signals we used, an impulse and a sine wave of 10 Hz. Figure 7c shows the corresponding output (continuous). The impulse amplitude was set large enough to produce a substantial transient reduction of the gain, from 0.83 to 0.40, as shown in Fig. 7d. The question is whether the output shown in Fig. 7c results from superposition of the responses to the flash and the sine wave, determined independently. To check this, we first determined the response of a feedback loop without gain control to an impulse (Fig. 1a). The gain in this case, however, was not kept constant but changed as a function of time in the same way as in the loop with gain control (Fig. 7d). The result is shown in Fig. 7f. With the same method, the response of the loop to a sine wave was determined (Fig. 7h). There is a modulation of the sine-wave amplitudes comparable to that observed in the experimental data (Fig. 4l, n), due to the modulation of the gain. It takes more than 200 ms before the sine-wave amplitudes reach their minimum. (This slow time course is determined by one parameter, the time constant of the low-pass filter Lp in the gain-control loop GC, Fig. 6). In order to prove the superposition law, we have to check whether superposition of the impulse response (Fig. 7f) and the sine-wave response (Fig. 7h) produces a curve that matches the output signal in Fig. 7c. The dotted function (slightly shifted vertically) in Fig. 7c is the sum of the functions in Fig. 7f and h. The coincidence of the two functions in Fig. 7c shows that the superposition law does indeed hold. It is noteworthy that there is no resetting of the phase of the sine wave by a flash stimulus, just as in a linear system (Fig. 2b).

Figure 7k shows the impulse response that would be obtained if the gain is not modulated, but remains fixed at 0.83. Comparing the impulse response in Fig. 7k with that in Fig. 7f reveals that gain modulation does affect the impulse response. The same happened to the flash-evoked potentials in Figs. 3a and f (light blue). This can be concluded from the fact that the evoked potentials last for more than 200 ms, during which time the gain was significantly decreased. Since the time course of the decrease of gain after the flash is known (Fig. 4l and n), the evoked potential without an influence of the gain modulation in principle can be reconstructed in order to arrive at a "true" evoked potential – that is, an evoked potential that is not modified by adaptation, that is a reduction of the gain.

The model presented in Fig. 6 is not yet sufficient to explain one other well-known property of visually evoked potentials, namely that attention modulates their amplitude: at a high level of attention their amplitude is larger for the same stimulus intensity, and vice versa (Hillyard et al. 1998). To take this property into account, the gain in the model has to be modulated not only via the channel GC, but also by other inputs, one of them being attention. The modulatory inputs I to III at the gain element in the loop shown in Fig. 6e take this aspect into account. It has been shown furthermore that evoked potentials have higher amplitudes in epochs in which the alpha-wave amplitudes are high (Lansing and Barlow 1972; Makeig et al. 2002), which happens in the model if the gain is modulated.

A prediction that follows from this model is that at high levels of attention not only evoked potentials should be large, but also the amplitudes of alpha waves.

In summary, the evidence presented above shows that alpha-wave activity in the EEG can be interpreted as comprising linear and nonlinear components: alpha waves and evoked potentials are superimposed as expected for a linear system. There is no resetting of the phase of the alpha

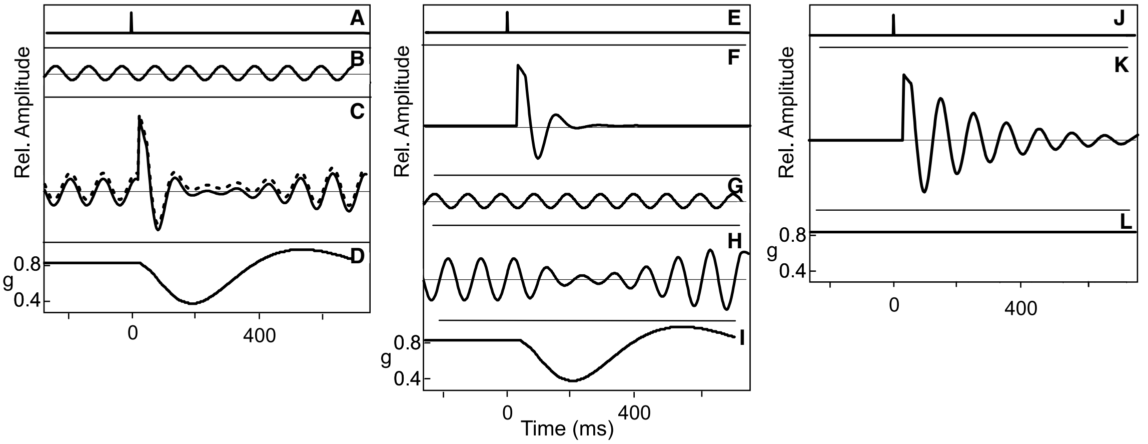

Fig. 7. Demonstration of the superposition law in a system with automatic gain control (Fig. 6e), model calculations. **a**–**d** Loop with gain control. **a**, **b** input. **c** Output. **d** Time course of gain in a loop with gain control as shown in Fig. 6. The low pass filter Lp in the gain control loop GC in this calculation was of second order and had an upper limit frequency of 1.5 Hz. **e**–**i** Loop with pre-programmed gain. **e**, **g** Input. **f** Output in response to impulse. **h** Output of a feedback loop in response to sine-wave input, when the gain of the loop was not automatically controlled as in Fig. 6e, but its time course was pre-programmed to produce the same time course as in (**d**). **j**–**l** Loop with constant gain. K Impulse response of a loop with gain fixed to 8.3. **l** Gain

waves by a light flash. In addition, a nonlinear gain-control mechanism is active: a light flash leads to a transient reduction of gain (light adaptation), which affects the responses to a subsequent flash, as well as the amplitudes of ongoing alpha waves. This gain-control mechanism is relatively slow compared to the alpha-wave frequency, so that the system does not become a self-sustained oscillator. Modification of the gain is also due to attention. The model implies that visually evoked potentials and alpha waves are generated by the same neuronal mechanism.

3 Discussion

3.1 Limits of the model

As far as the particular properties of the loop shown in Fig. 6e are concerned, it is clear that the suggested solution is highly simplified. It could well be, for instance, that in addition to the channel GC, there is also a direct input from the stimulus to the gain-controlling unit G. Furthermore, the loss of alpha-wave amplitude and sensitivity was tested only with flashes of light as the stimulus. How sensitivity and alpha waves are modified by longer-lasting stimuli, different stimulus modalities, attention or even motor activity (eye opening) is still an open question. It is also important to show how close the relationship between amplitudes of alpha waves and those of evoked potentials actually is. In principle, such details can be worked out by specifically designed experiments.

One remaining question is whether the conclusions drawn here for the alpha waves are also valid for EEG waves in other brain areas, or even in different frequency bands. Findings from the motor cortex are directly comparable. The motor response measured at particular muscles of the hand, for example, was found to be larger when transcortical magnetic stimulation (TMS) was applied at high EEG amplitudes in the alpha range (Rossini et al. 1991). This suggests that a loop with variable gain might also be operating in the motor cortex.

Visual stimuli to which the subject attends elicit visually evoked potentials of larger amplitudes than unattended ones do, indicating an increased gain under attention (Hillyard et al. 1998). In monkeys, it was shown that the amplitudes of EEG waves in the gamma range (frequency components greater than 20 Hz) increase if attention is directed to a location at which an object is to be expected (Cardoso de Oliveira et al. 1997). This indicates that the gain in a loop comparable to that shown in Fig. 6e could be present in the gamma range as well.

3.2 Relationship to results in the literature

Most electroencephalographic (EEG) studies of human visual perception have assumed that averaged-evoked potentials such as visually evoked potentials (VEPs) generated by brief visual stimuli reflect neural activity within discrete, functionally defined visual cortical processing units. It is also well known that different frequency bands contribute to evoked potentials (reviewed by Basar 1998a). By independent component analysis, Makeig et al. (2002) have shown that at least eight classes of components, including those producing central and lateral posterior alpha, left and right mu, contribute to visually evoked responses. In spite of this multitude of components, there are a number of arguments corroborating the view that 10-Hz components of VEPs and occipital alpha waves, such as are analysed in this paper, are in fact generated by a common neural substrate:

1. Makeig et al. 2002 have shown that alpha waves – that is, the components around 10 Hz of the EEG, and 10-Hz components of VEPs – are generated in the same occipital cortical region.
2. It was shown that evoked potentials have higher amplitudes in EEG epochs in which the alpha-wave amplitudes are high (Lansing and Barlow 1972; Makeig

et al. 2002) and vice versa, which indicates a functional relationship between the two waveforms.

3. As we have shown, light flashes not only generate evoked potentials, but in addition, they reduce the gain (sensitivity). The consequence is that the amplitude of VEPs is reduced, but also that of alpha waves (Fig. 5e). This means that the structures that generate alpha waves as well as those generating visually evoked potentials are both equivalently affected by visual input.

These facts favour the view that alpha waves and visually evoked potentials are generated by the same neuronal structures. This is the reason why we confined our analysis to occipital alpha waves, because only with these is a functional relationship between alpha waves and visually evoked potentials to be expected. With the noninvasive EEG technology, it seems impossible at present to identify the alpha-wave- and visually evoked potential-generating structures beyond the level worked out by Makeig et al. (2002).

Sometimes brain waves have been considered a mere consequence of linear processing, such as band-pass filtering or linear oscillation (van der Tweel 1964; Spekreijse 1966; Lopes da Silva et al. 1974). More recently, a resetting of the phase of alpha waves by visual stimuli was described (Brandt 1997; Makeig et al. 2002).

By using the data of Brandt (1997), we have shown that *phase-selective averaged visually evoked potentials* correspond to the superposition of *random-phase averaged evoked potentials* and alpha waves, supporting the inference of a linear mechanism and excluding the possibility of phase resetting by a stimulus.

A detailed analysis of phase relationships between alpha waves and evoked potentials was made by Makeig et al. (2002). They show in their Fig. 2 (upper panel) ongoing activity and how this activity is modified by a light stimulus. In their experiments, flashes were presented at all phases of alpha waves, not only at two specific phases as in the paper by Brandt (1997). They describe the response to the flashes as a stimulus-induced resetting of the phase of ongoing EEG activity. This seems to be inconsistent with the result presented here, namely that the phase of ongoing activity cannot be changed by a light stimulus. Analysis of Makeig et. al.'s data shows, however, that their results at least do not exclude a linear mechanism as proposed here. Since this is a lengthy analysis, it is illustrated in the *supplementary material*.

3.3 Functional considerations

Why does the brain exhibit electrical oscillations at all? Since Berger this has been a basic question of encephalography. If linear mechanisms like band-pass filtering by feedback loops generate brain waves in particular spectral bands, then some general conclusions can be drawn regarding the function of these waves. All theories that consider oscillations and periodic synchronization of spike activity in the context of increased attention are compatible with a mechanism based on band-pass filtering: if attention increases the gain, it increases the amplitudes of brain waves as well, with the additional consequence that spike frequencies in the corresponding neurons are modulated accordingly. This increases the probability of achieving synchronization. Such attention-induced synchronization was demonstrated in the visual and somatosensory cortices (Fries et al. 2001; Steinmetz et al. 2000). In contrast, theories in which the *oscillation phases* must be controlled by a stimulus or in which different neuronal assemblies have to become synchronized with different phases are difficult to reconcile with a band-pass filtering mechanism. The reason is that if signals in linear feedback loops are combined, they are simply superimposed, as illustrated in Fig. 2a–d and Fig. 7. The resulting phase depends on the instantaneous state of the components, i.e. their amplitude, relative phase, etc., parameters which are almost impossible to control with sufficient precision. Furthermore, there is no way that a stimulus can affect the phase of the ongoing oscillatory signal; there is no resetting of the phase, as can happen in nonlinear oscillators (Fig. 2b, f).

According to the data presented here, brain oscillations might be a means of controlling the gain of neurons and in this way keeping them within their working range. Light adaptation and increasing attention have opposing effects: light adaptation lowers the gain and reduces alpha amplitudes, whereas increasing attention magnifies it and increases occipital alpha amplitudes. Light adaptation and decreasing attention have equivalent effects (K. Kirschfeld, in preparation). A consequence of this type of mechanism is that thresholds, for instance to light stimuli, should not be constant but fluctuating in temporal correlation with alpha-wave amplitudes.

Quite early on, Berger made the following observation: if the hand of an observer is touched or stroked, alpha-wave activity is reduced. How can this happen? We know from functional magnetic resonance imaging studies that cortical areas are particularly active if they are associated with the modality of a presented stimulus. This implies that other areas are less active in comparison. In terms of alpha waves, this means that touching the hand increases the activity in the somatosensory cortex, but reduces activity and hence alpha-wave amplitudes in the visual cortex. These observations are corroborated by a finding made by Basar and co-workers (1998b). They showed that there is an *inverse relationship* between amplitudes of alpha components of the spontaneous EEG measured at the vertex and the amplitude of the visually evoked potential measured as usual at the occipital region. These observations show that the control of gain is a complicated process, in which not only the sensory input is relevant, but also attention, or, in more general terms, the distribution of brain activity in a particular behavioural context.

The distribution of alpha-wave activity resembles the distribution of the haemodynamic response as measured with functional magnetic resonance imaging techniques (BOLD effect); both are high in functionally active cortical areas. The BOLD effect correlates best with local field potentials rather than with spike activity (Logothetis et al. 2001). Local field potentials are also the main source of the EEG activity measured at the skull. Could it be that alpha waves are also the trigger for the haemodynamic response?

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Appendix

EEG recordings and evaluation

Data presented in Fig. 5 were measured as follows. Nine subjects (aged 20–50 years, five of them females, with normal vision or vision corrected to normal) participated in the experiments and gave their informed consent to the experiments. They sat in an armchair in front of a monitor (Iiyama Vision Master Pro 21, 39 × 29 cm, refresh rate 100 Hz) at a distance of 60 cm. The flash stimulus, a $3 \times 3^\circ$ square (luminance of $12\,\mathrm{cd/m^2}$), was presented for 20 ms on a background of $4\,\mathrm{cd/m^2}$. Data were collected from five electrodes, but only those from position Oz are presented, with the nose serving as reference. Impedance of the electrodes was 4–10 kΩ. The signals were band filtered between 0.1 Hz and 200 Hz, at a sampling rate of 1000 Hz. The electro-oculogram of the right eye was recorded, and trials with eye-blink artefacts were rejected.

The alpha amplitudes (Fig. 5) were determined as follows. To isolate alpha waves, signals were band-pass filtered (8–12 Hz, Butterworth Second order). This filtered function was rectified and then low-pass filtered (12 Hz, Butterwoth Second order); see inset in Fig. 5.

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