Brain oscillations differentiate the picture of one’s own grandmother

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Available online 25 September 2006

Abstract

The present report introduces, as a first study, the concept and methods of oscillatory brain dynamics to analyze well-known (familiar) and unfamiliar face processing in the 800 ms following a face presentation. We analyzed event-related oscillations in young, healthy subjects (N=26) by using three types of stimulation: (1) a simple light signal, (2) the picture of the face of an anonymous elderly lady and (3) the picture of the subjects’ own grandmother. We found a number of significant peak to peak amplitude measures in all frequency bands in the time period of 0–500 ms, allowing a differentiation between perception of the subjects’ own grandmother, the unknown elderly face and the light stimulation. The results showed increased event-related oscillatory responses elicited by the unknown face compared to the known grandmother a) in the theta responses (4–8 Hz) at T6 (46%), b) in the gamma (28–48 Hz) responses at Cz (22%) and C3 (38%) and c) in the beta responses at F4 (46%), Cz (47%) and P3 (105%). In contrast, the subjects’ own grandmother elicited 20% increased fast theta (6–8 Hz) oscillations at F4 compared to the unknown face. Delta responses dissociated face from simple light processing, as reflected in the observation of approx. 50% higher amplitudes at the occipital compared to the frontal locations during face perception. We conclude that the described multiple brain oscillations clearly differentiate the known and unknown faces with varied degrees of selective-responsiveness in a short time window between 0 and 800 ms. Furthermore, the results are in conceptual accordance with the “selectively distributed processing” hypothesis.

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Keywords: Delta; Theta; Alpha; Beta; Gamma oscillations; EEG; ERP; Face recognition; Semantic; Episodic; Memory

1. Introduction

The face recognition process in the brain has attracted increasing attention in neuroscience research (Haxby et al., 2001; Grill-Spector et al., 1999; Rotshstein et al., 2004; Quiroga et al., 2005). Although, several publications using functional Magnetic Resonance Imaging (fMRI) and conventional Evoked Potential (EP) reports are to be found in the literature, there are almost no reports taking into account the concept and approach of selective multiple oscillations and the long established fundamental physiological facts stated by Luria (1966), Lashley (1929), Fuster (1995, 1997), Mesulam (1990, 1994), Damasio and Damasio (1994), and Goldman-Rakic (1996). Their approaches include the concept that even a simple percept, such as a light stimulation, involves memory processing and that our memories are distributed across the entire brain, instead of being concentrated in specific regions (Lashley, 1929; Fuster, 1995, 1997). According to Luria (1966) mental functions too, are, similar to vegetative functions, a product of complex systems, a component part, which may be distributed through the structures of the brain. The task of neuroscience is therefore not to localize “centers”, but rather, to identify the components of the various complex systems that interact to generate the mental functions. Luria called this task “dynamic localization”. A recent study tested the possible interplay between the working and long-term memory systems and indicated the relevance of this dynamic localization (Sauseng et al., 2002). Especially Fuster (1995, 1997) emphasizes that complex stimuli processing includes simultaneous and successive activity of diffusely interconnected and another overlapping memory
networks. One neuron or group of neurons in the cortex can be part of many networks, and thus, many memories: this is why it is virtually impossible, by any method, to localize a memory. Nevertheless, many studies investigating face recognition have attributed functional correlates of this processing to the temporal cortex and not to distributed and interconnected neuronal networks.

The present report aims to fulfill this gap and introduces as a first study the concept and methods of oscillatory brain dynamics to analyze face recognition in the first 800 ms following a face presentation. In the Sherringtonian view, “the grandmother neuron” is defined as a neuron, which responds to nothing else but the face of one’s grandmother. According to Barlow’s (1995) concept we would have a specific neuron in the brain firing while seeing the face of a particular grandmother. Following the relevant work of Eckhorn et al. (1988) and Gray and Singer (1989) on gamma oscillations Stryker (1989) raised the question “Is grandmother an oscillation?”, commenting that neurons in the visual cortex activated by the same object, tend to discharge rhythmically and in unison.

The first results related to selectively distributed and selectively coherent multiple oscillatory responses as large-scale approach were described by Başar et al. (1975; Başar, 1980) in the cat and human brain (for reviews see Başar, 1999 and Başar et al., 2001). In the last years, the large-scale hypothesis has become a keyword in an increasing number of publications (e.g. Bressler and Kelso, 2001; von Stein and Sarnthein, 2000; Varela et al., 2001; Makeig et al., 2002; Fell et al., 2001; Mesulam, 1990, 1994).

In the analysis of the grandmother percept the experimenter is confronted with the process of face processing, which comprises (i) perceptual and memory processes required for the recognition of complex stimulation as a face, (ii) the identification of the particular face in view (here the grandmother), (iii) the analysis of facial expression (McCarthy, 2000) and (iv) the concept of dynamics in integrative brain function. In addition to the processes pointed out above, face recognition requires integration of attention, perception, learning and memory. Recent publications favor the idea that attention, perception, learning and memory are inseparable as described by Hayek (1952) (see also Fuster, 1995, 1997; Damasio and Damasio, 1994; Baddeley, 1996, Desimone, 1996, Başar, 2004). Therefore, face recognition can be considered as a prototype of complex signal processing in the brain.

From the methodological viewpoint, Mountcastle (1992) indicated that the paradigm change introduced by using brain oscillations became one of the most important conceptual and analytic tools for the understanding of cognitive processes. He further stated that a major task for neuroscience is to devise ways to study and to analyze the activity of distributed systems in waking brains, including particularly human brains. As a consequence of this chain of reasoning, the analytical and conceptual framework of the present study is premised on the methodological advice of Mountcastle (1992) and the conceptual statements of Luria (1966) and Lashley (1929). Furthermore, the study takes the principle of selectively distributed systems into account (Mesulam, 1990, 1994; Başar, 1999, 2004). Within this framework, the present study investigated event-related oscillations in young, healthy subjects using three types of stimulation assumed to activate partly overlapping and partly distinct neuronal networks: (1) a simple light signal, (2) the picture of the face of an anonymous elderly lady and (3) the picture of the subjects’ own grandmother.

2. Materials and methods

2.1. Experimental strategy and procedure

We used a strategy consisting of the application of three different types of visual stimulation:

1) A simple light stimulation as control signal, its luminance and size was approximately the same as for pictures 2 and 3 described in the following (app. 30 cd/m2).
2) The picture of an ‘unknown face’: an anonymous elder lady.
3) The picture of a ‘known face’: the subjects’ own grandmother.

A total of 26 subjects in the age range of 15–36 years (17 females and 9 males) participated in the study. They had normal or corrected to normal binocular visual acuity and were right-handed. The pictures were presented in black and white (17 × 17 cm) and displayed on a screen at a distance of 120 cm from the subjects. Stimulus duration was set to 1000 ms with intervals varying between 3.5 and 7.5 s. The subjects were instructed to minimize blinking and eye movements, and they sat in a soundproof and dimly illuminated echo-free room (Fig. 1).

Data recording set: The stimuli were randomly presented in 75 trials, such that each type of stimulation was similarly distributed. The grandmother (known face), unknown face and light responses were analyzed separately in subsets. All subjects reported clearly recognizing and differentiating the face of their own grandmother.

2.2. Electrophysiological recording

The EEG was recorded from F3, F4, Cz, C3, C4, T3, T4, T5, T6, O1, O2, P3, P4, O1 and O2 locations according to the 10–20 system (Jasper, 1958). For the recordings an EEG-CAP was used. For the reference and EOG recordings Ag/AgCl electrodes were used. Linked earlobe electrodes (A1 + A2) served as reference. EOG from the medial upper and lateral orbital rim of the right eye was also registered. The EEG was amplified by means of a Nihon Kohden EEG-4421 G apparatus with band limits 0.1–100 Hz 24 dB/octave. The EEG was digitized online with a sampling rate of 512 Hz. For the analysis stimulus-locked epochs of 2000 ms, with 1000 ms serving as the pre-stimulus baseline, were used.

2.3. Computation of selectively averaged event-related potentials (ERP)

Before the averaging procedure, the epochs that contained artifacts were rejected by an off-line technique. In the off-line procedure, single sweep EOG recordings were visually studied
and trials with eye movement or blink artifacts were rejected. Subject averages and grand averages were calculated for each electrode site, experimental condition. The data was digitally filtered according to determined frequency bands of interest. According to new approaches, the EEG consists of the activity of an ensemble of generators producing rhythmic activity in several frequency ranges. These oscillators are usually active in a random way. However, by application of sensory stimulation these generators are coupled and act together in a coherent way. This synchronization and enhancement of EEG activity gives rise to "evoked" or "induced rhythms". Evoked potentials representing ensembles of neural population responses were considered as a result of transition from a disordered to an ordered state. The compound ERP manifests a superposition of evoked oscillations in the EEG frequencies ranging from delta to gamma ("natural frequencies of the brain" such as alpha: 8–13 Hz, theta: 3.5–7 Hz, delta: 0.5–3.5 Hz and gamma: 30–70 Hz) (Yordanova and Kolev, 1998).

In the present study, two approaches were taken in determining the frequency responses of the system: the transient response frequency characteristics (TRFC) method and digital filtering (DF) method.

The computation formula of the TRFC method where the step response, $c(t)$, of the system is transformed to the frequency domain ($\omega = 2\pi f$, where $f$ is the frequency of the input signal) is as follows:

$$G(j\omega) = \int_0^\infty \frac{d\{c(t)\}}{dt} e^{-j\omega t} dt$$

The numerical evaluation of the formula was accomplished using a fast Fourier transform (FFT) of the following form: Let $X_n$ be a discrete time series ($X_n = X(n\Delta t)$, $T = ((N-1)\Delta t$). Then the Fourier transform of $Y_k$ of $X_n$ is:

$$Y_k = Y(\omega_k) = \sum_{n=0}^{N-1} X_n \exp(-i2\pi N^{-1} nk); \quad \omega_k = 2\pi kT^{-1}$$

Where $Y_k = a_k + ib_k$ are the complex Fourier coefficients whose geometric mean is the amplitude spectrum.

2.4. Digital filtering

Filtering produces visual displays of the time courses of oscillatory components within the frequency limits of the utilized filters. Digital filters are advantageous because they do not produce the phase shifts that are a characteristic of electronic filters. Digital filtering was employed in the present study for the digital pass-band filtering of the event-related potentials (ERPs) and thus to demonstrate the event-related oscillations (EROs) in selected frequency-bands (for a detailed explanation of the AFC method see; Başar et al., 2001; Karakaş et al., 2000a,b). The AFC is expressed in relative units and it reflects the amplification in the studied frequency channels. The presence of a peak in the AFC thus reveals the frequency selectivities of the system and these are interpreted as its most preferred oscillations when responding to stimuli. The AFC method has also the advantage to show the status of all frequencies in a combined manner.

2.5. Data analysis

We analyzed the oscillatory responses in five frequency ranges, and in each frequency window we categorized the results in two different ensembles of results: The first ensemble of results comprises the differences in peak to peak (p–p) oscillatory response amplitudes between the picture of the anonymous face and the picture of the subjects’ own grandmother in distributed locations in a time window of 800 ms following the stimulation. In the second ensemble, which could be specified as secondary or indirect differentiations, we describe topological differentiations (1) between the right and left hemispheres and (2) between the anterior and posterior hemispheres for the subjects’ own grandmother and for face responses separately. Wilcoxon matched pair test was used for the statistical analysis.

2.6. Remarks on the application of frequency analysis methods

A recently published paper by Bruns (2004) described that spectral signal analysis constitutes one of the most important and most commonly used analytical tools for the evaluation of neurophysiological signals. It is not only the spectral parameters per se (amplitude and phase) which are of interest, but there is also a variety of measures derived from them, including important coupling measures like coherence or phase synchrony. After reviewing some of these measures in order to underline the widespread relevance of spectral analysis, Bruns (2004) report compares the three classical spectral analysis approaches: Fourier, Hilbert and wavelet transform. Recently, there seems to be increasing acceptance of the notion that Hilbert- or wavelet-based analyses are in some way superior to Fourier-based analyses. The analysis by Bruns counters such views by demonstrating that the three techniques are in fact formally (i.e. mathematically) equivalent when using the class of wavelets that is typically applied in spectral analyses. Moreover, spectral amplitude serves as an example to show that Fourier, Hilbert and wavelet analysis also yield equivalent results in practical applications to neuronal signals.

Bazar et al. (1999) compared the outcome of adaptively filtered signals with wavelet analysis and found excellent equivalency. However, the consideration of spectral analysis, as
we perform here, provides a crucial advantage by seeing the entire spectral axis, instead of ad hoc estimation of used filtered limits in wavelet transforms. Accordingly, in this present paper, the analyses were performed with frequency analysis methods. This provided the basis for selection of cut-off frequency ranges in the sub-bands.

3. Results

3.1. Direct differentiations between grandmother and anonymous faces

In Fig. 2A and B delta and theta responses in 13 distributed scalp locations are illustrated as responses to the picture of an anonymous face and to the picture of the own grandmother. The large number of topological and stimulus-related significant differences are described in the form of histograms representing comparative peak to peak response amplitudes of 26 subjects in five frequency ranges (Figs. 3 and 4). The illustrations with histograms cover results only with statistical significance.

Fig. 3 illustrates the significant comparisons between anonymous and grandmother face in three frequency windows. In F3 there were no significant differences between the responses to the grandmother and to the anonymous face, whereas at F4 the amplitude of the grandmother fast theta (6–8 Hz) response was significantly larger (20%) than for the anonymous face response ($p = 0.018$). At T6 the amplitude of the anonymous face theta response was significantly larger (46%) than the grandmother response ($p = 0.035$). We also analyzed the differences between light response, grandmother and anonymous face at F4, and found no significant differences.

Beta responses reported in a recent study (Özgören et al., 2005) showed clear differences in distribution of the responses at anterior locations (Fig. 3). Beta responses to the unknown faces in the central and frontal areas were on average 40% higher than the grandmother response; additionally the grandmother responses showed prolonged beta responses.

Fig. 2. A. Delta (0.5–3.5 Hz) and B. theta responses (fast 6–8 Hz) at 13 scalp locations upon presentation of the picture of an anonymous face, the picture of the subjects’ own grandmother and the light stimuli. Zero marks the time point of stimulation.

Fig. 3. Significant differences between the anonymous face and grandmother face in three frequency windows (6–8 Hz, 15–30 Hz, 28–48 Hz). The responses to the grandmother (known) face are represented by black bars and to the unknown face by gray bars.
comparison of P3 anonymous face/grandmother face responses showed the greatest difference amounting to 105%.

In the gamma band (28–48 Hz) direct differences were also found. At the Cz electrode the amplitude of anonymous face gamma response was significantly larger (22%) than grandmother response (p=0.02). At C3 the amplitude of face gamma response was significantly larger (38%) than the grandmother response (p=0.04). The light response was 23% larger than the grandmother response at C3 (p=0.03).

3.2. Secondary (indirect) differentiations of grandmother responses

Fig. 4A illustrates the comparisons of grandmother responses between the anterior/posterior areas and left/right locations in the form of histograms. The amplitude of the delta response at O1 was significantly larger than at F3 (p=0.001) and the amplitude of delta response at O2 was significantly larger than at F4 (p=0.000). The alpha response at O1 was larger than F3 (p=0.000), the alpha response at O2 was significantly larger than at F4 (p=0.000).

Laterality of the grandmother responses is illustrated in Fig. 4B. Upon presentation of the grandmother picture, the amplitude of delta response at T6 was 121% larger than at T5 (p=0.008), the amplitude of 6–8 Hz theta responses at T6 is significantly larger (114%) than T5 (p=0.008). Upon presentation of the grandmother picture the alpha response at T6 was 96% larger than at T5 (p=0.025). The amplitude of alpha responses at P4 was significantly larger (22%) than at P3 (p=0.004). The T6 gamma response was 46% larger than at T5 (p=0.021) (Fig. 4B).

3.3. Secondary (indirect) differentiations of the anonymous face responses

Fig. 5 illustrates the comparisons of anonymous face responses between the anterior/posterior areas and left/right locations in the form of histograms. The delta response at O1 was higher than at F3 (p=0.007), the delta response at O2 was 55% higher than at F4 (p=0.000) (Fig. 5A). The upper alpha response at O1 was 64% higher than at F3 (p=0.000). The upper
alpha response at O2 was higher than the alpha at F4 ($p=0.009$) (Fig. 5A).

Anterior versus posterior differences are shown in Fig. 5A and differences in laterality are shown in Fig. 5B. The delta response at T6 was 106% higher than at T5 ($p=0.008$), the theta response at T6 was 194% higher than at T5 ($p=0.012$). The upper alpha response at T6 was 86% higher than at T5 (Fig. 5.B). In the gamma band T6 response was 59% higher than at T5 ($p=0.024$). It should be further noted that the differentiation in the theta band between T4 and T3 was only 20% ($p=0.03$) (Fig. 5.B), thus showing that the lateral differences were high in temporal–posterior locations.

3.4. Topological distribution of light responses and differences between anterior, posterior and laterality

The upper alpha response to light stimulus at O1 was 88% higher than at F1 ($p=0.000$) and respectively, the response to light stimulus at O2 was 86% higher than at F4 ($p=0.000$) (Fig. 6A). Laterality differences of light responses are shown in Fig. 6. There were significant (90–100%) increases of amplitude at right temporal locations (T6) as during face processing, indicating that there may be fundamental aspects observable in both facial and simple light processing (Fig. 6A–B). However, only in the theta band the differentiation was extremely high (194%) indicating that the theta response of the anonymous faces has been a differentiated response for unknown faces. In the gamma band the right/left hemisphere differences were higher for light stimulation in comparison to the grandmother and anonymous faces.

4. Discussion

4.1. Selected differences between light, grandmother and anonymous faces

The most important feature of our data is the existence of approx. 25 (8 direct, 17 indirect) significant differentiations in the delta, theta, alpha, gamma and beta responses between the anonymous, the grandmothers’ face and the non-face light stimulation in the frontal, central, parietal, temporal and occipital sites. The present report cannot discuss all 17 indirect differentiations in detail, therefore, specific results are selected for the discussion.

4.1.1. Differentiation between light, grandmother, and anonymous faces as indicated by varied degrees of response amplitudes

A simple light stimulation evokes selectively distributed multiple oscillations in the brain. The analysis of oscillatory responses to simple light provides a necessary control often neglected in strategies to understand brain function. Our results once more demonstrate that even the perception and/or remembering of simple light, evokes complex processing in the brain (see Fig. 6).

Occipital compared to frontal delta responses upon presentation of anonymous faces and grandmother faces were very high in comparison to the light stimulation. This suggests that the increase in occipital delta response is a consequence of face processing in general without differentiation between known and unknown faces (Fig. 2A). Earlier results demonstrated that the amplitude of the delta response is considerably increased during oddball experiments (Başar-Eroğlu et al., 1992; Karakaş et al., 2000a,b). Therefore, it was concluded that the delta response is related to signal detection and decision-making. Further, the delta responses to visual oddball targets have their highest response in parietal locations, whereas for auditory target stimuli the highest delta responses are observed in the central and frontal areas (Başar-Eroğlu et al., 1992; Schürmann et al., 1995). Accordingly, the increase of delta in the occipital areas in anonymous and grandmother pictures is a relevant finding as a component of the recognition of the presented picture as a face, but not a manifestation for the differentiation between different faces.

The amplitude differences in the theta response between frontal (F4) grandmother and anonymous face responses indicate differences in the processing of known and unknown faces. This may be associated with differences in individual episodic semantic memory contents related to the specific faces.

The right temporal (T6) in comparison to the left temporal (T3) theta responses are significantly higher upon both types of face presentations. Further, it is to note that the temporal theta responses to both types of face presentations are considerably high in comparison to light stimulation (Figs. 4, 5 and 6). This finding strongly indicates that temporal theta and frontal theta responses probably have different functional correlates: Frontal theta face differentiation may have a role for the differentiation of semantic and episodic memories, whereas, the tempo-posterior theta seems to be related to global face detection, similar to posterior delta responses. Accordingly, it can be assumed that the $T_6$ theta responses do not manifest a differentiation between episodic and semantic memories, as it is the case for $T_4$ theta responses, since no significant differences were noted at $T_6$ between known and unknown faces. Our results differ from results presented by Haxby et al. (2001), Kanwisher et al. (1998), and Grill-Spector et al. (1999) allocating absolute face recognition areas to the temporal lobes.
Although the alpha response merits special attention, this will be subject of a separate and detailed study considering the fluctuations due to higher and lower frequency bands and the joint alpha blocking process (Klimesch et al., 1994, see also preliminary results in Başar, 2004).

The beta responses topologically highly differed between grandmother and anonymous face stimuli. The frontal and parietal beta response was higher upon anonymous face presentation, hence, showing largest differences with 100% increase at parietal locations. It is to note that occipital beta responses did not show any differentiation between grandmother and anonymous faces. It is to note that, various other functions have been assigned to beta oscillatory responses such as visual attention (Marrufo et al., 2001), movement related changes (Müller et al., 2003), excitation–inhibition (Whittington et al., 2000), sensory memory (Haenschel et al., 2000), recollection and familiarity (Burges and Ali, 2002). Recently, linkage and linkage disequilibrium between beta frequency and a GABAA receptor gene has been reported (Porjesz et al., 2002).

Gamma responses showed differentiations in the C3 and Cz locations, but not in the posterior and right locations. As we stated, gamma responses are assumed to be one of the essential oscillatory components, but its contribution to all brain functions, and consequently to the processing of face recognition should be described in parallel or in superposition with the activation of other oscillatory components (Başar, 1999, 2004). According to the presented results the gamma response is more sensitive (with higher activation) to the unknown face, in comparison to the known face. It is also to note that the beta response showed a higher sensitivity to differentiate both face presentations, in comparison to the gamma response.

4.2. Differentiation of percept by selectively distributed oscillatory patterns

Our analysis of both types of faces showed 25 significant peak to peak amplitude differences in oscillatory responses at 13 different locations. This suggests that the activation of oscillations to each type of facial stimulus show significant selectively distributed activation patterns. Therefore, our results support and extend the concept that integrative brain functions are based on multiple oscillations. We would like to emphasize that the analysis of conventional ERPs and single frequencies may lead to restricted interpretations (Başar, 1980, 1999). This view finds support by several recent publications (Gruzelier, 1996; Makeig et al., 2002; Klimesch et al., 2004; Başar, 1999). Different functions are often correlated with different oscillations at distinct locations. According to the results, only ensembles or combinations of alpha, beta, gamma, delta and theta that act in parallel are tenable and essential for the specific shaping of an individual percept; not only one recording area or a unique frequency.

4.3. Recognition of percepts and faces. A short survey

Physiological correlates of face processing have been studied by means of lesion studies, functional neuroimaging, and conventional evoked potentials (McCarthy, 2000; Kanwisher et al., 1998; Kuskowski and Pardo, 1999). The electro-physiological studies have pointed out face specific potentials within the range of 120–210 ms (Bötzel et al., 1989; Endl et al., 1998; Taylor et al., 1999; Herrmann et al., 2002; Balconi and Pozzoli, 2003, Jemel et al., 2003). Depending on the study designs both MEG and EEG studies suggest that face selective processing may start either in the range of 100–130 ms (Linkenkaer-Hansen et al., 1998) or around 150–170 ms (Sams et al., 1997). In addition, the stages of face processing have been suggested to be separated into structural face encoding which would take place at around 170 ms and recognition that would take place around 400–600 ms (Eimer, 2000).

Several research groups have reported distinct ERP components during face presentation localized at temporal areas (Bentin and Golland, 2002; Eimer, 2000; Zhang et al., 2001). Face selective changes in the activation of the human fusiform gyrus was demonstrated by Klopp et al. (1999). Gruber et al. (2001) found significant interactions in the gamma range between electrode sites over more distant cortical areas, however this group did not analyze slow frequency responses. Neurons in the occipito-temporal cortex have been observed by single-cell recordings in primates and in intracranial electrophysiological recordings in humans (McCarthy, 2000).

Begleiter et al. (1995) showed that for recognition of familiar faces both the temporal and frontal regions are involved. Schweinberger et al. (2002) also reported that for the familiar faces, responses were recorded from the parietal, central and prefrontal areas.

Fuster (1995, 1997) hypothesizes that cortical dynamics evoked by episodic memory is identical to that evoked by a familiar stimulus, such as a cue given in a delay task. Although the cue is represented in the posterior cortex, the prefrontal cortex is essential for its retention towards prospective action. Further, memory networks overlap and are diffusely interconnected with one another. Thus, one neuron or group of neurons anywhere in the cortex can be part of many networks, and thus, many memories: this is why it is virtually impossible, by any method, to localize a memory. This statement is physiologically fundamental.

Damasio and Damasio (1994) state that our brains use dynamic records, and that the record of the face of a person is a set of neuronal circuit changes, which can be reactivated, rather than assuming the activation of a “picture” that is stored somewhere in the brain. The experimental studies of Klimesch’s group show the possibility of differentiating the role of alpha and theta oscillatory activity during memory tasks (Klimesch et al., 1994; Sauseng et al., 2002). Our earlier and the present findings are in accordance with the scope of all these authors: The neural representations of different memory forms (e.g. semantic, episodic memory) involve the activation of neural populations firing in all common frequencies ranges (delta, theta, alpha, beta, and gamma). Thus these findings are in accordance with these fundamental physiological statements stated above (Fuster, 1995, 1997; Damasio and Damasio, 1994). The distinct behavior of theta responses at the right frontal (F3) and temporal (T6) areas showed an opposite trend (Figs. 4B, 5B and 6B). The beta response of the anonymous face was larger than the grandmother.
response, opposite to the behavior of the theta response at F4. The results suggest and emphasize the importance of investigating multiple oscillations at different locations as a tool for recognizing differences in episodic and semantic events.

4.4. Comparison with fMRI and single cell studies

Courtney et al. (1997) presented subjects with pictures of human faces, and asked them to recall whether the picture being shown was the same, or different, from one that had been presented 8 s earlier. The authors found that the activation in the prefrontal areas correlated most strongly with delay periods, compared with the activation in the visual areas, which were more strongly correlated with sensory stimulation.

The results of Haxby et al. (2001) indicate that the representations of faces and objects in the ventral temporal cortex are widely distributed and overlapping; Grill-Spector et al. (1999) describe that the fusiform face area is involved in both detection and identification of faces. However, the results’ interpretation that the percepts of several objects are localized only in restricted given substructures of the temporal cortex is physiologically questionable, since such statements are not in accordance with physiologically anchored theories by Mesulam (1990, 1994), Fuster (1995, 1997), and Goldman-Rakic (1996). Although, fMRI studies merit important consideration, a word of caution should be stated, because of the very low temporal resolution (Grill-Spector et al., 1999) and the missing of frontal activation although the co-activation of frontal lobes is almost obligatory from the physiological viewpoint (Fuster, 1995, 1997).

Using single cell recordings, Quiroga et al. (2005) reported subsets of neurons that are selectively activated in the human medial temporal lobe. These authors recorded in restrictive operative conditions and they could not have recorded the changes in fusiform area, occipital or frontal cortices. Thus, results of Haxby et al. (2001) and Grill-Spector et al. (1999) are highly contradictory, possibly supporting the concept of selective distribution.

4.5. Components of emotion

In the present study the influences of emotion cannot be discussed explicitly: It can be hypothesized that grandmother pictures would anyhow evoke various degrees of emotional components among subjects. However, unpublished data from our laboratories indicate enormous changes in the multiple oscillations and topology space upon emotion induced by selective presentation of face pictures with different emotional valence.


Although our results show that the grandmother percept can be differentiated from the anonymous face by multiple and selectively distributed oscillations, such an analysis cannot completely exclude the existence of a group of face sensitive neurons somewhere in the brain. However, according to Libet (1991) the brain needs at least 300–500 ms for building percepts and all oscillatory responses take place in parallel at multiple locations of the cortex approx. 300–400 ms following the stimulation. Therefore, it can be hypothesized that mechanisms leading to the perception of the grandmother picture are manifested with parallel activation of neural assemblies in different cortical locations and that a percept cannot be localized in a given specific region.

Goldman-Rakic suggested that it might be more useful to study the cortex in terms of information processing functions and systems rather than traditional but artificially segregated sensory, motor, or limbic components and individual neurons within only one of these components. In Mesulam’s model of cognition the formation of specific templates belonging to objects and memories occurs as selectively distributed processing with considerable specialization. This functional selectivity exists in anatomically differentiated localizations. Further, Fuster (1997) states that memory reflects a distributed property of cortical systems.

Supported by the present results, the question of Stryker (1989) can be answered by stating that the grandmother percept is manifested by distributed multiple oscillations.

5. Conclusion

Survey of various approaches to the analysis of face recognition demonstrates that face recognition requires a profound analysis with various methods; a simple measurement cannot be representative and may lead to erroneous statements. The analysis with EEG-oscillations requires also special care by including (1) measurements of a baseline with simple light, (2) topologically distributed locations, (3) the consideration of multiple oscillatory components. Steps (2) and (3) are often neglected not only in the EEG but also in most of fMRI studies. (4) The presented data do not favor statements related to absolute localizations and preferred frequency channels; for the time being the presented results should be only physiologically described and shortly commented. (5) The presented evidence of selectively distributed multiple oscillations for the differentiation of facial stimuli is in conceptual accordance with the “selectively distributed processing” in neurocognitive networks of Goldman-Rakic (1996), Fuster (1995, 1997) and Mesulam (1990, 1994). The large-scale approach of several investigators is also confirmed by recent results (Bressler and Kelso, 2001; Varela et al., 2001; von Stein and Sarnthein, 2000). Upon facial stimuli a given location can show a considerable selected activation; but the shaping of percepts is manifested by multiple oscillations, with differentiated weight, in large neural populations.

Acknowledgements

The experiments of this collaboration study were supported by the TÜBITAK-DFG grant 446 TUR 112/14/01, DEÜ 02 KB. SAG.012/027-03.KB. SAG.064.

References


Sauseng, P., Klimesch, W., Gruber, W., Doppelmayr, M., Stadler, W., Schabus, M., 2002. The interplay between theta and alpha oscillations in the human electroencephalogram reflects the transfer of information between memory systems. Neuroscience Letters 324, 121–124.


