The modulation of alpha-wave amplitude in human EEG by the intention to act with a motor response

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The most conspicuous signal in the human EEG is the so-called alpha wave, oscillations in the frequency range of 8 to 12 Hz. Visual stimulation of the retina suppresses the amplitude of alpha waves (Berger effect), and increased attention can reduce them. Here I show that one more parameter significantly affects the amplitudes of alpha waves: the intention to act by a motor response. Together with data from the literature, these results show that alpha waves are not part of the visual processing network but rather part of a long-range neuromodulatory network. The modulation modifies latencies in perception or motor response. The relevant mechanisms are located in early cortical visual areas; their activity may contribute to hemodynamic changes in these areas and thus explain dissociations between *Bold* signals and spike activities mentioned in the literature.

In spite of intensive research on the electroencephalogram (EEG) over more than 70 years, there is still no generally accepted theory on the functional meaning of occipital alpha waves. There are, however, a number of robust findings on how the amplitude of alpha waves can be modulated.

For instance, alpha-wave amplitude is large as long as subjects keep their eyes closed, and it is reduced when eyes are opened (alpha blocking, Berger effect). The conclusion drawn from this observation is that the state with reduced alpha-wave amplitudes is an activated state with enhanced processing of information and increased excitability of cortical neurons[1]. Fitting with this interpretation is the finding that increased attention also can induce a reduction in alpha-wave amplitudes[2-5].

A new aspect came into focus through experiments on visual suppression in monkeys. These experiments showed that the power of alpha-range field potentials, measured with extracellular electrodes in early cortical processing areas (V1 and V2), is closely related to the representation of stimulus visibility. Quite unexpectedly, this is even the case if, at the same cortical location, the spiking activity of neurons is not modulated according to stimulus visibility[6]. In the meantime, it has become clear that spikes and field potentials represent different aspects of cortical activity[7,8], insofar it is not to be expected that both show equivalent behavior. Why alpha range field potentials seem to be closer to perception at these locations than nearby spiking neurons is still not understood.

In the monkey experiments, perceptual suppression was induced in the so-called generalized flash suppression paradigm: first a salient target was presented, followed 1.4 s later by an extended surrounding pattern. This pattern can suppress the target's visibility, and its parameters can be adjusted so that pattern suppression happens only in a subset of trials. The monkeys were trained to hold a lever as long as the target remained visible and to release it as soon as the target disappeared. The consequence of this paradigm is that disappearance of the target from perception is always coupled with a motor (muscle) response, but persistence is not.

Even if it does not seem likely that motor responses affect the amplitude of alpha frequency oscillations in the visual cortex, the possibility that they could do so has not yet been excluded; it could be that it is rather the motor response and not the target’s persistence/disappearance from perception that is the origin of the alpha range field potential modulation.

No functional relationship has yet been established between alpha waves in the human EEG and alpha range local field potentials measured within the monkey brain. A correspondence seems possible, however, and we therefore devised an experiment in humans analyzing whether motor action in context with visual stimulation affects alpha-wave amplitudes.

We used primarily an approach recently worked out by Harris, called differential conditioning, because it allows determining with high sensitivity how different parameters affect the amplitude of alpha waves[9]. It relies on the fact that the amplitude of alpha waves can be modified in a Pavlovian conditioning paradigm: To a participant two consecutive stimuli are presented, a conditional stimulus (CS), which does not elicit a response, and an unconditional stimulus (US), which is response evoking. After several learning trials, a conditional response (CR) is elicited to the CS.

In the differential conditioning paradigm not only one CS is presented but, in random order two (a tone of either 600 or 1200 Hz), whereby only one of the tones is followed by an US, in our case a visual stimulus, which suppresses alpha-wave amplitudes (the Berger effect); the other one is not followed by an US, therefore no alpha suppression will occur.

After a number of learning trials, the amplitude of alpha waves will be suppressed whenever that CS (tone) is given which is followed by the US (visual stimulus). Remarkably, the alpha suppression starts more than 500 ms before the visual stimulus itself is presented, it occurs in anticipation of the suppression due to a light stimulus, which, as the participants have learned, will happen later. If , however, this conditional stimulus is given which is not followed by a visual stimulus, no anticipatory suppression of alpha waves takes place. We also included motor responses in this paradigm, as described in the Results section.

Pavlovian conditioning is a rather specific experimental paradigm. To check the generality of our conclusion, we also used a simpler approach in which alpha amplitudes were modulated by light flashes that suppress alpha-wave amplitudes (classical test of the Berger effect) with and without a motor response. The data, which confirm the conclusion drawn from the conditioning experiments, are presented in the **Supplementary Figure 1** and **Supplementary Table 1** online.

Results

Conditioning experiments

Figure 1 shows the outcome of different types of experiments that followed the scheme of differential conditioning. Figure 1a shows the standard case as introduced by Harris[9]: either tone 1 was presented (beginning at $t = -1$ s, ending at 0.1 s) without a flash and button press (red), or tone 2 which was combined with a flash and button press (blue). As is visible in the red track, onset of tone 1 induced a small transient depression of occipital alpha amplitudes. In contrast, onset of tone 2 induced a stronger depression of alpha-wave amplitude, which arrived at a minimum at $t = - 0.5$ s and maintained a low level until time $t = 0$, at which the flash was presented. Following this flash, alpha amplitudes were strongly suppressed, a manifestation of the Berger effect. To make Figure 1 easily readable, whenever participants in a particular trial were asked to press a button, the time course of alpha amplitude over time is drawn in blue; if participants were not required to react by pressing a button, red was used.

The interpretation of Figure 1a is as follows: By the onset of tone 1, no long-lasting decrease in alpha-wave amplitudes was triggered because participants had learned that no alpha-wave suppressing flash would follow. After onset of tone 2, however, because it was expected to be followed by an alpha amplitude-suppressing flash, alpha amplitudes were suppressed in anticipation of the following Berger effect. This result basically is in agreement with the outcome of the experiment by Harris[9].

Figure 1 about here

The two cases, illustrated in Figure 1a, differ with respect to the flash, which is presented in only one of them. There is, however, a second difference; namely, that only in one of the scenarios were participants asked to respond by pressing the button. Because alpha waves are considered to be relevant in the context of vision, it seemed unlikely that button pressing would affect the modulation of occipital alpha-wave amplitudes. We nevertheless tested the influence of button pressing as follows: Participants were asked to press the button not only in response to the end of tone 2 with the flash but also at the end of tone 1 without a flash. In Figure 1b, the two cases are compared: as it shows, there is an anticipatory alpha depression in both cases before t = 0, also in the case when no flash has been presented. In this case, the anticipatory alpha depression must have been attributable to the button press that happened later.

To verify this finding still further, we included some more experimental conditions in the differential conditioning scheme. In the experiment illustrated in Figure 1c, participants were asked not to respond to the flash by pressing the button (red) but to respond with a button press at the end of the tone that was not followed by a flash. As the figure shows, the decrease in alpha amplitude after initiation of the tones in the two conditions is similar. This finding indicates that in a conditioning experiment, a flash without button pressing can generate anticipatory alpha depression.

For some idea about the relative contribution of button pressing and the Berger effect to the anticipatory alpha-wave suppression, we combined the conditions: flash with or without button press. As can be seen in Figure 1d, the anticipatory alpha-amplitude suppression is significantly more pronounced in the case with (blue) compared to the case without (red) button pressing.

There is general agreement that low alpha-wave amplitudes correlate with increased attention[2-5]. Additionally, one might argue that after onset of that conditioning tone followed by a button press, the increased attention suppresses the alpha amplitudes. On the other hand, the light flash in the experiments described in Figure 1 a–d was so strong that there was no danger that it could have been overlooked. Therefore, with respect to detection of the flash and with respect to the time of the flash (always 1 s after onset of the conditioning tone), no increased level of attention seemed to be necessary.

To obtain additional information on this point, we modified the light flash: We made it smaller and darker so that it could be detected only with >90% probability. In this case, it was to be expected that attention, in expectation of the just-detectable flash, would be higher compared to the case with a strong flash.

Figure 1e shows the outcome of this experiment: In the combination tone without flash and motor response (red) and just-detectable flash with motor response (blue), it is obvious that the result is similar to that shown in Figure 1a, in which a strong flash was used. Anticipatory alpha suppression seems to be independent of whether the flash followed by a button press is large and intensive or small and weak.

We also compared the two flash types (strong and weak) directly in a differential conditioning experiment, as shown in Figure 1f. Obviously, under our experimental conditions, there is no difference in the anticipatory alpha-amplitude suppression, regardless of whether the conditioning tone is followed by a strong or a weak flash. This outcome supports the view that the intention to act by motor response is the relevant factor for the anticipatory alpha-amplitude suppression but not the level of attention.

The data shown in Figure 1a–f were recorded from the occipital cortex. The effects described by Harris[9] have been largest at the parietal cortex. We therefore present in Figure 1g–l data recorded simultaneously with those illustrated in Figure 1a–f from position Pz. Except for panels c and i, the results are the same.

The experiments illustrated in Figure 1 showed that a significant anticipatory alpha-wave suppression in Pavlovian conditioning can be induced as follows:

1. by flashes with a button press
2. by flashes without a button press
3. by a button press without a flash

The significance of the results is summarized in Table 1. When analyzing the data, the fact must be considered that the differential conditioning paradigm is rather sensitive only with comparison of the data collected within individual pairs, as they are presented in Figure 1. Only in this condition is the alpha-generating system, subject to modification by learning, in a similar state when the two different stimuli are presented. Details on this point are given in the statistics description in the Methods. Under our experimental conditions, the anticipatory alpha-amplitude depression was largest in the case of a flash with a button press (Fig. 1d,j). We could not identify a difference in the size of this effect when comparing large and bright with smaller and darker flashes (Fig. 1f, l).

Table 1 about here

Discussion

The paradigm of differential conditioning

We used Harris' approach of differential conditioning[9]; however, with some modification affecting the results. In Harris' approach, presentation of the conditional stimulus was delayed until spontaneously occurring large alpha waves were detected, defined by a threshold. As a consequence, for statistical reasons, in his data there was always a significant increase in mean alpha amplitudes before presentation of the conditioning stimulus. In our experiments, we always presented the conditioning stimulus 8 s after the last one, regardless of the actual alpha-wave amplitude. Therefore, for statistical reasons, here the mean alpha amplitude, before presentation of the conditioning stimulus, remained basically constant (Fig. 1).

Following the light flash (unconditional stimulus), Harris' data showed a small transient increase in alpha amplitudes, which was not followed by a strong decrease, indicative for a

Berger effect. In contrast, in our data, every light flash was followed by a strong Berger effect. This distinction is also a consequence of the difference in our experimental paradigms: Alpha waves spontaneously are modulated in the shape of “spindles”; they wax and wane continuously. Thus, if the tone (conditional stimulus) is presented at a spontaneous large alpha amplitude, as in Harris’ experiments, the alpha amplitude will spontaneously decrease so that the later-presented light (unconditional) stimulus is given at low alpha amplitudes. It is known that at low alpha amplitudes, the Berger effect is small or can even be inverted[10]. In our experiments, following the tone, alpha amplitudes were reduced only moderately; thus, in response to the flash, a significant further reduction of alpha amplitudes (Berger effect) was still possible.

Is there perception-related alpha activity?

Our experiments demonstrated that the intention to generate a motor action can modulate occipital alpha waves beyond the Berger effect (suppression by visual stimuli). The question is whether this finding can help with interpretation of the results in monkeys on the modulation of alpha range field potentials by perceptual suppression[6].

In these experiments, in a subset of trials, a high-contrast visual stimulus (target) vanished completely from perception. The spiking of neurons in cortical areas V1 and V2 was uncorrelated with the perceptual visibility of the target; however, unexpectedly, the alpha range local field potentials, recorded with the same electrodes, showed significant perception-related power modulation[6].

Assuming that alpha range field potentials in the monkey visual cortex are functionally related to alpha waves in the human EEG, the results presented in this paper offer an explanation for this unexpected result. The monkeys had been trained to release a lever when the object vanished but to hold it if the target remained visible. This design meant that perceptual disappearance was always combined with motor (muscle) activity, but perceptual persistence was not. Thus, it may be that the motor activity rather than the change in perception contributed to or even caused the demonstrated stronger perception-related modulation of alpha range field potentials in monkeys.

Wilke and co- workers previously considered this possibility as an explanation, but it has been viewed as doubtful because the perception-related alpha modulation was observed well before the execution of the monkey's motor response; thus, it seemed unlikely that this response could be the origin of the earlier alpha modulation[6].

A closer look at the monkey experiments shows that regarding the motor response, the paradigm of generalized flash suppression can be considered a Pavlovian conditioning setup: After presentation of the surround, whenever the target disappeared from perception, the monkey responded by releasing the lever. Thus, by learning, the monkey would eventually already know as soon as the target disappeared that he will later release the lever. It may well be—as it is in humans—that this intention to act by the motor response induced the stronger decrease in the power of the alpha range field potentials compared to the case of a persistent target. In addition, this stronger power depression may happen before the actual motor response. Qualitatively, this behavior corresponds to the behavior of the human alpha-wave amplitudes demonstrated in Figure 1d: Here, also after the beginning of the conditional stimulus, the amplitude was more strongly depressed in the case of a subsequent motor response. The findings on human alpha-wave amplitudes and those from the monkey experiments are compared in more detail in the **Supplementary Figure 2** online. This Figure shows equivalent behavior between the human alpha waves and the monkey alpha range local field potentials in connection with the intention to act by a motor response. This equivalency supports the view that human alpha waves and alpha range field potentials in monkeys may be relevant in an equivalent functional context.

Alpha waves are part of a long-range neuromodulatory network, not part of the visual processing network

The experiments illustrated in Figure 1 show that a visual stimulus can suppress alpha amplitudes (Berger effect). But they can also be modulated independently of any visual stimulus, e.g., if participants have learned that later a visual stimulus will be presented or that a motor response will be executed. This dissociation of alpha amplitudes from visual stimuli shows that alpha waves are not part of the visual processing network that leads to perception of a visual object. I argue that they belong to a different network that prepares the perception-related neurons for adequate processing of a visual stimulus. "Adequately processed" could mean, for example, that the gain of the information processing network is adjusted so that an expected stimulus is neither overlooked nor drives neurons into saturation. Such a gain modulation happens, for example, by attention (increased sensitivity) or by adaptation (reduced sensitivity). Increased attention can induce a reduction of alpha-wave amplitudes[2-5], emphasizing the possible functional role of alpha waves in gain control, as in a neuromodulating network. Regarding alpha range field potentials in monkeys, they carry little information about a visual stimulus and therefore have been considered rather to reflect neuromodulatory inputs[7].

Instead of adjusting the gain, adequate processing can also mean that the processing speed is made as fast as possible, usually an advantage for an organism. Data from different approaches unanimously show that the modulation of latencies is widespread in the early stages of the visual system, and evidence indicates that alpha waves are functionally important in this context. Furthermore, this latency modulation is not confined to the retinotopic location of the stimulus that triggers the effect but spreads over large areas of the cortex, affecting processing speed of perception of stimuli presented later elsewhere in the visual field. The psychophysical experiment described below illustrates this point.

When a dot is briefly presented against a homogeneous background, the participant can see the dot (because of the visual processing network) but cannot see any change in the background. Nevertheless, for the next 100–1000 ms, there are significant modifications in visual projection centers of the surrounding background. If a second visual stimulus is presented within this time span, even at distances many degrees apart, it will be perceived with a latency up to 100 ms shorter than if the second stimulus had occurred alone. This latency arises from activity of a neuromodulatory network. The mechanism is the basis of the impressive so-called line-motion illusion[11,12], illustrated in the supplementary information of a paper by Jahnke et al.[13]. There are many other psychophysical demonstrations in which the time to perception is modified according to stimulus context, with several discussed in the context of the so-called flash-lag effect[14].

Clearly, the mechanism that mediates this latency decrease is localized in the early visual cortex. The most direct evidence comes from experiments in anesthetized cats[13]. A line-motion illusion stimulus was presented, and cortical activity recorded by a real-time optical-imaging technique. The results showed that a small, briefly presented square created gradually propagating subthreshold cortical activity that extended far beyond its retinotopic projection. A closer look at the data shows that the parameters of this subthreshold activity corresponded to what is expected from the line-motion illusion[11,12].

Using brief, small visual stimuli and real-time optical imaging also showed that in awake monkeys after stimulus onset, cortical activity spreads from its retinotopic site of initiation with a velocity of 1–2.50 cm in 100 ms. The area finally covered by this activity was at least 10 times larger than the retinotopic representation[15]. This activity has been considered as reflecting subthreshold synaptic activity. The similarity to the cat cortical signals suggests that both reflect long-range latency-modulating activity.

Occipital alpha waves in humans can be seen in the context of this latency control. If a peripheral short visual stimulus (e.g., 10 degrees apart from the fovea) is presented to a person, two things happen: (1) the reaction time given to a foveal stimulus in a time window of 100–1000 ms after the peripheral stimulus is significantly reduced; and (2) the amplitude of occipital alpha waves in the equivalent time window also is reduced: the smaller the alpha amplitude, the shorter the latency. In addition, the traveling speed of the modulating signals as derived from these experiments is 1 cm in 100 ms, i.e., of the same order as the velocity determined by optical-imaging techniques in the monkey visual cortex[16].

The conclusion from these findings is that any visual stimulus activates at least two pathways: the visual perception pathway and a latency-shortening neuromodulatory pathway. In addition, activity of both pathways is already reflected in neuronal activity in the early stages of the visual cortex. As emphasized by Logothetis[17], it is to be expected that both pathways will contribute to signals, depending on hemodynamic responses such as the blood-oxygene-level-dependent (Bold) contrast mechanism[18]. This dual involvement might explain dissociations between *Bold* signals and multi-unit activity because the latter most likely reflects only the visual perception pathway[7].

Single-cell recordings in areas V1 and V2 in binocular rivalry show minimal or no modulation in firing rate during perceptual suppression[6,19,20]. The interpretation has been that perceptual visibility of a stimulus is determined only at later stages. In contrast, functional imaging (fMRI) studies in equivalent experiments in humans have revealed a strong correlation of functional imaging signals with visibility also in early cortical areas[21,22] and even in the lateral geniculate nucleus[23,24], indicating that mechanisms relevant for binocular rivalry occur already in these early visual centers.

A possible interpretation on the basis of the results presented here is as follows: In rivalry paradigms in early visual centers, not only are alpha range local field potentials and fMRI signals modulated in synchrony with perception, but spike activity is, as well. The latter occurs, however, not with respect to spike rate but with respect to latency. Latency modulation is expected in the order of 100 ms. Such a modulation in perception latency is easily detected in psychophysical experiments; however, it can scarcely be seen in spike activity recorded in experiments on binocular rivalry because in these experiments the times of persistence or disappearance of the patterns are not known with sufficient precision to detect such latency differences. Spike rate in correspondence with perception then is modulated in higher centers only .

Methods

Participants

The study included 11 healthy participants, 8 men and 3 women, in the conditioning experiments, and 4 more men and 2 women in the experiments on the Berger effect. Age ranged from 20 to 40 years, and they had normal or corrected-to-normal vision and had given their written informed consent to the experiments. These participants are a selection of the population of our institute that had proven to exhibit large alpha-wave amplitudes. The Ethics Committee of the Medical Faculty of the University of Tübingen approved this study.

Data collection

Data were collected from five EEG electrodes, but only those from positions Oz and Pz (Fig. 1) or Oz (Supplementary Figure 1online) are presented, with the two earlobes serving as reference. Impedance of the electrodes was 4–8 kΩ. The signals were band-filtered between 0.1 and 200 Hz, at a sampling rate of 1000 Hz. An electro-oculogram of the left eye was recorded; it signaled eye movements in the vertical and horizontal directions. Trials with artefacts, arising from eye-blinks, for example, were rejected.

The amplitude of alpha waves was determined as follows: An EEG trace was band-filtered (8–12 Hz, Butterworth second order). This trace, rectified and low-pass filtered (Butterworth digital filter of fourth order; upper-limit frequency, 12 Hz) represents the alpha-wave amplitude as shown in Figure 1 and Supplementary Figure 1 online.

Conditioning experiments

The participant, sitting in an armchair in front of a monitor screen (Ijama Vision Master Pro 21, 39 × 29 cm; refresh rate 100 Hz) at a distance of 100 cm, focused on the fixation point (diameter 0.1 degree, intensity 2 cd/m^2).

The conditioning stimuli were tones with frequencies of 600 and 1200 Hz, of 1.1 s duration. They were switched on at t = -1 s (inset Fig. 1) and presented by headphones. Intensity was adjusted so that they were easy to hear but not unpleasantly loud. Two different unconditional stimuli were used. The first was a large checkerboard (18 degrees horizontal × 13 degrees vertical; size of squares 4.5 degrees × 3.25 degrees, presented on a monitor 22 degrees × 16 degrees). The intensity of the bright squares was 10 cd/m^2 and that of the dark ones 0.1 cd/m^2, as was the intensity of the monitor screen not covered by the checkerboard. The second was a small checkerboard (9 degrees × 8 degrees; same size of squares). The intensity of these bright squares was 0.15 cd/m^2 and that of the dark ones 0.1 cd/m^2, as was the monitor screen background. Checkerboards were flashed for one frame that corresponded to 10 ms. The time from beginning of one conditional stimulus to the next was always 8 s.

During the learning session we presented one block of 30 trials. Within this block 15 trials were in condition 1 (as in Fig. 1a,g, the tone of 600 Hz followed by flash and button press) and 15 trials in condition 2 (tone of 1200 Hz without flash and button press); the two conditions were randomely intermixed. In pilot experiments, it turned out that this number of trials was sufficient for participants to learn the connection between conditional und unconditional stimuli. This corresponds with the result presented by Harris[9].

One to two minutes after the learning session, in the actual experiment, we presented the participants first a block of 30 trials. Within this block 15 trial were in condition 1 (as in Fig.1a,g, the tone of 600 Hz followed by flash and button press) and 15 trials in condition 2 (tone of 1200 Hz without flash and button press); the two conditions were randomely intermixed. The same block was presented three more times, and after each block a pause of 1 to 2 minutes was inserted. These 60 trials for each condition and participant were averaged. Figure 1 shows the grand averages from either 11 (Fig. 1a,e,f,g,k,l) or 10 (Fig. 1b,c,d,h,i,j) participants.

Method used in the experiments on the classical Berger effect are described in **Supplementary Method** online.

Statistics

Conditioning experiments

To achieve statistical significance in this kind of experiment is difficult: The amplitudes of alpha waves wax and wane spontaneously, and because the system can "learn", it is modified according to boundary conditions. This means that one of the prerequisites for classical statistical analysis, namely that the system is "stationary" during data collection, is not fulfilled. We applied two strategies to improve the situation:

1. We selected participants with high alpha-wave amplitudes. This attribute is person specific and maintained over many years. In these participants, signals are large and experiments can be shorter; therefore, the probability that the system is changing during data acquisition is reduced. It means, however, that our results will be reproducible only if a similar selection of participants is used in the experiments.

2. We used a method of differential conditioning introduced by Harris[9]. In this approach, two different experimental conditions in temporal random order are intermixed. Therefore, changes in the system, if they are not too fast, affect both conditions in a similar way.

The statistical significance of the data in Figure 1 was validated as follows: From time t = - 0.25 to - 0.15 s for each participant, the alpha-wave amplitude was averaged. This time span was selected because the differences between the data of the two conditions used in the differential conditioning scheme appeared to be maximal in this study. Afterwards, the mean from the respective 10 and 11 participants was calculated and together with the standard error plotted at time t = - 0.2 s. The question was whether the mean values for the two conditions in each differential conditioning experiment at t = - 0.2 s were significantly different or not. Parameter *p* values from pairwise t-tests of data presented in Figure 1a–l are shown in Table 1. Red numbers in the table show those cases in which the data at the 0.05 level were significantly different.

The fact that the system is learning—it is modified according to boundary conditions—means that in the paradigm of differential conditioning, the result is valid only for the particular pair of conditions used. If one compares results from different pairs, they may be contradictory. The combination "flash without motor response," for instance, has been used twice: first in combination with "motor response without flash" (Fig. 1c) and second in "flash with motor response" (Fig. 1d). The alpha-amplitude depression due to the stimulus "flash without motor response" in the first case was 5.05 ± 0.58; in the second case, it was 6.33 ± 0.60. These numbers at the 0.05 level are significantly different (pairwise t-test: $p = 0.0017$; $t = -4.42$). If the system had not been modified by the partner in the differential conditioning scheme, the outcome in the two cases of course would be the same.

Given this particular situation, applying an alpha correction did not seem to be adequate for the statistical analysis of all data.

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Figure legend

Figure 1. Grand average of alpha amplitudes in several differential conditioning experiments. At time -1 s, a tone of either 600 or 1200 Hz was switched on, ending at time +0.1 s (inset on top). At time 0 s (inset on top), a strong flash (*F*), a weak flash (*f*), or no flash was presented. In the left panel, the flashes are indicated by letters, which apply also for the right panel. Participants were instructed to respond either by button press after the flash or at the end of the tone (blue tracks) or not to respond (red tracks). Whenever a flash was presented, the alpha amplitude shortly after t = 0 decreased strongly within 300 ms (Berger effect), which did not happen without a flash. The relevant signal in this figure is, however, not this well-known Berger effect, but the fact that some 500 ms after the beginning of the tone at -1 s, a significant decrease of alpha-wave amplitudes appeared if either a flash or a motor response or both followed. The calibration of the alpha amplitudes is indicated by two horizontal bars on the ordinate in every individual drawing; they mark 4 and 6 μV, respectively (see numbers down the left). The points mark averages over 100 ms; the bars indicate standard error of the mean. Data in figures a, e, f, g, k, and l are averages from 11 participants; those in b, c, d, h, i, and j are the averages from 10 participants. Data in the left panel were recorded at electrode position Oz and those in the right panel at Pz .

Table 1

Significance of the data from Figure 1.

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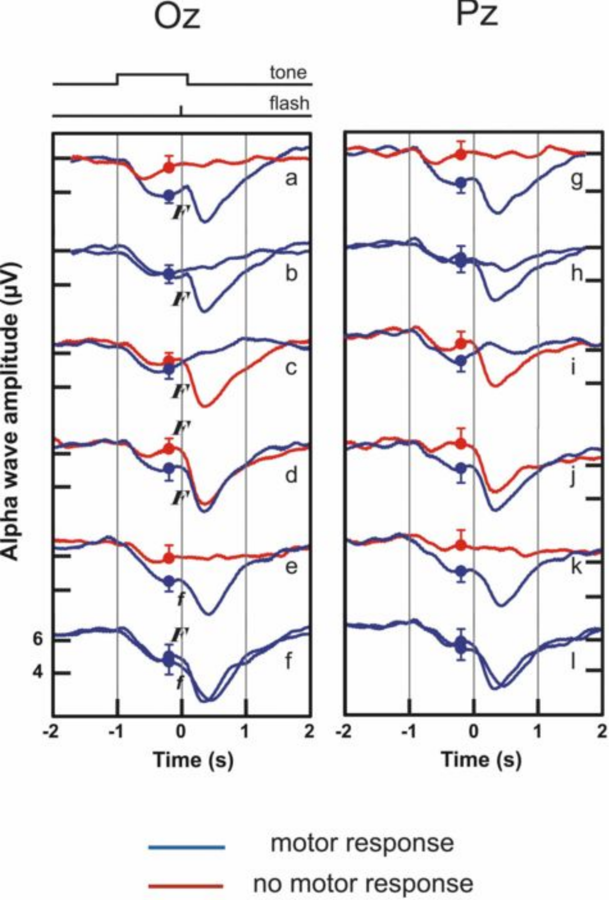

Kirschfeld Figure 1

Table 1 Significance of data Fig. 1

	p		p
a	0.0014	g	0.0034
b	0.6899	h	2.2639
c	0.0926	i	0.0000
d	0.0040	j	0.0000
e	0.0009	k	0.0032
f	0.0627	l	0.0753

Kirschfeld Table 1